

## MINIREVIEW

# Diversity and function of soil microbes on montane gradients: the state of knowledge in a changing world

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**One sentence summary:** Patterns of diversity vary across elevation, but unlike plants and animals, which often show a mid-elevation peak, the majority of studies in this review find that soil microbial diversity declines or shows no trend with increasing elevation.

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## ABSTRACT

Mountains have a long history in the study of diversity. Like macroscopic taxa, soil microbes are hypothesized to be strongly structured by montane gradients, and recently there has been important progress in understanding how microbes are shaped by these conditions. Here, we summarize this literature and synthesize patterns of microbial diversity on mountains. Unlike flora and fauna that often display a mid-elevation peak in diversity, we found a decline (34% of the time) or no trend (33%) in total microbial diversity with increasing elevation. Diversity of functional groups also varied with elevation (e.g. saprotrophic fungi declined 83% of the time). Most studies (82%) found that climate and soils (especially pH) were the primary mechanisms driving shifts in composition, and drivers differed across taxa—fungi were mostly determined by climate, while bacteria (48%) and archaea (71%) were structured primarily by soils. We hypothesize that the central role of soils—which can vary independently of other abiotic and geographic gradients—in structuring microbial communities weakens diversity patterns expected on montane gradients. Moving forward, we need improved cross-study comparability of microbial diversity indices (i.e. standardizing sequencing) and more geographic replication using experiments to broaden our knowledge of microbial biogeography on global gradients.

**Keywords:** archaea; biogeography; bacteria; climate change; community composition; diversity; elevation gradients; fungi; microbial ecology; mountains; soil

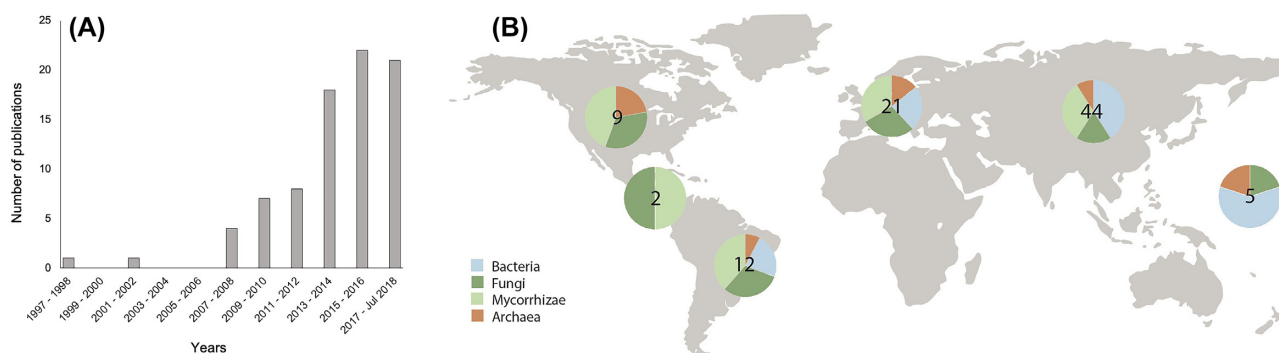
## INTRODUCTION

Mountains are hotspots of biodiversity, covering only ~12% of the global terrestrial surface outside of Antarctica (Körner, Paulsen and Spehn 2011), yet supporting ~33% of terrestrial species diversity (Körner and Paulsen 2004) and half of the planet's biodiversity hotspots (Chape et al. 2005). Mountains also create steeply compressed gradients in abiotic and biotic conditions (Martin and Bellingham 2016), providing natural space-for-time settings to assess *in situ* responses to environmental change (Malhi et al. 2010), while minimizing the confounding effects of dispersal limitation. These conditions have long helped ecologists understand drivers of biogeography

(Sundqvist, Sanders and Wardle 2013), as montane gradients highlight the fundamental influence of climate on composition, diversity and dynamics (e.g. Sherman et al. 2012). At the same time, mountains serve as important indicators of change, as warming is generally occurring much faster at higher elevations than in lowland ecosystems (Pepin et al. 2015), and mountains are proving to be among the most climate-sensitive ecosystems worldwide (Seddon et al. 2016). Finally, as a primary source of global terrain complexity, mountains play a disproportionate role in global biogeochemical cycles, and the ecosystems they harbor have particularly important influences on global carbon cycling (Reyes et al. 2017).

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**Figure 1.** (A) The recent surge in studies on soil microbes and elevation shown by the number of publications on Web of Science, and (B) geographic locations studied. Pie charts in panel (B) show the proportion of studies that investigated bacteria (light blue), fungi (dark green), mycorrhizal fungi (light green) and archaea (orange). The number on each pie chart represents the total number of studies in each geographic location. In panel (B), a total of 93 entries were included as some studies were included more than once as they investigated more than one microbial group (i.e. fungi and bacteria; fungi, bacteria and archaea; bacteria and archaea; or fungi and mycorrhizal fungi). The total number of entries in each geographic area is denoted in the chart. See Table S1 (Supporting Information) for the search criteria and the full list of publications considered in this review.

It was long thought that patterns in aboveground species richness on montane gradients emulated patterns on latitudinal gradients, but it is now generally accepted that species richness patterns on mountains defy a single model and vary by taxa (Rahbek 2005). Moreover, there is good reason to ask whether the patterns reported for macroscopic and aboveground taxa are informative for microbial communities of bacteria, fungi and archaea, whose biology is generally distinctive from flora and fauna. Free-living microbes are especially sensitive to abiotic conditions and external biotic factors, like litter quantity and quality. Indeed, microbial abundance frequently peaks in areas with high soil organic matter (SOM), which develops in conditions different from what fosters high plant productivity (Xu et al. 2013). Soil microbes also depend on specialized processes like decomposition to complete their life cycles, requiring necromass for energy (Allison, Wallenstein and Bradford 2010; Trivedi, Anderson and Singh 2013). These processes may be highly dynamic on montane gradients given the large stocks of both living and dead carbon (C) that mountains contain in biomass and soils, and soil C typically increases markedly with elevation (Tanner, Vitousek and Cuevas 1998). For instance, along a 2010-m gradient in Ecuador, SOM increased nearly 7-fold with elevation, from 11 to 75 Mg C ha<sup>-1</sup> (Moser et al. 2011).

