# Research review

# Embracing mountain microbiome and ecosystem functions under global change

Author for correspondence:
*Jianjun Wang*
*Email: jjwang@niglas.ac.cn*

**Jianjun Wang**[1,2]* (iD), **Ang Hu**[1,3]* (iD), **Fanfan Meng**[1,2]* (iD), **Wenqian Zhao**[1,2], **Yunfeng Yang**[4] (iD), **Janne Soininen**[5] (iD), **Ji Shen**[6] and **Jizhong Zhou**[7,8] (iD)

[1]State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academic of Sciences, Nanjing 210008, China; [2]University of Chinese Academy of Sciences, Beijing 100049, China; [3]College of Resources and Environment, Hunan Agricultural University, Changsha 410128, China; [4]State Key Joint Laboratory of Environment Simulation and Pollution Control, School of Environment, Tsinghua University, Beijing 100084, China; [5]Department of Geosciences and Geography, University of Helsinki, Helsinki FIN-00014, Finland; [6]School of Geography and Ocean Science, Nanjing University, Nanjing 210023, China; [7]Institute for Environmental Genomics and Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA; [8]Earth and Environmental Sciences, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA

## Summary

Mountains are pivotal to maintaining habitat heterogeneity, global biodiversity, ecosystem functions and services to humans. They have provided classic model natural systems for plant and animal diversity gradient studies for over 250 years. In the recent decade, the exploration of microorganisms on mountainsides has also achieved substantial progress. Here, we review the literature on microbial diversity across taxonomic groups and ecosystem types on global mountains. Microbial community shows climatic zonation with orderly successions along elevational gradients, which are largely consistent with traditional climatic hypotheses. However, elevational patterns are complicated for species richness without general rules in terrestrial and aquatic environments and are driven mainly by deterministic processes caused by abiotic and biotic factors. We see a major shift from documenting patterns of biodiversity towards identifying the mechanisms that shape microbial biogeographical patterns and how these patterns vary under global change by the inclusion of novel ecological theories, frameworks and approaches. We thus propose key questions and cutting-edge perspectives to advance future research in mountain microbial biogeography by focusing on biodiversity hypotheses, incorporating meta-ecosystem framework and novel key drivers, adapting recently developed approaches in trait-based ecology and manipulative field experiments, disentangling biodiversity–ecosystem functioning relationships and finally modelling and predicting their global change responses.

## Introduction

Mountains are landforms that rise prominently above their surroundings (e.g. > 300 m in elevation) and are generally characterised by steep slopes, a relatively confined summit area and considerable local relief (Kapos *et al.*, 2000; Antonelli *et al.*, 2018). Mountain building, resulting from the interplay of tectonic and volcanic processes, establishes high topographic heterogeneity

and steep climatic gradients within a relatively compressed geographical extent. It also creates highly interacting terrestrial and aquatic habitats such as soils, streams, rivers and lakes to maintain high biodiversity and endemism and further ecosystem services for humans (Rahbek *et al.*, 2019a). Specifically, by covering just 25% of all land area, mountains host one-third of the world's terrestrial plant species and 85% of the amphibian, bird and mammal species and supply half of the human population with water (Körner, 2007; Rahbek *et al.*, 2019a). Mountain regions are

*These authors contributed equally to this work.

biodiversity hotpots of both large and small organisms that play key roles in regulating global carbon, nitrogen and water cycles and are thus fundamental for sustaining life on Earth (Myers *et al.*, 2000). The variation in plants and animals across climate zones on mountainsides is first characterised by Carolus Linnaeus in 1743 (Linnaeus, 1781). Humboldt's enigma of extraordinarily high mountain biodiversity has been studied dating back to his famous vegetation zonation discovery of Mount Chimborazo in the Andes in 1802 (Morueta-Holme *et al.*, 2015; Rahbek *et al.*, 2019b). For over 250 years, mountains have served as an area for natural experiments for generations of ecologists to test biodiversity gradient theory, seek underlying ecological mechanisms and predict biodiversity loss and ecosystem functioning under global change for diverse taxonomic groups from higher plants and animals to microorganisms (Lomolino, 2001; Rahbek *et al.*, 2019b).

Microbes are abundant and diverse in mountain regions, play an essential role in virtually all biogeochemical cycling processes and are an important component of ecosystem response to global change (Battin *et al.*, 2016; Cavicchioli *et al.*, 2019; Zhu *et al.*, 2021). Mountains offer contrasting ecosystem types and continuous environmental gradients for their biota (e.g. energetics, resources and stress). For example, temperature and primary productivity decline with elevation, which leads to increased plant litter decomposition and soil carbon loss due to not just a kinetic effect on microbial reaction rates but results from plant inputs stimulating microbial growth (Nottingham *et al.*, 2019; Peters *et al.*, 2019; Albrecht *et al.*, 2021). Unravelling diversity patterns of microorganisms in parallel with macroorganisms (e.g. plants) is needed to provide a more unified framework for understanding biodiversity patterns and predicting system-wide ecological responses to global change. However, the distribution, characteristics and diversity of microorganisms along elevational gradients have been examined only for a decade, as the first study appeared for soil Acidobacteria in 2008 (Bryant *et al.*, 2008) followed by stream bacteria and diatoms (Wang *et al.*, 2011). Such studies show that microorganisms may not always follow the hump-shaped or decreasing elevational diversity patterns that are traditionally observed for plants and animals but rather show much more diverse and nuanced diversity patterns for terrestrial (Bryant *et al.*, 2008; Fierer *et al.*, 2011; Shen *et al.*, 2013) and aquatic ecosystems (Wang *et al.*, 2017). The biogeographical literature comprises prevalent ecological and evolutionary hypotheses to explain competing diversity patterns of microorganisms, such as climatic hypotheses (Grytnes & McCain, 2007), elevational Rapoport's rule (Stevens, 1992), mid-domain effect (Colwell & Lees, 2000) and scale effects (Rahbek, 2005).

Such observations and mechanistic drivers are affected by the ongoing Anthropocene. Notably, mountains belong to the most climate-sensitive ecosystems world-wide (Seddon *et al.*, 2016) and become more urbanised with increasing settlements and transport networks (Becker & Bugmann, 2001). Mountain diversity is thus inevitably and strikingly affected by global change, such as climate change and human activities. For instance, warming is shifting the fundamental features of species such as elevational range and optima, driving plant species upwards in elevation, such as on Mount Chimborazo over two centuries (Morueta-Holme *et al.*, 2015), and further affecting global patterns of mountain biodiversity (Rumpf *et al.*, 2018). Globally, nearly 60% of the mountainous areas are under intense human pressure such as downstream eutrophication and mountaintop removal, and generally more extensively in the lower than upper elevations (Elsen *et al.*, 2020). Climate can modulate the effects of human activities, and their interacting effects reshape elevational patterns in biodiversity, including microorganisms, and ecosystem functions at an unprecedented pace (Peters *et al.*, 2019).

Despite the long-term interest in mountain biota, a comprehensive synthesis of elevational patterns and drivers in biodiversity and ecosystem functions is still lacking for microorganisms across mountainous ecosystems. In this literature review, we analyse 152 studies on various microbial taxonomic groups, including bacteria, fungi, archaea and diatoms, to synthesise our current understanding of elevational diversity patterns across terrestrial and aquatic ecosystems (Fig. 1). We further address the underlying mechanisms that drive these elevational diversity patterns, that is the relative importance between deterministic and stochastic processes and the main environmental drivers. Finally, we identify the important knowledge gaps and propose 21 key questions from seven cutting-edge perspectives to guide future studies on mountain microbial biogeography under global change. These perspectives include ecological theories for decrypting extraordinarily high mountain biodiversity, namely Humboldt's enigma, novel drivers underlying biodiversity change, ecological interactions between terrestrial and aquatic ecosystems, and biodiversity–ecosystem functioning relationships and the state-of-the-art approaches, including trait-based ecology, manipulative field experiments and modelling approaches to predict global change responses.