An improved understanding of belowground diversity patterns and community structure along montane gradients is needed for insights into how microbial communities interact with ecosystem processes, especially as measurements of microbial diversity have been found to strengthen predictions of microbial function on key processes (e.g. respiration) more than estimates of microbial abundance alone (Graham et al. 2016). Via decomposition, microbes are a key determinant of C storage and release in soils, and systematic changes in microbial function across montane ecosystems will have global consequences. Moreover, high-elevation soils are often organic-rich and waterlogged, making them particularly vulnerable to environmental change (Bradford et al. 2016). In general, it is likely that decomposition rates will increase significantly in C-rich montane sites as they warm, especially given the temperature sensitivity of extracellular enzymes—that strongly influence decomposition rates—at high elevations (Nottingham et al. 2016). However, to move beyond broad generalities, we need an improved understanding of how the diversity and functional composition of microbial communities will shift as climatic and edaphic conditions change.

Soil microbial community structure on montane gradients was a hitherto largely unexplored aspect of microbial biogeography, but in the last decade it received new attention (Fig. 1A) as ecologists utilized mountains as proxies to study the effects of climate change (Malhi et al. 2010). There is now sufficient literature to summarize patterns in montane microbial biogeography, explore mechanistic and empirical relationships, and provide directions for future studies. Utilizing this new research, we used Web of Science to compile all relevant literature on soil microbial diversity and function patterns along montane gradients (see Table S1, Supporting Information, for full search criteria). We focus on free-living microbes, as patterns of fungal symbionts with elevation were addressed in a recent synthesis (see Kivlin et al. 2017). We only included studies that sampled an entire fungal, bacterial or archaeal community in three or more sites on an elevation gradient, and to avoid other confounding effects, sampled exclusively in primary vegetation communities, predominantly forests and alpine habitats (e.g. dominated by herbs, shrubs, etc.). In secondary vegetation communities, confounding factors may mask whether microbial responses are artifacts of land use or due to elevation and covarying environmental properties (e.g. Fichtner et al. 2014). We found a total of 77 studies that met these criteria (Table S1, Supporting Information). In this literature, most studies do not detail how soil microbial distributions are directly linked with ecosystem processes like decomposition, as overall the relationship between microbial community structure and ecosystem processes remains poorly understood (Graham et al. 2016); hence, this review does not aim to provide an in-depth look at the role covarying ecosystem processes play in structuring microbial communities on elevation gradients (see Sundqvist, Sanders and Wardle 2013 for a general review of ecosystem processes and elevation). Given the methodological limitations in comparing species richness across studies of microbial communities (see below), a formal meta-analysis of the data was not performed at this time, and hence our review is generally descriptive. Synthesizing and summarizing this literature, we ask what are the overarching patterns of soil microbial diversity and turnover in species composition on montane gradients, and what are the driving forces behind shifts in composition. We also ask how changes along elevation gradients alter microbial roles in ecosystem function. We conclude the review with suggestions for future research directions on this topic.

## MONTANE ECOSYSTEMS AND ABIOTIC FACTORS THAT VARY WITH ELEVATION

Mountains occur on every continent and house a diverse variety of terrestrial ecosystems, often juxtaposed over short distances. Per Körner *et al.* (2011), mountains are defined as areas with an increase in elevation of greater than 200 m with a concomitant decrease in total land area. Many environmental conditions change in montane ecosystems and these often covary with elevation. Associated environmental gradients in temperature, solar radiation and atmospheric pressure change rapidly and predictably with elevation (Körner 2007). Of these factors, declining temperature at higher elevations is likely the most important driver shaping microbial communities on mountains, as temperature is well known to directly and indirectly affect soil microbe biology (Davidson and Janssens 2006). Variation in UV-B radiation levels may also directly structure microbial communities, but most likely only in alpine ecosystems above the treeline where unfiltered solar radiation reaches the soil surface. Although decreasing land area with elevation can directly impact the ecology of plants and animals, it is not clear whether this affects microbial communities.

Warmer temperatures at lower elevations influence many community- and ecosystem-level ecological processes, both above- and belowground (Sundqvist *et al.* 2013). Certain species of fungi favor warmer temperatures based on their evolutionary history (Treseder *et al.* 2014) and functional traits (Treseder and Lennon 2015), which in turn can affect diversity and community composition. Warmer temperatures at lower elevations also result in increased rates of decomposition in most instances, causing less accumulation of SOM and more soluble nutrients to be released in the soil matrix, dynamics that generally favor bacteria over fungi [i.e. lower fungal to bacterial (F:B) ratios; Thébault *et al.* 2014; Whitaker *et al.* 2014b; Kotas *et al.* 2018]. At broad scales, concentrations of foliar nitrogen (N), phosphorus (P) and potassium usually decrease with elevation, leading to nutrient-poor litterfall in montane forests compared with lowland forests, in part due to reduced litter inputs, but also because N and P concentrations are lower in montane forests, especially above 1500 m on tropical mountains (Tanner, Vitousek and Cuevas 1998). Montane soils usually have more soil organic matter per unit area, N mineralization levels are lower at higher elevations, and on tropical montane gradients, it is thought that lowland forests are generally P-limited while montane forests are N-limited (Tanner, Vitousek and Cuevas 1998).

There are also indirect effects of temperatures on microbial communities, through climate's influence on plant communities. Warmer ecosystems at lower elevations generally are richer in tree species (e.g. Martin, Sherman and Fahey 2007) and have higher levels of plant photosynthesis, biomass and productivity. In such settings, the quantity, quality and diversity of leaf litter increase, influencing the composition and abundance of soil microbes (Hättenschwiler, Tiunov and Scheu 2005; Hättenschwiler and Jørgensen 2010). Likewise, as plant ecological processes change and the quantity and quality of carbon inputs decline with cooler temperatures at higher elevations, microbial communities are strongly affected by the changes in both the abiotic and biotic conditions. Indeed, changing substrate quality was a main factor affecting mineralization and priming of soil organic matter decomposition across a 3190-m elevation gradient in the Peruvian Andes (Whitaker *et al.* 2014a). The cooler temperatures prevailing at higher elevations lead to slower rates of decomposition, which, along with poor