## Patterns of global mountain microbial diversity

In recent decades, microbial ecologists and biogeographers have challenged the Baas Becking hypothesis that states 'everything is everywhere, but the environment selects' (Baas Becking & Nicolai, 1934; O'Malley, 2007) and finds that microorganisms also show biogeographical patterns on mountainsides in terms of species richness and community composition (Bryant *et al.*, 2008; Fierer *et al.*, 2011; Wang *et al.*, 2011, 2012b; Shen *et al.*, 2013). For instance, a macroecological experiment on mountainsides showed clear segregation of aquatic bacterial species along elevations or climatic zones, with community compositions at higher elevations in subtropical regions being more similar to those in subarctic regions (Wang *et al.*, 2016) (Fig. 2). Such a phenomenon agrees with climatic zonation of plants and animals, which was first documented by Linnaeus in his PhD dissertation in 1743, showing a compressed and very orderly succession of climate, vegetative zones and animals along elevational gradients (Linnaeus, 1781; Lomolino, 2001). However, given their high dispersal ability and high population densities, microorganisms tend to show weaker elevational segregation in their community composition and more complex elevational diversity patterns than macroorganisms.
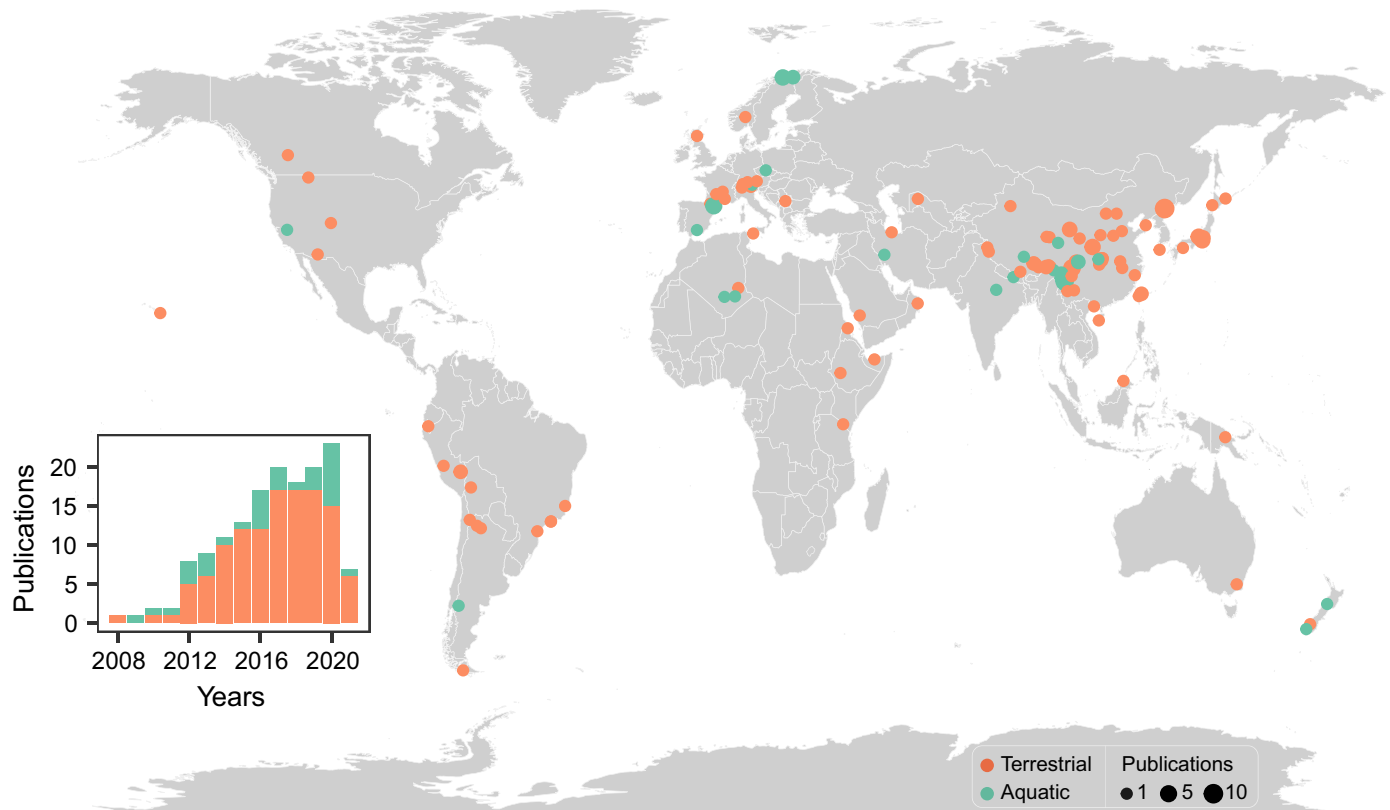
**Fig. 1** The studies on elevational diversity patterns of microorganisms across global mountains. We compiled the data of terrestrial and aquatic ecosystems from the literature by searching the Web of Science with the following keyword combinations: (microorganism* OR microb* OR bacter* OR archae* OR fung* OR diatom*) AND (elevation* OR altitud*) AND (diversity OR biodiversity OR richness). Our review only includes the studies that investigate bacteria, fungi, archaea, diatoms and/or functional groups across more than one elevation. We obtained a total of 238 data sets from 115 mountains reported in 152 studies, some of which investigate more than one taxonomic group (i.e. bacteria, fungi, archaea and diatoms). The geographic locations of each mountain are shown with light brown and dark green dots for terrestrial and aquatic ecosystems, respectively, and the number of studies on each mountain is indicated by the dot size. Inset figure shows the publication trend of papers in the two ecosystems from the first elevational diversity study in 2008 (Bryant *et al.*, 2008) to May 2021. The full publication list for this review is shown in Supporting Information Table S1.

Here, we present a quantitative review of 238 data sets of microorganisms from 115 mountains of six continents reported in 152 studies (Fig. 1; Supporting Information Table S1). The elevational ranges varied substantially, spanning an average of 1479 (±897) m. The minimum and maximum elevational ranges were 152 m in Mountain Kosciuszko and 4350 m in Mountain Himalaya, respectively. These data sets comprised three biodiversity facets, taxonomic, functional and phylogenetic diversity, the former of which was dominant in 89.1% of all data sets and included major microbial taxonomic groups such as bacteria (91), fungi (83), archaea (12) and diatoms (26). The data sets were mainly from terrestrial ecosystems (160), whereas only 32.8% of the data sets originated from aquatic ecosystems, most of which were from China with 45.0% and 47.4% for these two ecosystems, respectively (Fig. 1).

Over half of these data sets (152 out of 238) across ecosystems showed a wide range of elevational patterns in alpha and beta diversity on a global scale (Fig. 3). Taxonomic alpha diversity (e.g. species richness and Shannon–Wiener diversity) showed various patterns with elevation for terrestrial and aquatic microorganisms, including decreasing, increasing, hump-shaped, U-shaped or no