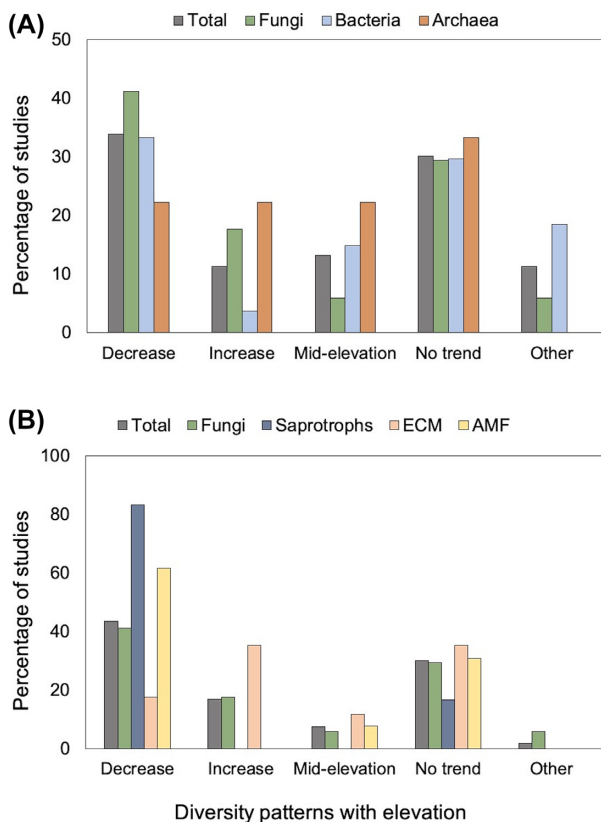
litter quality, generally favors fungal growth (i.e. higher F:B ratios; Zhou *et al.* 2014) and leads to organic matter buildup despite lower organic inputs (Schuur, Chadwick and Matson 2001; Girardin *et al.* 2010; Dieleman *et al.* 2013), ultimately making mountains an important reservoir of global carbon stocks. The accumulation of SOM in high-elevation ecosystems may have potentially important feedbacks on the structure and diversity of microbes in ways that run counter to richness patterns in aboveground taxa, as global studies have found that bacterial (Delgado-Baquerizo *et al.* 2016), fungal (Tedersoo *et al.* 2014) and archaeal (Angel *et al.* 2010) diversity are positively correlated with soil carbon levels.

Changes in precipitation and associated soil moisture on elevation gradients also have important direct and indirect effects on soil microbial diversity and composition, but unlike temperature gradients, precipitation regimes on montane gradients do not have globally consistent patterns (Körner 2007). When soil moisture increases, the microbial habitat is wetted and in turn soil oxygen levels decrease (Silver, Lugo and Keller 1999; Schuur 2001), both of which affect microbial physiology, abundance and the ecosystem-level processes microbes influence. Many montane ecosystems do receive high levels of precipitation; when combined with low evapotranspiration due to cooler temperatures, frequent orographic cloud cover and shallow montane soils, waterlogging and anoxic soil conditions can occur at high elevations, especially on tropical mountains (e.g. Silver, Lugo and Keller 1999). Likewise, important edaphic factors also vary with elevation, such as decreasing soil depths at higher elevations, but can be idiosyncratic in their spatial patterns. Nevertheless, soils generally become more acidic with increasing elevation, as a by-product of higher organic carbon stocks. Soil pH is a well-known driver of bacterial community composition (Fierer *et al.* 2009; Lauber *et al.* 2009), and at small spatial scales is an environmental filter for soil fungi (Glassman, Wang and Bruns 2017).

## HOW DOES SOIL MICROBIAL DIVERSITY RESPOND TO CHANGES IN ELEVATION?

Recent studies of soil microbial diversity patterns on montane gradients have mostly focused on bacteria, followed by fungi and archaea. The majority of investigations occurred in Asia (~47%) primarily on the Tibetan Plateau (~14% of all studies), followed by Europe (~23%), South America (~13%), North America (~10%), Oceania (~5%) and Central America (~2%; Fig. 1B). The elevation ranges studied in our literature search were substantial, spanning on average a total of 1477 m in elevation across the sample locations with a SD of  $\pm 936.8$  m; the minimum elevation range spanned was 115 m and the maximum was 4392 m. The mean starting elevation of sampling was 1191 m and the mean end elevation was 2668 m. An important limitation of microbial datasets, such as this one, is not all the studies use the same methods to determine species richness (e.g. next-generation sequencing and phospholipid fatty acid analysis (PLFA) methods), which limits the scope of diversity comparisons between microbial studies. Rather than attempting to compare absolute values in species richness, we address this limit in our study by first determining the patterns of diversity with elevation within each study separately, and then summarizing the overall trends across studies and taxa.

Studies in our review show a wide range of patterns in soil microbial diversity with elevation including declines, increases, mid-elevation peaks and peaks at the extremes of the gradient



**Figure 2.** Studies of diversity patterns of (A) soil microbes and (B) fungal functional groups on montane gradients. Values denote the percentage of studies that found a decrease, increase, mid-elevation peak, no change or other patterns with increasing elevation (e.g. when diversity was the highest at the extreme of the gradient, often referred to as U-shaped or hollow). Panel (A) only includes studies that investigated an entire free-living soil bacterial (light blue), fungal (green) or archaeal (orange) community across three or more elevations; the total category (gray) shows fungi, bacteria and archaea combined ( $n = 53$ ). Panel (B) shows patterns of diversity in fungal communities with elevation, including the total (gray) of all free-living and mycorrhizal fungi combined ( $n = 53$ ), all free-living fungi (green) combined and patterns of functional groups: saprotrophs (decomposers; dark blue), ectomycorrhizal (ECM; pink) and arbuscular mycorrhizal (AMF; yellow) communities.

(also referred to as U-shaped, hollow and mid-elevation minimum; these patterns are pooled as ‘Other’ in Fig. 2), or no discernible trend at all (Box 1). Indeed, though soil microbial communities are thought to be strongly structured by elevation gradients across the globe (Tedersoo et al. 2014; Delgado-Baquerizo et al. 2016), 33% of the studies in our review found no consistent trend with elevation for all microbial taxa combined and 34% observed a decrease in diversity (Fig. 2A), with the remainder divided between an increase, mid-elevation and other trends. For each taxon separately, fungi showed the strongest trends with 41% of studies finding a decline in diversity with elevation, while 33% studies found a diversity decline for soil bacteria. Diversity patterns of archaea with elevation were the least consistent, but only 13 studies of archaea met our review criteria, so this information should be considered preliminary.