discernible trend at all (Figs 3a, S1). Such a variety of patterns has also been observed for higher plants and animals, the species richness of which was traditionally thought to simply decline linearly with elevation and was revealed later to show mostly hump-shaped patterns (50–63%), while only < 25% followed monotonically decreasing patterns (Rahbek, 2005). In terrestrial ecosystems, however, bacteria and fungi typically decreased with increasing elevation (24.3% and 32.4%, respectively) and, in some instances, followed alternative patterns such as hump-shaped and nonsignificant patterns (Figs 3a, S1). By contrast, studies in aquatic ecosystems, mostly focusing on bacteria and diatoms, have remained rare (36.8%) and lagged behind terrestrial ecosystems (Figs 3a, S1). Based on a few freshwater studies, diatoms mainly showed alternative elevational patterns, including increasing (27.8%) and nonsignificant patterns (44.4%), rather than a decreasing pattern (16.7%). Most aquatic bacteria showed a typically decreasing elevational pattern (34.6%), followed by a nonsignificant pattern (23.1%) (Figs 3a, S1). It should be noted that a novel discontinuous pattern with elevational breakpoints is discovered for microorganisms and attributed to treeline (Li *et al.*, 2016) and even suture zone fault (Li *et al.*, 2018; Hu *et al.*, 2020).
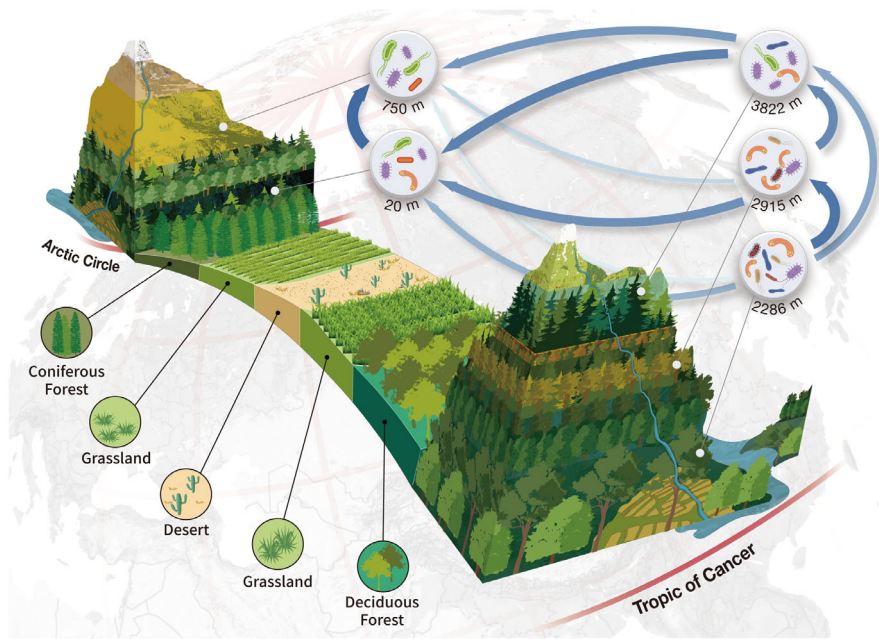
**Fig. 2** The habitat segregation of microbial species along elevations or climatic zones. That is, microorganisms show similar community composition in the same climatic zone (or vegetation zone). For instance, Balggesvarri Mountain in Norway (0–1270 m) and Laojun Mountain in China (2280–3820 m) are located in the subarctic and subtropical regions, respectively, along the latitudinal gradient with clear vegetation zones. The bacteria at higher elevations in the subtropical mountain are more similar in community composition to those at lower elevations in the subarctic mountain, indicated by the simplified network plot modified from fig. S8 in Wang *et al*. (2016). Each mountain is drawn according to the plant species and climate zones along elevational gradients. The circle with microbe cartoons indicates a local species pool of each elevation, and thicker arrows between cycles refer to higher similarity of species between climatic zones and regions. More detailed support of habitat segregation of bacteria is shown in Wang *et al*. (2016).
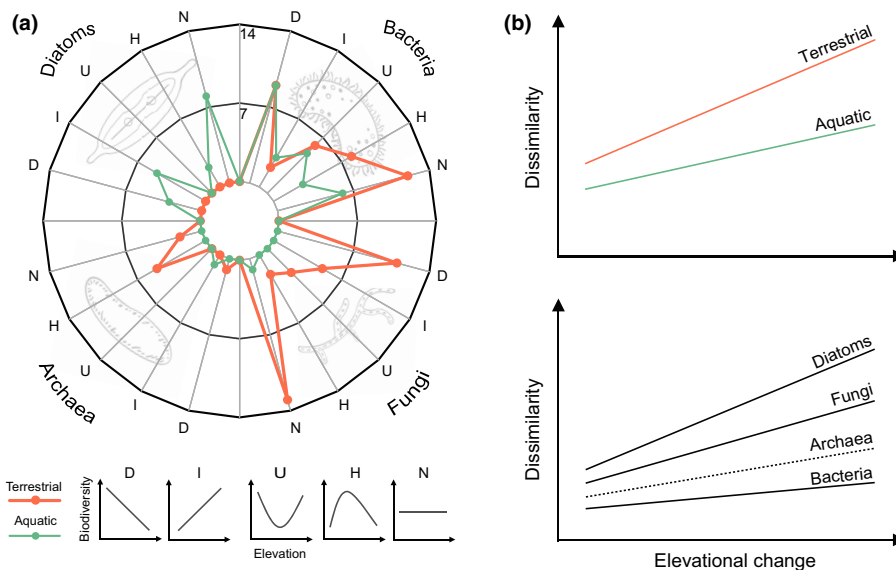


**Fig. 3** Microbial diversity patterns along elevational gradients in terrestrial and aquatic ecosystems. We considered two facets of microbial diversity: alpha diversity (a) and beta diversity (b). Alpha diversity pattern analysis only includes the studies that investigate species richness, Chao1, Shannon–Wiener or Simpson across more than three elevations and that test the significance of alpha diversity patterns along elevational gradients using linear regression or Pearson correlation analyses. The full list of publications considered for alpha diversity patterns is shown in Supporting Information Table S1. (a) Radar plot shows the number of data sets with a decreasing (D), increasing (I), hump-shaped (H), U-shaped (U) or no discernible (N) alpha diversity elevational pattern for bacteria, fungi, archaea and diatoms in terrestrial (light brown) or aquatic (dark green) ecosystems. The percentages of data sets for each pattern are shown in Fig. S1. (b) Beta diversity indicated by elevational distance–decay relationships for the four taxonomic groups in terrestrial and aquatic ecosystems. The distance–decay relationship quantifies the increase in compositional dissimilarity between communities with increasing elevational distance, and the linear slopes indicate the hypothesised trends across taxa and ecosystems based on literature synthesis. The slope is generally the highest for diatoms and the lowest for bacteria, while unclear for archaea indicated by the dotted line.

By contrast, there are consistent elevational patterns in microbial community composition, supported by beta diversity analyses including ecological uniqueness and distance–decay relationships. Ecological uniqueness of community composition quantified with local contributions to beta diversity shows a U-shaped elevational pattern for biofilm bacteria in mountain streams and lakes, which is consistent with benthic diatoms or macroinvertebrates along the same elevational gradients (Teittinen *et al.*, 2017; Wang *et al.*, 2020), and suggests higher uniqueness of community composition at both elevational ends. The elevational distance–decay relationship, which quantifies the increase in compositional dissimilarity between communities with increasing elevational distance (Soininen *et al.*, 2007), has been repeatedly observed for microorganisms in the collected 48 data sets from 20 studies. However, there were substantial variations among various taxonomic groups in a range of habitats regarding the species turnover rates and strength of distance–decay relationships, indicated by the slope (Fig. 3b) and Mantel correlation (Fig. S2), respectively. For example, eukaryotic organisms like diatoms and fungi show higher elevational turnover than bacteria (Fig. 3b), perhaps indicative of high dispersal ability and good adaptability of bacteria to harsh environmental conditions (Wang *et al.*, 2012b; Vacher *et al.*, 2016). In contrast to soil environments, the elevational distance–decay pattern may be weaker in streams (Fig. 3b) due to the greater connectivity and higher dispersal between sites (Wang *et al.*, 2013a). In addition, the strength of the elevational distance–decay pattern also showed significant variations among terrestrial and aquatic habitats after accounting for taxonomic group via a linear mixed-effects meta-regression model ($F$ (df = 5) = 6.60, $P < 0.001$; Fig. S2a,b; Table S2). Although scale effects usually determine the elevational patterns of species richness (Rahbek, 2005), such effects were not found for elevational distance–decay relationships of microorganisms as indicated by the nonsignificant correlations between elevational ranges and the strength of the relationships (Fig. S2c).

Notably, only a few studies about functional aspects of microorganisms emerged in our review (25 out of 238 data sets), including the functional groups involved in biogeochemical cycling (11) and the composition of functional genes (14) (Table S1). Microbial functional groups relevant to carbon and nitrogen cycles like nitrifiers, denitrifiers, methanogens and methanotrophs exhibit significant elevational patterns (Picazo *et al.*, 2020; Kou *et al.*, 2021). For instance, the Shannon–Wiener diversity and evenness of ammonia-oxidising archaea monotonically increase with elevation, while richness is relatively stable in meadow soils on the Tibetan Plateau (Zhao *et al.*, 2017). Furthermore, microbial functional genes also show significant elevational patterns in alpha diversity and elevational distance–decay relationships in soils (Shen *et al.*, 2016; Qi *et al.*, 2017) and streams (Picazo *et al.*, 2020). In the mountainous streams of Eurasia, for example, the Shannon–Wiener diversity of microbial functional genes involved in carbon, nitrogen, phosphorus and sulphur cycling shows consistently declining elevational patterns (Picazo *et al.*, 2020).