Fungal functional groups (e.g. saprotrophic fungi) showed much more consistent patterns with elevation than other microbes, but the patterns were individualistic for each fungal group (Fig. 2B), indicating patterns of diversity between fungal functional groups diverge along montane gradients despite broad taxonomic affinities. Most notably, the diversity of

free-living saprotrophic fungi was found to consistently decline with elevation in all but one study (83%), while the diversity of mycorrhizal groups diverged with 62% of studies finding arbuscular mycorrhizal fungal (AMF) diversity declined with elevation and 35% finding ectomycorrhizal fungi (ECM) increased.

Overall, patterns of microbial diversity on mountains are notably variable and differ between taxonomic groups. This is in contrast with other aboveground taxa that show a much more consistent patterns in diversity with elevation, in that ~50% of studies of all plant and animal species show a mid-slope peak with elevation (Rahbek 2005); we found that this is comparatively uncommon for microbes. Indeed, our findings suggest there are fundamentally different abiotic and biotic mechanisms structuring aboveground and belowground diversity pattern on mountains. Based on the central role of soil and edaphic conditions serve in structuring microbial communities (see the section below on mechanisms), we hypothesize that unsystematic and idiosyncratic variation in soil properties with elevation weakens the broad pattern of microbial diversity on montane gradients.

When comparing microbial diversity trends between studies, it is important to acknowledge the role of DNA sequencing-based approaches in measuring biodiversity in microbial communities. The primary metric of richness in these communities, operational taxonomic units (OTUs), is quite different than traditional taxonomic approaches used to describe macroscopic species (i.e. morphology). Rather, OTUs are user-defined similarity thresholds of DNA sequences (Schloss et al. 2009; Caporaso et al. 2011). About 77% of the studies included in this review used sequencing-based approaches, and many reported multiple richness and diversity indices in the same study, or richness estimators (e.g. Chao1, OTU richness) to measure diversity (see Table S1, Supporting Information). Results derived from OTU richness and diversity indices (i.e. Chao, Shannon and Simpson indices) are inherently interconnected (Chao, Chiù and Hsieh 2012; Alberdi and Gilbert 2019), and a consensus on how to best measure diversity has yet to be reached (Deagle et al. 2019). Given the inherent constraints on such data (e.g. limiting the strength of inference in comparisons of richness between studies), cross-study patterns should be interpreted with caution.

## MECHANISMS DRIVING CHANGES IN COMMUNITY COMPOSITION

Sixty-five studies in our review provided the primary mechanism driving shifts in microbial community diversity and composition on montane gradients (see Table S1, Supporting Information, for details): 66% reported changes in climate (36%) and edaphic factors (mainly soil pH; 30%), 16% reported changes in soil organic matter and nutrients (e.g. C, N) and 18% reported changes in vegetation composition as the principal mechanism. The main drivers of microbial community composition were not uniform across taxa. For fungi, 48% reported climate as the main mechanism driving changes in composition and 24% reported edaphic factors, primarily nutrients (Fig. 3). For bacteria, 48% reported edaphic factors (mainly soil pH) as the main mechanism and 30% reported climate. For archaea, 71% of studies reported edaphic factors as the main mechanism. Finally, for mycorrhizal fungi, climate (44%) and vegetation (38%) were the main mechanisms driving shifts across elevation. These results highlight how changes in climate and edaphic factors along the gradient play the predominant and taxon-specific role in structuring soil microbial community composition.

### Box 1 Patterns in elevational response of soil microbes



A **decline** in diversity with elevation is the most common pattern observed across studies. Fungal diversity declined along elevation gradients in the Cordillera de Tilarán in Costa (Looby *et al.* 2016), the White Mountains in California (Collins *et al.* 2018), and Mount Gongga in the Tibetan Plateau (Tian *et al.* 2017). Bacterial diversity also declined across numerous mountain ranges in Asia (Lin *et al.* 2010, Meng *et al.* 2013, Zhao *et al.* 2017), the Peruvian Andes (Nottingham *et al.* 2018), and the Italian Alps (Siles and Margesin 2016). Li *et al.* (2018) found a unique stair-step decline in diversity that coincided with changes in pH along the gradient in the Tibetan Plateau.



An **increase** in diversity with elevation is frequently seen in mountain ecosystems where water is a limiting factor, and moisture and rainfall increase along the gradient. Fungal diversity increased along elevation gradients in a grassland in the Swiss Alps (Pellissier *et al.* 2014) and dry forests in Mexico (Caiafa *et al.* 2017). An increase in bacterial diversity was observed in a tropical forest in Brazil (Lima-Perim *et al.* 2016) and along a tropical to high altitude temperate gradient in southwest China (Singh *et al.* 2013).



In some cases, conditions at **mid-elevations** (i.e. freeze-thaw, lack of nutrients, temperature fluctuations) minimizes competition allowing a greater diversity of soil microbes to thrive (Zhou *et al.* 2017). On Mount Fuji, Japan, bacterial (Singh *et al.* 2012b) and archaeal (Singh *et al.* 2012a) diversity peaked at mid-elevations, and trends did not mirror plant diversity along the gradient.



Although there were many studies that found **no trend** with elevation, there were no instances where neither fungal diversity (taxonomic, functional groups, or otherwise) or community composition responded across elevation gradients, while this was the case for bacteria. In the Andes, soil bacterial diversity did not vary with elevation in organic or mineral soil, while plant diversity peaked at mid-elevations (Fierer *et al.* 2011). Soil fungal diversity did not differ between three forest types in the Yungas in Argentina, but functional groups preferred certain forest types (Geml *et al.* 2014).



In few cases, microbial diversity is highest at the extreme ends of the gradient. Decreases at mid-elevations (referred to hollow or **u-shaped** patterns in the literature) are rarely observed (Rahbek 2005), and in this review, were only found with bacteria (Wang *et al.* 2012, Singh *et al.* 2014, Liu *et al.* 2016).

Box 1. General patterns in the elevational response of soil microbial diversity. Unlike plants and animals, which often show a mid-elevation peak, the majority of studies that found a trend showed a decline in soil microbial diversity with increasing elevation.

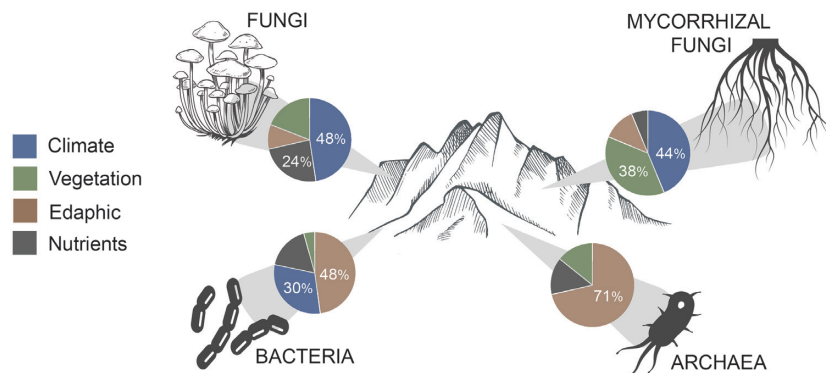


Figure 3. Climate, edaphic factors, nutrients and vegetation were the principal mechanisms identified in determining soil microbial community composition across elevation in 65 studies. Climate and edaphic factors were the primary mechanisms reported (~66% of studies). Climate was the primary mechanism for fungi ( $n = 21$ ), while edaphic factors (mainly pH) were the primary mechanism for bacteria ( $n = 23$ ) and archaea ( $n = 7$ ). In studies focusing on mycorrhizal fungi, climate, followed by vegetation, were the main drivers of community composition across elevation ( $n = 16$ ). Climate (blue) includes temperature, precipitation, or soil temperature or moisture. Edaphic factors (brown) include soil pH, cations or electrical conductivity. Nutrients (gray) include SOM, C, N or C:N. Vegetation (green) includes forest type, composition, host identity and shrub expansion.

In addition to cross-site patterns for individual taxa, we are also interested in whether fungi, bacteria and archaea communities show coordinated responses across the gradient, ideally in studies where the conditions are uniform for each taxon (Peay *et al.* 2017). This is best accomplished in single studies, which simultaneously compare the responses of different microbial groups to change in elevation. We found 10 such studies, and these report that diversity patterns generally diverge between taxa on the same elevation gradient, along with the factors causing these patterns (Box 2). In particular, studies on tropical montane gradients found changes in temperature and precipitation shape diversity patterns differently for each class of microbial taxa (Peay *et al.* 2017; Nottingham *et al.* 2018a). For instance, along a 950-m elevation gradient on the island of Hawai'i, the factors associated with an increase in richness were different for each taxa: fungal richness increased most strongly with soil C, ammonia-oxidizing archaea increased with N mineralization, and bacteria increased with higher soil C and pH (Peay *et al.* 2017). Given the distinctive and nonlinear climatic patterns common on tropical mountains (e.g. Giambelluca and Nullet 1991; Martin and Fahey 2014), future changes in tropical climates are likely to have complex effects on microbial communities found in these species-rich ecosystems.

## MANIPULATIVE EXPERIMENTS, MONTANE GRADIENTS AND MICROBIAL RESPONSES TO CLIMATE CHANGE

There has been increase in the use of experimental studies on elevation gradients to assess how microbes, and the processes they mediate, respond *in situ* to change in conditions mediated by elevation, while controlling for the roles of abiotic and biotic properties in structuring soil microbial communities. In particular, studies have increased that mimic warmer temperatures by moving intact, high-elevation soil communities to lower elevations, while also exposing high-elevation microbes to litter and other C-sources from lower elevation flora predicted to move upslope (e.g. Lenoir *et al.* 2008). When microbes are exposed to more labile sources of C and N in warmer and usually drier soil conditions at lower elevations, net increases in decomposition rates and changes in the structure of microbial communities are expected. Indeed, decomposition of SOM (Zimmermann *et al.* 2009) and litter (Salinas *et al.* 2011) increase markedly when transplanted to lower elevations in the tropics. Activities of C-degrading enzymes also increased in litter transplanted to lower sites along a dry elevation gradient in California (Baker *et al.* 2018) and a wet elevation gradient in Costa Rica (Looby and Treseder 2018). Along the gradient in Costa Rica, fungal diversity also increased in soils moved to lower elevations.

Biotic conditions are also changing on mountains as ongoing climate change alters communities. Close relationships between species ranges and community composition with the abiotic environment have already led to elevational range shifts and local extinctions of aboveground taxa in response to climate change (e.g. Wiens 2016). In turn, altered and potentially novel aboveground assemblages of species are forming in montane regions, which is already impacting soil microbial communities. For instance, along an elevation gradient in the White Mountains in California (3200–3800 m) experimental evidence suggests high-elevation microbial diversity may decline in response to the recent expansion of woody sagebrush shrub communities into alpine areas (Collins *et al.* 2018). However, bacteria and fungi both reverted back to pre-sagebrush expansion

diversity levels and community compositions after 4 years of experimental shrub removal (Collins *et al.* 2016, 2018), indicating these shifts can occur rapidly. Depending on the scale of vegetation shifts, concomitant changes in the microbial community may have cascading feedbacks on decomposition and nutrient cycling, altering the structure and function of these alpine areas at least in the near term. Such studies demonstrate the utility of combining manipulative experiments with elevation gradients for understanding environmental influences—and the rapidly changing conditions characteristic of the Holocene—on microbial ecology.

## CHANGING FUNCTIONAL ROLES OF MICROBES ON MONTANE GRADIENTS

Changing climate and increasing topographic complexity increase stress and isolation, promoting endemism and speciation, and leading to high turnover rates along elevation gradients (Decaëns 2010; Steinbauer *et al.* 2016). Rapid changes in biotic and abiotic conditions on montane gradients serve as trait filters, and functional diversity of microbes has been linked to changes in climate across elevations (Caiafa *et al.* 2017). The steep gradients on mountains accentuate microbial traits, nutrient status and sensitivity to specific climatic and edaphic conditions. Such turnover primarily affects many key ecosystem functions, like decomposition and N cycling, in which soil fungi and bacteria often interact synergistically. In particular, soil fungi and bacteria promote plant nitrogen uptake and fixation, increase plant stress tolerance (Giauque and Hawkes 2013) and play synergistic and tailored roles in decomposition (de Boer *et al.* 2005; Schneider *et al.* 2012), each of which can be altered when taxa turn over at different rates on montane gradients. A better understanding of shifting functional roles in the microbial community on montane gradients is a promising avenue to improve our understanding of how microbially mediated nutrient cycles, especially of carbon and nitrogen, vary with elevation in montane systems.