Collectively, consistent with the climatic zonation of higher plants and animals, microbes showed clear segregation in community compositions for both terrestrial and aquatic ecosystems on mountainsides. They also showed largely consistent elevational distance–decay relationships, but terrestrial microbes had higher species turnover rates across elevations than aquatic microbes. However, elevational patterns in alpha diversity varied between the two ecosystems, showing decreasing pattern dominantly in terrestrial ecosystems while decreasing and nonsignificant patterns in aquatic ecosystems. These microbial elevational studies from taxonomic to functional compositions have been continuously increasing over the past decade (Fig. 1 inset), but there are gaps left to be fulfilled by future studies regarding ecosystems, geographical regions and taxonomic groups (e.g. virus). For instance, mountains in tropical and Arctic regions are still poorly studied, especially for aquatic ecosystems, where biodiversity and ecosystem functions are perhaps most vulnerable to global change.

## Mechanisms driving elevational patterns in microbial diversity

The balance between deterministic and stochastic processes represents plausible explanations for the generation and maintenance of spatiotemporal patterns of biodiversity also along elevational gradients (Wang *et al.*, 2013a). Deterministic processes are driven by local and regional environmental filtering and biotic interactions, while stochastic processes include dispersal limitation, diversification, mass effects and random drift (Stegen *et al.*, 2013; Wang *et al.*, 2013a; Zhou *et al.*, 2013, 2014). These processes have been disentangled by approaches shifting from traditional multivariate statistical methods and correlation-type analyses to neutral theory-based models and null model analysis, the latter of which is becoming more popular and is still under intensive development (Zhou & Ning, 2017). Current evidences on mountainsides overwhelmingly support the dominant role of deterministic processes underlying a broad range of taxa, including bacteria, archaea, fungi, diatoms and also microbial functional groups, in both terrestrial and aquatic ecosystems (Fig. 4). Furthermore, we developed a novel approach to quantify the relative importance of environmental drivers by calculating their weighted frequency across the 179 data sets in our review. Specifically, we scored the three most important drivers for each data set from high to low, summed the scores for each driver and then normalised the sum scores as weighted frequency (Fig. 4a). We revealed the environmental drivers to be dominant for the elevational variations in microbial diversity and composition (Fig. 4a; Table S3): pH (37.6% of weighted frequency across the data sets), temperature (35.5%) and plants (33.6%) for terrestrial ecosystems, and temperature (46.3%), pH (33.8%) and phosphorus (34.5%) for aquatic ecosystems.

In terrestrial ecosystems, pH has been widely recognised as a dominant driver influencing mountain biodiversity and community composition, especially for bacteria (Singh *et al.*, 2012; Shen *et al.*, 2013; Wang *et al.*, 2015; Zhang *et al.*, 2015). The effects of pH on microorganisms could stem from its direct influence on enzyme activity and indirect influence through constraining the availability of nutrients. Compared with bacteria, fungi are usually less influenced by soil pH due to the wider pH ranges for their optimal growth (Rousk *et al.*, 2010). Furthermore, climate exerts less influence on soil microorganisms compared with pH (Fig. 4a).

**(a)**



**(b)**
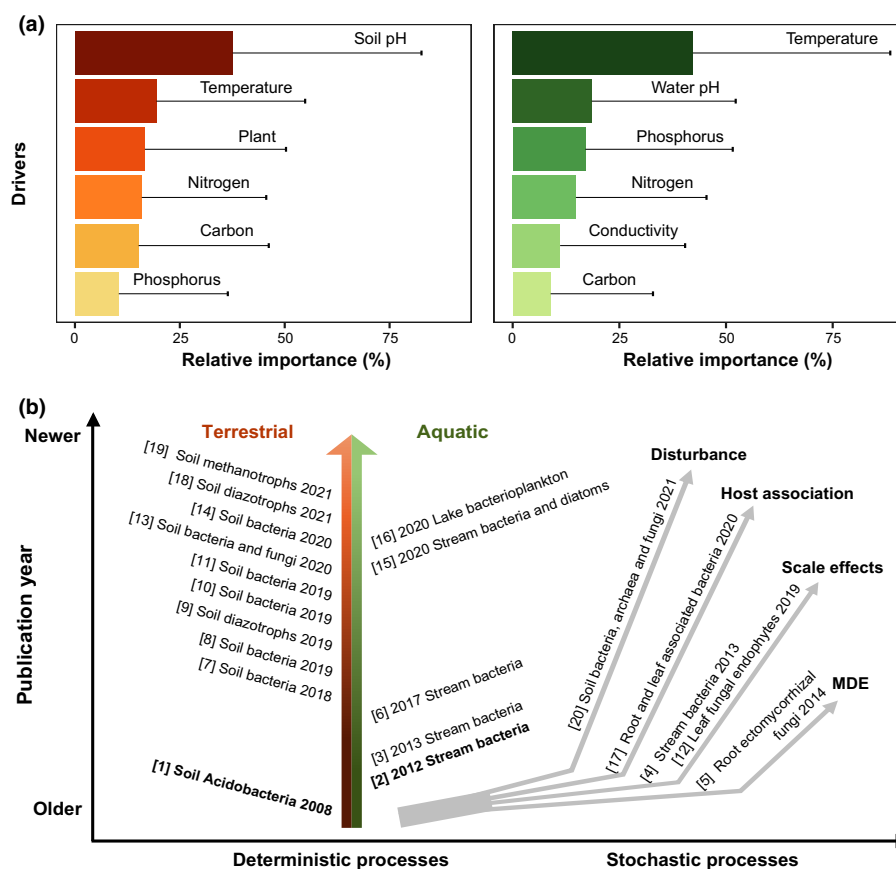


**Fig. 4** Synthesis of ecological mechanisms underlying elevational diversity patterns of microorganisms. (a) The relative importance of main abiotic and biotic drivers for shaping microbial elevational patterns in the terrestrial or aquatic ecosystems. We developed an approach to quantify their relative importance measured by weighted frequency across the data sets in the literature with percentages by following three steps: scoring the three most important drivers for each data set from high to low as the values of 3, 2 and 1, summing the scores for each driver across data sets, and then normalising the sum scores by dividing three times of the total data set number and multiplying by 100. The higher the percentage value, the higher the weighted frequency of a driver across the entire data sets. For better visualisation, we show here the top six drivers based on their weighted frequency. Error bars indicate the standard deviation of weighted frequency for each driver. Details of the general terms of drivers such as temperature and plant for categorising different measured variables are shown in Supporting Information Table S3. (b) Illustration of the progresses on relative importance of deterministic and stochastic processes and the influences of factors on ecological processes. We only show the references explicitly considering the two processes. Arrows running near the left suggest that deterministic processes dominate, while arrows running to the right suggest that stochastic processes may increase with the factors such as disturbances, host association, small elevational scales and strong mid-domain effect (MDE). The details of the references indicated by the numbers in square brackets are shown in Table S4.

Nevertheless, microtopographic temperature, especially the 5-year developments of near-ground soil and air temperature, rather than other environmental factors such as pH, mainly drives soil bacterial communities responding to elevation on Arctic–alpine mountains (Frindte *et al.*, 2019). Evidence from ectomycorrhizal fungi, an ecologically important group of soil and plant root-associated symbionts, also shows strong responses to climate on Mount Fuji, Japan (Miyamoto *et al.*, 2015). In addition, precipitation is more important in arid environments in driving soil bacterial communities than temperature (Yuan *et al.*, 2014). Finally, plants are also important for structuring microbial communities by determining the quantity and quality of litter substrate supply and modifying the soil physical environment (Zhang *et al.*, 2015). For instance, bacterial, fungal and plant diversity show congruent patterns on mountainsides (Nottingham *et al.*, 2018), and there are also plant phylogenetic imprints for the taxonomic compositions of bacteria (Shen *et al.*, 2013) and fungi (Yang *et al.*, 2019), and the functional gene composition (Shen *et al.*, 2016).