### Decomposers, montane conditions and nutrient limitation

Rates of decomposition are slow at higher elevations due to cooler temperatures, wetter soils and lower soil fertility, which perpetuates a feedback between nutrient limitation, poor litter quality (i.e. more recalcitrant) and slower rates of detrital breakdown in montane forests. This cycle is especially evident in forests on mountains in the humid tropics—particularly at elevations that receive regular orographic cloud cover—where thick deposits of dead organic matter accumulate due to cool and anoxic soil conditions (Silver, Lugo and Keller 1999), forest productivity is low and trees are generally short-statured (Fahey, Sherman and Tanner 2016). Microbial function and the distribution of dominant soil taxa are highly sensitive to such shifts in the abiotic and biotic conditions that shape decomposition dynamics.

Microbial communities also track gradients in ecosystem fertility common in montane ecosystems, as found in the Changbai Mountains in China where the elevational distribution of soil taxa mirrored nutrient conditions (Yao *et al.* 2017): the diversity of oligotrophic bacteria (Acidobacteria) and fungi (Basidiomycota) peaked at mid-elevations under nutrient-poor conditions, and copiotrophic taxa (e.g. Acidobacteria and Ascomycota) were most diverse at the extremes

## Box 2 Comparing responses of soil bacteria, fungi, and archaea



**Fungi, bacteria, and archaea** all responded strongly, yet differently to an elevation and precipitation gradient in Hawai'i (Peay *et al.* 2017). Fungal diversity increased, bacterial showed a mid-elevation peak, and archaea decreased with increasing elevation. Shifts in microbial communities varied based on resource ecology and limiting conditions for each group: fungi responded most strongly to C, bacteria to pH, and archaea to N.

Across an elevation and temperature gradient in the Peruvian Andes, Nottingham *et al.* (2018) found coordinated changes between **plants, bacteria, and fungi**. Diversity decreased with elevation for all three groups. However, plant responses were more drastic than those for bacteria and fungi. Responses were primarily temperature driven, and microbial diversity was strongly correlated with activities of enzymes used in organic matter cycling.



On Taibai Mountain along the Qinling Mountain range in China, **bacterial and fungal** diversity showed a mid-elevation peak and no trend with elevation, respectively (Ren *et al.* 2018). Shifts in community composition for both bacteria and fungi were mainly driven by soil moisture and temperature.

In the Italian Alps, **bacterial and fungal** diversity was highest at the lowest elevations and declined at higher elevations (although not linearly; Siles and Margesin 2016). Shifts in bacterial community composition were caused by many environmental factors, especially pH. There were no shifts in soil **archaea**.



**Box 2.** Studies that investigated the diversity patterns of more than one microbial group (bacteria, fungi and archaea) along a single montane gradient. Such studies that incorporate more than one microbial group help drive the field forward, allowing cross-taxa trends in elevation to be determined. In our literature search, 10 studies investigated diversity patterns across elevation in more than one microbial group. See Table S1 (Supporting Information) for elevation ranges in each study.

of the gradient (i.e. U-shaped or hollow pattern). Likewise, Nottingham *et al.* (2018b) observed a transition in microbial traits towards slower-growing, oligotrophic taxa at higher elevations (e.g. Acidobacteria). Such shifts in organic substrates and soil taxa can alter C-source utilization, with microbes focusing on decomposing more recalcitrant forms of carbon at higher elevations and more labile forms at lower elevations (Xu *et al.* 2014). Nutrient limitation at higher elevations also affects the balance of fungal versus bacterial decomposition of cellulose. For instance, an abundance of genes associated in the breakdown of C, isopullulanase and exoglucanase was found at higher elevations along a gradient in the Tibetan Plateau using GeoChip4 (Yang *et al.* 2014). Overall, more C-degrading enzymes and higher F:B ratios suggest a greater capacity for soil microbes to decompose recalcitrant C at high elevations.

### Nitrogen cycling and microbial function

Our understanding of microbial-mediated changes in nitrogen cycling along elevation gradients is not as resolved as for decomposition, and most of this research has focused on tropical mountains. There is general evidence that nitrogen limitation increases at higher elevations (Vitousek and Sanford 1986; Fisher

*et al.* 2013), and in turn, soil C:N ratios usually increase (Thébault *et al.* 2014), leading to fungal-dominated communities (Fierer *et al.* 2009) and greater microbial demand for N (Nottingham *et al.* 2015) in upper montane ecosystems.

Although some studies have investigated how nutrient availability affects N-fixation in mountain ecosystems (e.g. Matson *et al.* 2015), there is little information on how N-fixing bacteria vary with elevation. In contrast, elevational responses of fungal symbionts have been studied extensively, with arbuscular mycorrhizal fungi species richness generally declining and ectomycorrhizal fungi species richness generally increasing with elevation (Kivlin *et al.* 2017). How N-fixing bacteria vary with elevation is a much-needed area of research as climate change and other global change drivers like anthropogenic N-deposition may fundamentally alter these dynamics.

As nitrogen availability declines with elevation, the functional influences of free-living microbes on N-cycling change along with the changing activities of symbiotic microbes on the same gradients. Ammonia-oxidizing bacteria and ammonia-oxidizing archaea play important roles in total ammonia oxidation—the rate limiting step in N-cycling—and some studies have found trade-offs in their abundances with elevation, where abundance of these archaea declined at higher elevations

as the bacterial abundance increased (Zhang *et al.* 2009; Yuan *et al.* 2015). More studies like these will help reveal biotic and environmental constraints on N-cycling in the face of ongoing global change.