However, in mountain aquatic ecosystems, the climate is usually prominent for shaping microbial diversity, taxonomic and functional compositions (Wang *et al.*, 2016, 2020; Picazo *et al.*, 2020). For example, the mean temperature of the warmest quarter or the mean precipitation of the coldest quarter best predicts microbial functional alpha diversity and community structure at both mountain and continental scales in the mountain streams of Eurasia (Picazo *et al.*, 2020). A macroecological experiment on mountainsides illustrates that temperature jointly with nutrient enrichment shows direct effects on bacterial diversity and indirect effects via primary productivity in subtropical and subarctic regions (Wang *et al.*, 2016). Among local environmental variables, phosphorus, an essential nutrient for primary producers, is the main local environmental variable shaping the alpha diversity of diatoms and further bacteria (Wang *et al.*, 2017). Water pH is associated with the primary productivity of algae in affecting bacterial community composition (Wang *et al.*, 2016) and is a key determinant of aquatic autotrophs such as diatoms and

cyanobacteria, followed by catchment conditions (Teittinen *et al.*, 2017; Yeh *et al.*, 2019).

Notably, the importance of deterministic processes varies with elevational scales, disturbance events and habitat types, indicating that stochastic processes are important in shaping mountain microbial communities under certain conditions (Fig. 4b; Table S4). For instance, a small elevational scale may increase the likelihood of dispersal effects through higher connectivity among sites (i.e. mass effects), leading to stronger stochastic processes that contribute to microbial elevational patterns (Wang *et al.*, 2013b). This scale effect has also been noted by Cobian *et al.* (2019) who show that local abiotic conditions do not shape foliar fungal endophyte communities, possibly due to sampling of too small elevational gradients on the Island of Hawai'i. Disturbance events like forest harvesting and habitat fragmentation could also shift the relative importance of deterministic and stochastic processes, the former of which dominate microbial community assembly in the early succession of forest recovery and decrease in the late succession (Liu *et al.*, 2021). At high elevations with varying harsh environmental conditions, deterministic processes may often dominate, as indicated by stronger phylogenetic clustering towards high elevations for bacteria in streams (Wang *et al.*, 2012a) and lakes (Li *et al.*, 2017). Across multiple habitats, deterministic processes underlying bacterial assemblages are prominent for soils but weak for host-associated communities like root and leaf endophytes (Cai *et al.*, 2020).

## Key questions and perspectives

Over two and half centuries from the Linnaeus' and van Humboldt's footprints of mountain biodiversity, mountain biogeography has evolved from descriptive science to theory development. Review papers on mountain biodiversity have summarised mostly for macroorganisms the major achievements and novel insights of the elevational diversity patterns (Rahbek, 1995, 2005), the geological and evolutionary effects for Humboldt's enigma (Rahbek *et al.*, 2019a,b) and the climate change impacts using field experiments (Tito *et al.*, 2020). Recently, reviews on mountain microorganisms and their responses to climate change have appeared for soils (Donhauser & Frey, 2018; Looby & Martin, 2020), while aquatic environments remain understudied (Battin *et al.*, 2007; Wang *et al.*, 2017). In the light of classical ecological hypotheses for biodiversity gradients, we are now facing emergent objectives for mountain microorganisms in how to advance our understanding of the patterns in biodiversity and ecosystem functioning and their responses under global change from multidisciplinary and multitrophic perspectives across multiple ecosystems. We identified the key questions and cutting-edge perspectives of theories, approaches and predictions for future studies in the following seven topics (Fig. 5; Table S5).

### Biodiversity hypotheses

The search for the underlying processes of mountain biodiversity has identified a list of potential but not mutually exclusive theories or hypotheses also applicable for microorganisms. These hypotheses can be grouped into four primary categories: climatic hypotheses based on current abiotic conditions, spatial hypotheses of area and spatial constraints, biotic hypotheses involving biotic interactions and feedback among communities, and historical hypotheses invoking processes occurring across evolutionary time scales (Lomolino, 2001; Grytnes & McCain, 2007). Climatic hypotheses are mostly documented for mountain microorganisms, followed by spatial hypotheses, but the other two hypotheses are rarely tested, especially considering the evolutionary importance of microbial adaptation across environmental gradients and mountain habitats (Ren & Wang, 2022).

Among the possible environmental drivers of climatic hypotheses, temperature and the associated factors, such as precipitation, primary productivity and human disturbances, vary predictably with elevation, while other factors including pH, moisture, cloud cover, riparian shading, slope and lithology are not elevation-specific (McCain, 2007; Wang *et al.*, 2011; Bertuzzo *et al.*, 2016; Thornton *et al.*, 2021). Although our collected empirical observations often result in complicated elevational patterns of microbial alpha diversity without general rules, we propose that the environmental drivers identified across terrestrial and aquatic ecosystems could be grouped into two divergent processes: physiological tolerance hypotheses and energetic hypotheses. In terrestrial ecosystems, local environmental factors like pH are frequently reported in structuring soil microorganisms, while energetic constraints imposed by climate and resource availability mainly drive the alpha and beta diversity of aquatic microorganisms at local and continental scales (Fig. 3). In Eurasian streams, for instance, climate primarily explains the diversity and community compositions of microbial functional genes (Picazo *et al.*, 2020). Such temperature dependency of diversity gradients is also supported by the decreasing elevational patterns in sediment bacterial species richness in microcosm experiments (Fig. 5) and could be explained by the metabolic theory of ecology that is primarily caused by the kinetics of biological processes, including rates of dispersal, species interactions, reproduction, speciation and evolution, and further ecosystem processes such as organic matter production and decomposition (Wang *et al.*, 2016; Zhou *et al.*, 2016). The discrepancy between terrestrial and aquatic ecosystems may stem from their contrasting environmental constraints, for instance, the varying water availability for terrestrial biota that is confounded by the high variations of precipitation and local moisture (McCain, 2007). Nevertheless, our review suggests that environmental filtering along steep environmental gradients on mountains dominantly drives microbial assemblages across climatic zones (Fig. 4).

Another alternative explanation is a spatial hypothesis that focuses on spatial constraints for species distributions, such as geographical range. The trends in geographic ranges are fundamental to our understanding of evolution, range expansion and contraction, and are also the potential mechanisms underlying at least two elevational diversity patterns: decreasing and hump-shaped (Grytnes & McCain, 2007). For instance, the decreasing richness pattern could be contributed to the more generalist species at high elevations depicted by Rapoport's rule, which postulates that species ranges increase towards higher elevations because
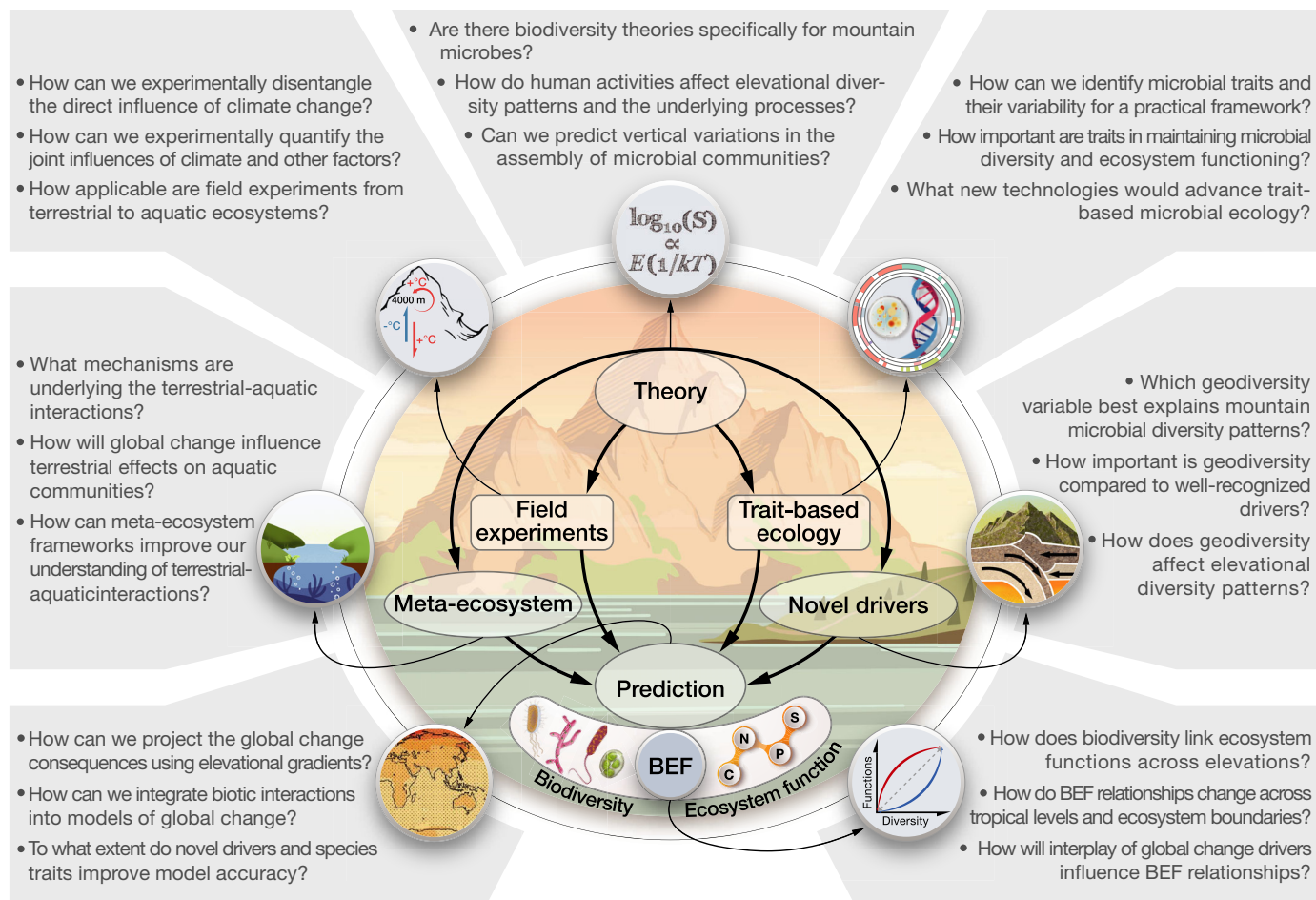
**Fig. 5** Seven primary topics of perspectives and the relevant 21 key questions. These topics (inner ring with a mountain as background) and questions (outer ring) are proposed to advance future research in mountain microbial biogeography and disentangle elevational patterns in microbial communities and ecosystem functions and their responses to global change from theories and approaches to predictions. These perspectives include ecological theories for decrypting Humboldt's enigma, novel drivers underlying biodiversity change, ecological interactions between terrestrial and aquatic ecosystems, and biodiversity–ecosystem functioning relationships (BEF) and the state-of-the-art approaches, including trait-based ecology, manipulative field experiments and modelling approaches to predict global change responses. The formula $\log_{10}(S) \propto E(1/kT)$ above the 'Theory' circle indicates metabolic theory of ecology (MTE), which could assess the temperature dependency of microbial diversity (Wang *et al.*, 2016). Specifically, log-transformed species richness is a linear function of the inverse absolute temperature; where $S$ is species richness, $k$ is Boltzmann's constant, $T$ is absolute temperature and $E$ is activation energy (Brown *et al.*, 2004). More details of key questions are shown in Supporting Information Table S5.

species inhabiting higher elevations are exposed to a wider range of climatic conditions and thus evolve wider physiological tolerances and are less affected by climatic variability (Stevens, 1992; McCain & Bracy Knight, 2013). To date, the Rapoport's rule is not always successful such as for the stream bacteria and diatoms on six mountains in Eurasia (Wang & Soininen, 2017), but is supported by only one study across New Zealand showing an increased elevational range size towards higher elevations for stream bacteria (Lear *et al.*, 2017). By contrast, the hump-shaped pattern could be explained by a neutral model, namely mid-domain effect, where species elevational ranges are randomly distributed within a geometrically constrained domain (Colwell & Lees, 2000). Specifically, the mid-domain effect can lead to the hump-shaped pattern because, by chance, more taxa could have elevational ranges that overlap at mid-elevations, rather than overlap at extremely high or low elevations, due to the geometrically bounded ends of the elevation gradient. However, we identified only one study

supporting this pattern in ectomycorrhizal fungi on Mount Fuji, which shows the maximum overlap in species ranges in middle elevations (Miyamoto *et al.*, 2014). Considering that this is a special case for plant-associated fungi and that hump-shaped patterns are often reported for plant diversity, we expect that the mid-domain effect would be less evident for free-living microorganisms in soils and aquatic environments. The spatial hypotheses have special implications for aquatic environments such as mountain streams and rivers, where the dendritic network organisation and the associated physical unidirectional flows (e.g. water, matter and biased dispersal) exert strong controls on metacommunity dynamics and the consequent distribution of microbial biodiversity (Altermatt, 2013; Tonkin *et al.*, 2018). Network structure could sufficiently explain large-scale biodiversity or override other typically strong drivers of biodiversity such as climate for freshwater microorganisms (Tonkin *et al.*, 2018), but it is needed to be explicitly incorporated for future microbial studies.

It is intriguing to see that the discipline of mountain biodiversity for microorganisms is evolving rapidly, as some hypotheses once viewed as hot debates are receding. Our synthesis shows that questions once considered important have still not been clearly resolved. The focus is, however, shifting in the light of our improved understanding of mountain microorganisms and the current practical needs of mountain ecosystem conservation facing global change. If this perspective on biodiversity hypotheses was discussed 5 or more years earlier, key questions would be 'Do the same elevational patterns in species richness apply to micro- and macroorganisms, and are they caused by similar ecological processes?' Today, the consensus is that microorganisms do not necessarily follow the same richness patterns as higher plants and animals, but they do have similar elevational succession in community composition across climatic zones (Fig. 2). The debate of the relative importance of deterministic and stochastic processes in structuring microbial assemblages on mountainsides has also been resolved as deterministic processes have now been found to dominate (Fig. 4). At the moment, the topical question could be 'how the diversity gradients and the associated ecological processes vary under global changes' (Fig. 5).

## Novel drivers underlying biodiversity variations

As an important but largely unanticipated consequence, geodiversity is increasingly recognised as key drivers of current biodiversity and further ecosystem functions (Knudson *et al.*, 2018; Schrodt *et al.*, 2019). The term 'geodiversity', introduced by Gray (2004), summarises geological and geographical processes such as geological (rocks, minerals and fossils), geomorphological (landforms, topography and physical processes), soil and hydrological features. This is especially true for mountain regions, largely because mountains are created and affected by different geological processes such as tectonic, volcanic and erosional processes over both geologically long and short scales and thus form varying topographies in space and time (Antonelli *et al.*, 2018; Rahbek *et al.*, 2019a).

Geodiversity has direct impacts on mountain biodiversity by modifying the rates and properties of speciation, dispersal, persistence and extinction (Hoorn *et al.*, 2013; Rahbek *et al.*, 2019a). Along with mountain building, speciation bursts occur due to evolutionary adaptation to the new environment. The biodiversity of higher plants and animals is often greater at lower elevations as a result of high speciation and low extinction (Rahbek *et al.*, 2019a). Compared with macroorganisms, there is a higher likelihood for microbial species to disperse across elevations with contrasting geology context due to small size and high dispersal capacity, and to be more constrained by local contemporary environmental filtering. Geodiversity can also indirectly shape soil bacterial diversity by imparting lasting legacies on contemporary environments (Hu *et al.*, 2020). Although there is a theoretical foundation for the links between geological processes and biological communities, only a handful of empirical studies and analytical frameworks have incorporated geological processes into the understanding of mountain biodiversity patterns. For example, mountain-building processes, such as erosion rates and heterogeneity of soil types, show prominent links to species richness of terrestrial tetrapods at regional and global scales (Antonelli *et al.*, 2018). Such links are also profound for soil bacterial communities and ecosystem functions, generally showing consistent abrupt changes at the elevation range of 2000–2800 m that coincide with the Indus-Yalu suture zone fault on the Tibetan Plateau; parent rock and weathering exert considerable direct effects on bacterial diversity but indirectly influence ecosystem functions via interactions with diversity and contemporary environments (Hu *et al.*, 2020).

To better understand geodiversity–biodiversity relationships, more empirical investigations, especially in aquatic ecosystems based on quantitative methods, are urgently required to unravel which geodiversity variables are most relevant and how the interplay of geodiversity and other environments influences microbial communities. Future studies are encouraged to consider geodiversity as a parallel framework to biodiversity to better gain the generality of geodiversity–biodiversity relationships across different ecosystems and regions. Such a framework may be facilitated by quantifying the relative importance of different aspects of geodiversity and by adopting indices and approaches already employed in ecology.