### Trade-offs in fungal functional groups

Biotic filtering—via microbe–microbe competition—may play an important role in structuring soil communities across elevation. Most studies investigating fungal functional groups note a trade-off in decomposer and ECM diversity patterns along elevation gradients. This is known as the Gadgil effect (Gadgil and Gadgil 1971, 1975), where plants invest more in ECM when soil C:N ratios are high and nitrogen is limiting. Under these scenarios, ECM fungi can serve as a biotic filter on free-living decomposer fungi as both compete for the organic N and C in SOM, and in the process ECM can suppress overall decomposition rates, increase C sequestration and reduce overall fungal abundance and diversity (Fernandez and Kennedy 2016; Zak *et al.* 2019; Stuart and Plett 2020). Indeed, higher diversities of ECM at higher elevations and higher diversity of decomposer fungi at lower elevations have been noted in tropical montane forests (Gómez-Hernández *et al.* 2012; Looby, Maltz and Treseder 2016; Eduardo *et al.* 2018), and on a Mediterranean elevation gradient (Saitta *et al.* 2018) among others, and in most cases the trade-off coincided with an overall decline in fungal diversity at higher elevations. Some of the mechanisms behind the Gadgil effect remain unclear; however, montane gradients are an important avenue to further study this phenomenon. For instance, future studies may consider soil transplant experiments and plant–soil reciprocal transplants to disentangle the effects of biotic filtering across elevation.

### Climate change and variation in microbial traits across elevation

When using mountains to study climate change impacts, tracking the differential responses of microbial traits along the gradient is important. Many free-living fungi possess traits that place them into broad groups as stress tolerators or decomposers (Treseder and Lennon 2015). Stress tolerators contribute to SOM accumulation in soil by producing recalcitrant compounds, while decomposers reduce SOM stocks. As climate conditions change, there may be trade-offs between these microbial groups that shift mountains towards carbon sinks or sources. In a boreal forest, for instance, mycorrhizal necromass is a greater component of SOM than even plant litter (Clemmensen *et al.* 2015), and similar shifts in microbial composition in montane settings have important implications for C-cycling via changes in C storage. In particular, melanin is a polymer abundant in ECM cell walls and offers protection against environmental stresses that are common at high elevations (e.g. UV radiation, drought, extreme temperatures, etc.). Melanin accumulation slows decomposition (Koide, Fernandez and Malcolm 2014), which can cause shifts in microbial decomposer communities (Fernandez and Kennedy 2018). If a greater abundance and diversity of ECM at higher elevations results in more melanin in soils, this can directly (i.e. slowing down rates of decomposition) and indirectly (i.e. shifts in microbial decomposer composition) affect C cycling in mountain ecosystems. Although not included in our literature search, dark septate endophytes (DSEs) are fungal symbionts that frequently colonize the roots of high-elevation plants (Casanova-Katny *et al.* 2011; Urcelay, Acho and Joffre 2011). In the Himalayas at extreme elevations above

5800 m, DSEs can even replace AMF, helping plants acquire nutrients and acting as surrogate mycorrhizae (Kotlínek *et al.* 2017). DSEs also produce large amounts of melanin in their cell walls, which may also act as a mechanism to slow decomposition at high elevations. Overall, investigating traits like this may provide important insights into the role of soil microbes in mountain ecosystems.

Tracking microbial traits across elevation gradients is also important as greenhouse gases are emitted from soil during microbially mediated processes, such as carbon dioxide (CO<sub>2</sub>), nitrous oxide (N<sub>2</sub>O) and methane (CH<sub>4</sub>). Bacteria and fungi both denitrify nitrate and nitrite, releasing N<sub>2</sub>O as a by-product and release CO<sub>2</sub> as a by-product during decomposition. In addition, archaea and bacteria are producers and consumers of CH<sub>4</sub>, respectively. Indeed, an increase in denitrification and methane-producing genes has been observed with increasing elevation (Yang *et al.* 2014), and the distribution of methanotrophic bacteria is dependent on temperature (Hofmann *et al.* 2016), which shifts along elevation gradients. In fact, CH<sub>4</sub> concentrations in extremely wet, tropical soils can be as high as 24%, and are also associated with reduced oxygen concentrations (Silver, Lugo and Keller 1999), suggesting a higher electron acceptor limitation for decomposers.

Soils in tropical forests are especially important for global greenhouse gas budgets. Along a 900-m elevation gradient in the Brazilian Atlantic Forest, greenhouse gas emissions were strongly linked to soil temperature (CO<sub>2</sub> and N<sub>2</sub>O) and moisture (N<sub>2</sub>O), suggesting that climate warming may support increases in decomposition and gross inorganic N fluxes (Sousa Neto *et al.* 2011). Other studies in the tropics have also found higher N emission rates at lower elevations in Peru (Teh *et al.* 2014) and Ecuador (Wolf *et al.* 2011), suggesting that warmer and drier conditions predicted with climate change in the tropics may increase gross N emission into the atmosphere. More research is needed on functional groups whose functions mediate greenhouse gas emissions into the atmosphere. Determining how soil microbes and the fate of greenhouse gas emissions will shift is a key challenge that many are beginning to tackle using mountain ecosystems.

## CONCLUSIONS AND FUTURE DIRECTIONS

Elevation gradients are useful for determining the patterns and mechanisms that drive the distribution of microbial diversity, composition and functional types. After a decade of new research on the topic, we have delved deeper into how the interactions between microbes, ecosystem function and climate change all come together on mountains. Overall, the patterns in our review make clear the centrality of climate and soil interactions on montane gradients in structuring microbial communities, and highlight how global change will fundamentally impact microbial diversity, composition and function. As the atmosphere warms, decomposition rates will likely increase rapidly at higher elevations and the composition and diversity of microbial communities will change in turn, causing significant feedbacks on carbon dynamics as microbes decompose previously sequestered organic matter in warming, drying and thawing soils. Such shifts could turn montane ecosystems from a global carbon sink into a net source of CO<sub>2</sub>. Persistently cold or wet climates common in montane ecosystems generally store large quantities of SOM, and increased temperatures in montane ecosystems are likely to result in rapid decomposition of this sequestered SOM (Biskaborn *et al.* 2019), especially at the highest elevations where significant SOM is stored in montane



permafrost soils (mountains comprise a significant portion of global permafrost; Gruber and Haeberli 2009). Likewise, the drying of anoxic soils due to shifting patterns in precipitation and cloud formation on montane gradients, especially on tropical mountains that are characterized by regular cloud formation at consistent elevations (e.g. Martin and Fahey 2014), will have fundamental implications of microbial function in hitherto wet and saturated ecosystems.