## Ecological interactions between terrestrial and aquatic ecosystems

Aquatic and terrestrial ecosystems are often studied separately, while their tight natural links are largely ignored via the fluxes of matter and organisms (Soininen *et al.*, 2015). These two fluxes are associated with the two primary contrasting ecological processes underlying aquatic microbial assemblages, that is deterministic processes and stochastic processes, the latter of which is posed mainly by dispersal effects. For example, catchment variables like terrestrial productivity (Teittinen *et al.*, 2017), riparian shading (Wang *et al.*, 2017) and soil-type richness (Kärnä *et al.*, 2019) show significant influences on bacteria and diatoms through controls on the inputs of materials, energy and light in aquatic environments. Such catchment effects are strong largely because regional terrestrial variables reflect long-term environmental conditions and are more robust than snapshot measures of local aquatic variables (i.e. water chemistry) for explaining downstream aquatic diversity patterns (Soininen *et al.*, 2015). By contrast, the strong dispersal effects linking a set of local communities, namely mass effects, could explain downstream microbial community composition, which are determined by large cell influx rates and short residence times that limit environmental influence (Ruiz-González *et al.*, 2015).

Notably, global change is altering mountain hydrological and landscape patterns from high to low elevations, such as glacier retreat and upward vegetation shifts, thereby influencing microbial elevational diversity patterns in both terrestrial and aquatic ecosystems. For example, climate change-induced glacier retreat can increase microbial species richness in glacier-fed streams via dispersal effects, especially at lower elevations, due to more diverse sources of catchment microorganisms upstream (Wilhelm *et al.*, 2013). Furthermore, an upward treeline shift could also foster the strong links

between terrestrial and aquatic systems via the inputs of terrestrial organic matter and nutrients to influence lake metabolism and the dominance of heterotrophic processes (Rofner *et al.*, 2017). We therefore expect a higher frequency and magnitude of terrestrial impacts on aquatic ecosystems towards low elevations, such as in the light of the river continuum concept and subsequent conceptual theories for mountain stream networks and surrounding terrestrial ecosystems (Altermatt, 2013; Tonkin *et al.*, 2018).

Researchers are encouraged to explore the generality of microbial elevational patterns in changing environments towards using more integrated ecosystem approaches in terrestrial and aquatic environments. We advocate the meta-ecosystem framework for achieving this aim, which is defined as a set of ecosystems connected by spatial flows of energy, material and organisms across ecosystem boundaries and has the potential to integrate the perspectives of community and landscape ecology (Loreau *et al.*, 2003). This framework could be expanded to explicitly consider cross-system fluxes of matter and organisms and the inclusion of cross-system analyses such as remote-sensing applications at broader spatial extents (Soininen *et al.*, 2015).

## Trait-based ecology

Functional traits are the key properties related to physiology, morphology or genomic information of an individual organism, reinforcing a mechanistic understanding of linking microbial diversity to ecosystem processes and further their responses to changing environments (Krause *et al.*, 2014; Zhou *et al.*, 2015; Escalas *et al.*, 2019; Yang, 2021). It is reasonable to consider the species-level perspective for complex microbial communities largely because each species has a unique physiology and consequently functional roles. Microbial traits can be inferred directly from genomes or metagenome assembly, which are referred to as 'genomic traits' (e.g. genome size, rRNA operon copy number and the presence of functional genes) (Hu *et al.*, 2021b; Ren & Wang, 2021). Some ecologically important traits are referred to as 'phenotypic traits' like temperature preferences, maximum growth rate and substrate use. Phenotypic traits are traditionally measured only from pure cultures and can now be quantified for natural communities with novel culture-independent techniques like quantitative stable isotope probing (qSIP) (Hungate *et al.*, 2015).

The use of traits to infer performance (i.e. phenotypic traits), processes and their responses to environmental changes are often evaluated in pure cultures in the laboratory (Treseder *et al.*, 2011; Roller *et al.*, 2016). Nevertheless, a few validations have also been recently reported for complex microbial assemblages on mountainsides. For example, similarity in species-specific traits such as growth rates or carbon assimilation rates diminishes as the elevational environmental conditions become more dissimilar (Morrissey *et al.*, 2019). Furthermore, genomic traits could potentially predict ecological performance and its environmental response in natural habitats, which shifts under different environmental scenarios. For instance, genomic traits such as 16S rRNA gene copy number and genome size can predict growth rates under nutrient-amended conditions in soil habitats, while the prediction is poor under native soil conditions (Li *et al.*, 2019). Bacterial

genomic traits such as Kyoto Encyclopedia of Genes and Genomes orthologues have been recently shown to explain species performance responses to environmental changes in mountain soils quantified by a novel approach 'effect-size qSIP' (Hu *et al.*, 2021b).

Strong natural environmental gradients on mountains provide a good opportunity to examine the relative contributions of inter- and intraspecific trait variations driven by climate and local environments. We advocate integrating elevational gradients with the emerging trait-based approaches to advance future mountain microbial ecology by explicitly developing new approaches to infer trait values, applying a quantitative strategy concept to select informative traits and subsequently estimating functional diversity indices to assess community assembly and predict functional reorganisation of microbes under global change. However, simplifying the complexity of microbial traits is required but challenging (Westoby *et al.*, 2021). The complexity of hyper-dimensional traits can be qualitatively simplified by microbial life history strategies such as oligotrophy–copiotrophy (Fierer *et al.*, 2007), competitor–stress tolerator–ruderal (C-S-R) (Krause *et al.*, 2014) and growth yield–resource acquisition–stress tolerance (Y-A-S) strategies (Malik *et al.*, 2020). Different strategies should be favoured from low to high elevations due to spatial variability in resource status and environmental stress. For example, at the lower elevations with high availability of polymeric resources (e.g. recalcitrant carbon) but fewer simple resources (e.g. simple sugars) (Dai *et al.*, 2021), A-strategists should outcompete other strategists by investing in extracellular enzyme machinery, and thus catalyse polymer decomposition, likely leading to declined microbial litter decomposition and soil carbon loss with increasing elevations. The complexity of microbial traits could also be quantitatively simplified by a newly developed framework into synthetic axes to define a low-dimensional trait space and to cluster species based on their traits while identifying those species with unique combinations of traits (Mouillot *et al.*, 2021).

## Manipulative field experiments

Inferring climate change impacts on microbial diversity and ecosystem functions determined by elevation gradient methods is difficult because we still lack a general understanding of the confounding influence of indirect factors that covary with elevation and temperature, such as rainfall, lithology, nutrients and plants (Körner, 2007). By contrast, manipulative experiments on mountainsides are a promising new technique for disentangling the direct influence of temperature and/or the interacting influence of temperature and other environments because they provide explicit control (Elmendorf *et al.*, 2015). In terrestrial ecosystems, translocation experiments and field warming experiments are two approaches widely used to assess direct climate change impacts (Yang *et al.*, 2014; Donhauser & Frey, 2018). The translocation experiments could reveal the direct influence of warming, which causes elevated litter decomposition rates (Salinas *et al.*, 2011) and soil carbon loss (Nottingham *et al.*, 2019), being mediated by microbial physiology, such as microbial carbon use efficiency and extracellular enzyme activity, and shifts in community composition. Furthermore, the interacting influence of temperature and

other environments can be disentangled. For example, a trans-location experiment in which microbial decomposers are deliberately inoculated onto common leaf litter disentangles the effects of microbial community vs temperature on the litter decomposition rates and re-evaluates the role of microbial community composition in its decomposition responses to climate (Glassman *et al.*, 2018).

Compared with terrestrial ecosystems, manipulative field experiments are fewer in mountain aquatic ecosystems, largely because water transplantation and the continuous heating of flowing water are challenging. Wang *et al.* (2016) recently established field aquatic microcosms by including different nutrient levels at each elevation and allowing microbes from each elevation to colonise into common sediments, which allows the investigation of interactions between temperature change and eutrophication and their independent impacts on bacterial communities.