Recent advances in the field allow us to provide directions for future study to better examine broad-scale responses of microbes and the drivers behind them, building on the insights of elevation gradients as proxies for climate change. We recommend four key areas for future study of soil microbes along elevation gradients. First, there should be further effort to better identify and quantify the mechanisms (i.e. environmental, edaphic, spatial, biotic, etc.) driving turnover in microbial diversity, composition and functional traits across elevation gradients. A good model is studies like Zhou et al. (2017) that integrated environmental selection, competition and spatial properties in structuring bacterial communities along a 2000-m elevation gradient on the Tibetan Plateau. Likewise, this effort should help to better connect how changes in microbial communities feed back on ecosystem processes and how these feedbacks in turn are conditioned by the environment. There are many environmental properties that vary along elevation gradients, but most likely climate will play the overarching role, governing direct (e.g. trait selection) and indirect (e.g. edaphic properties) functions in free-living microbes (though not necessarily for fungal symbionts; see Kazenel et al. 2019). Geographic factors, such as latitude, or smaller scale variation, such as terrain complexity (e.g. slope angle), may largely determine whether temperature or precipitation is more important. For example, soil moisture is generally more limiting in arid mountains, while temperature is likely to be more limiting in temperate than tropical mountains. Overall, an even better understanding of how microbial diversity and function shift with elevation, and how this varies between free-living microbes and symbionts, will provide insights into how montane systems will function in a changing climate.

Second, while there has been important progress in the last decade, we need more long-term manipulative experiments along elevation gradients to help observational studies better identify the specific mechanisms driving microbial communities. The observational studies in this review have been instrumental in developing the leading theories of the ecological and evolutionary factors that shape microbial diversity and communities—such as, that the richness of microbial communities are shaped by resource ecology (Peay et al. 2017), and that the compositions of fungal and bacterial community are tightly linked to temperature (Nottingham et al. 2018a). In addition, future climate conditions may increase rates of decomposition through changes in extracellular enzyme activity (Baker et al. 2018) and changes in the fungal community (Looby and Treseder 2018). However, a greater emphasis on manipulative experiments is needed to improve our predictive power and provide information that can be used in dynamic models. To this end, future experiments may include throughfall exclusions (i.e. drought shelters), soil transplants and plant-soil reciprocal transplants among others. Moreover, manipulative experiments highlighting functional traits will move the field beyond descriptions of diversity towards the key question of how ecosystem processes (i.e. soil inputs and atmospheric outputs dynamics) will be altered under projected climate change.

Third, both observational and experimental studies need standardization of high-throughput sequencing techniques to

allow for quantitative analyses of multi-study datasets and more extensive geographic and temporal replication to determine whether patterns are scale or season dependent. When estimating microbial richness and diversity, spatial resolution is important (Martiny et al. 2011; Bahram et al. 2012; Singh, Shi and Adams 2013). Standardizing methods to replicate sampling on the same mountain, and across mountains regionally and globally, is an essential next step to improve our ability to determine whether strong, universal patterns exist and the mechanisms that drive them. Furthermore, montane landscapes are topographically complex, which has marked effects on landscape-scale patterns in climate, soils and vegetation. This requires intensive sampling to account for spatial heterogeneity, which can help clarify the mechanisms driving soil microbial structure along elevation gradients (Yashiro et al. 2016), and whether the mechanisms differ for local or regional scales (Tripathi et al. 2014). As such, at smaller scales variation in topography can even be more important than elevation in shaping soil bacterial communities (Wu et al. 2007; Bardelli et al. 2017) and the mechanisms that drive diversity patterns can differ based on these effects (Singh et al. 2014). Sharp contrasts in conditions across slope and aspect at the same site—e.g. on mountains with rain shadows—provide important natural experiments to help understand how gradients in environmental conditions interact with a single local species pool. How variation in the geometry, shape and size of mountain ranges and regional contrasts in weather regimes interact with the effects of montane gradients needs to be considered as well. In particular, mountain geometry can alter the elevation where features like treelines and forest types are located, via the ‘Massenerhebung’ or mass elevation effect (e.g. Martin, Fahey and Sherman 2011), a phenomenon where the size of a mountain range influences local climate and hence vegetation patterns; at a given elevation, bigger mountains have higher temperatures than smaller ones as larger land masses absorb more solar radiation. Likewise, there is a general lack of information on the effects of seasonality as a driver of temporal changes in community composition, even though some studies have found pronounced seasonal shifts in microbial community composition (e.g. Siles et al. 2017). Once we have more thorough replication and better standardization of sequencing techniques across studies, quantitative analyses such as a formal meta-analysis of multi-study datasets will be an important next step. Such a study may account for additional factors between studies such as variation in elevation range and mountain geometry, and study site location details such as latitude (e.g. tropical versus temperate) and distance from the ocean.

Fourth, studies should investigate elevational diversity patterns through the lens of functional traits. A focus on taxonomic diversity rather than functional diversity is potentially precluding our ability to better understand microbial ecology and function. Rather, an increased focus on what the microbes are doing instead of which microbes are present will advance the field, and studies should also incorporate direct measurements of function (i.e. extracellular enzyme activity). For fungi at least, traits are a more powerful lens than diversity in determining patterns of fungal function (Crowther et al. 2014; Zanne et al. 2020). Labeling microbes by their nutrient status or function is more useful in linking microbes to ecosystem-level properties as well. This information will be more valuable for ecosystem models that account for trade-offs between stress tolerance and enzyme production (Allison 2012), and in turn improve montane gradients as tools for studying climate change. Finally, assessing traits associated with growth, resource acquisition and stress are important metrics for determining trade-offs between

microbially mediated decomposition and carbon storage affecting the overall carbon balance within ecosystems (Malik et al. 2020).

Future research that incorporates these recommendations will better advance our understanding of the underlying mechanisms and key environmental attributes that drive patterns of microbial diversity and communities in montane ecosystems and help us improve predictions of the ecosystem-level consequences of climate change. We expect that because soil microbial communities are so diverse, generalizable patterns may remain elusive until the roles of specific taxonomic and functional groups are addressed and progress is made in standardizing sequencing techniques. The field has advanced rapidly, but more work is needed to fully synthesize the biogeography and functional ecology of soil microbes in montane biomes.

## SUPPLEMENTARY DATA

Supplementary data are available at [FEMSEC](https://femsec.org) online.

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