To predict future climate change impacts, we need to strengthen the understanding of the potential influences of synergies between components of climate change (e.g. warming, atmospheric and hydrological changes) and with other abiotic (e.g. eutrophication) and biotic interactions (e.g. multitrophic levels). We further suggest applying the field warming experiments from terrestrial to aquatic ecosystems such as to continuously heat the flowing water by employing a long-term mesocosm system (Liboriussen *et al.*, 2005) and even at the stream level (Ferreira & Canhoto, 2015). Finally, we advocate combining manipulative field experiments with survey data, models and novel tools for a better mechanistic understanding of climate change impacts. For example, the qSIP approach can be integrated into translocation experiments to examine species-level growth responses to warming (Purcell *et al.*, 2022). The extended 'effect-size qSIP' approach has a potential to directly quantify species-level responses to climate change and further understand these responses from the perspectives of their genomic traits (Hu *et al.*, 2021b).

## Biodiversity and ecosystem functioning relationships

Biodiversity–ecosystem functioning research concerns how processes in ecosystems are influenced by species richness and other facets of biodiversity, and growing studies have revealed compelling positive relationships between microbial communities and ecosystem functioning (Bardgett & Van Der Putten, 2014). Such relationships can also be observed on mountainsides. For example, species richness enhances a set of ecosystem functions related to the biomass stocks of microbes, plants or animals, and the processes rates such as pollination, brood parasitism or litter decomposition across 13 ecosystem types along a broad elevational gradient (850–4550 m) on Mount Kilimanjaro in Eastern Africa (Albrecht *et al.*, 2021). Considering species-level effects on ecosystem functioning, the functional composition represented by the diversity of microbial traits (i.e. community-level aggregated gene orthologues) improves the explanatory power of nutrient-induced responses of growth rates along the C. Hart Merriam elevation gradient in North America (Hu *et al.*, 2021b). However, the strength of diversity effects on ecosystem functioning is strongly context-dependent, such as environmental heterogeneity (Peters *et al.*,

2019; Albrecht *et al.*, 2021; Hu *et al.*, 2021a), due to strong environmental gradients such as climate and ecosystem types on mountainsides. For instance, Albrecht *et al.* (2021) show that environmental heterogeneity across ecosystem types shapes the effects of diversity on ecosystem functioning and contributes to the diversity effects by the increases from explaining 49% to 72% of the variation in ecosystem functions.

Given that mountain regions are experiencing rapid environmental changes caused by climate change combined with human activities, it is critical to understand how the interplay of multiple global change drivers constrains the strength of biodiversity–ecosystem functioning relationships to determine the consequences of global change for mountain ecosystems. Hu *et al.* (2021a) performed manipulative field experiments on mountainsides and showed that the interplay of temperature change and eutrophication influenced the relationship between microbial composition and molecular-level metabolite composition (i.e. dissolved organic matter composition) via the indirect effects of energy supply and both the diversity and traits of microbes and organic matter. Elevational gradients are encouraged to integrate with meta-ecosystem and landscape level to add new dimensions and realism for the assessment of the functional role of biodiversity by explicitly considering cross-ecosystem linkages and the multitrophic levels of biotic interactions. Biodiversity change in one ecosystem can propagate across ecosystem boundaries to affect the functioning of other ecosystems, mediated by multiple connecting vectors such as water, wind, gravitation and organisms (Scherer-Lorenzen *et al.*, 2022). Multitrophic diversity can better predict ecosystem functioning than a single trophic level because the functional effects of taxa from different multitrophic levels may complement or oppose each other (Soliveres *et al.*, 2016). Among these multitrophic levels, indirect biodiversity changes caused by one trophic level or across different ecosystem boundaries can also influence overall ecosystem functioning (Eisenhauer *et al.*, 2019). Consequently, we suggest future biodiversity–ecosystem functioning studies need to be broadened across ecosystem boundaries to evaluate the general significance, such as focusing on aboveground–belowground and terrestrial–aquatic linkages.

## Modelling and prediction of global change responses

Model-based approaches have been widely applied in mountain microbial biogeography, which provides quantitative insights into the relative contributions of different assembly processes and predictions of the spatiotemporal dynamics of microbial communities and associated ecosystem functions under global change. Traditionally, there are disparate statistical tools for connecting environmental variables with microbial alpha and beta diversities, the former of which includes regression-based techniques and machine learning algorithms, and the latter includes the raw data approaches like canonical analysis and the distance-based approaches such as generalised dissimilarity modelling (GDM) (Legendre *et al.*, 2005). GDM is designed specifically to accommodate the nonlinearity and special types of environmental and biological data such as phylogenetic relationships between species (Ferrier *et al.*, 2007). Given that elevational gradients offer greater

changes in abiotic conditions and biotic communities than lateral distributions, elevation-derived models can be extended to predict spatiotemporal dynamics of microbial communities at regional or continental scales. This space-for-time substitution strategy is widely used to infer past or future trajectories of ecological systems, with *c.* 72% accuracy as time-for-time predictions (Blois *et al.*, 2013). A recent novel application uses linear regression and GDM models derived from elevational gradients in Norway, Spain and China to project functional gene assemblages of stream biofilm microbes across the Eurasian river network under future climate change scenarios, and shows the highest sensitivity of alpha diversity and assemblage composition primarily occurring in northern and central Eurasian regions in 2061–2080, respectively (Picazo *et al.*, 2020).

Recent species-level modelling approaches like species distribution modelling (SDM) have been widely used to explore the relationship between geographical occurrences of species and corresponding environmental variables (Norberg *et al.*, 2019). For example, SDMs in a temperate mountain area show that factors related to soil (especially pH), climate and/or topography explain and predict part of the abundance distribution of most bacterial species and that the extent of predicted bacterial community changes between current and future environmental conditions varies as a function of elevation (Mod *et al.*, 2021). Since both abiotic environments and biotic interactions ultimately drive species distributions, joint species distribution models (JSDMs) have emerged as extensions of SDMs to simultaneously explore interspecific interactions and the response of abundance to environmental variables (Warton *et al.*, 2015). JSDMs can also be extended to community levels by explicitly acknowledging the multivariate nature of species assemblages to capture more mechanistic and predictive insights into assembly processes. For example, the co-occurrences among mycorrhizal fungal species, especially positive interactions, play an important role in shaping fungal communities in arctic plant roots along an elevational gradient ranging from 33 to 479 m (Abrego *et al.*, 2020).

In summary, we highlight here the current knowledge gaps for the roadmap of future studies by linking theory, approaches and predictions based on our comprehensive syntheses of the biodiversity patterns, main drivers and underlying mechanisms in the recent decade of microbial biogeography studies on mountainsides (Fig. 5). Across mountain terrestrial and aquatic ecosystems, human activities are increasingly influencing the dwelled biological communities and the ecosystem properties, processes and services. Compared with higher plants and animals, we are just scratching the surface of microbial lives on mountainsides, and thus know far less about their roles of biogeochemical cycling, their effects on and feedback responses to anthropogenic global change. Owing to the increasing demands for models in biodiversity assessments and biogeochemical cycles on mountainsides, a better mechanistic model is required for the improvement of prediction accuracy. The big challenge for projecting microbial responses to future global change scenarios is to incorporate models with more necessary local- and landscape-level predictors and biotic information such as catchment characteristics, geodiversity, interspecific interactions, species traits and phylogenetic relatedness. We therefore strongly encourage future studies to take advantage of elevational gradients as a 'natural experiment' to mechanically understand microbial diversity patterns and the associated ecosystem functioning in mountain regions from theoretical and evolutionary perspectives and further improve our predictions of the species-, community- and ecosystem-level consequences under global change.

## Author contributions

JW conceived the review. FM synthesised the data with contributions from AH and WZ. AH and JW finished the first draft. JW and AH finalised the manuscript with contributions from FM, WZ, YY, JSoininen, JShen and JZ. JW, AH and FM contributed equally to this work.

## ORCID

Ang Hu https://orcid.org/0000-0002-5755-2442
Fanfan Meng https://orcid.org/0000-0001-5718-1621
Janne Soininen https://orcid.org/0000-0002-8583-3137
Jianjun Wang https://orcid.org/0000-0001-7039-7136
Yunfeng Yang https://orcid.org/0000-0001-8274-6196
Jizhong Zhou https://orcid.org/0000-0003-2014-0564

## References

Abrego N, Roslin T, Huotari T, Tack AJ, Lindahl BD, Tikhonov G, Somervuo P, Schmidt NM, Ovaskainen O. 2020. Accounting for environmental variation in co-occurrence modelling reveals the importance of positive interactions in root-associated fungal communities. *Molecular Ecology* 29: 2736–2746.

Albrecht J, Peters MK, Becker JN, Behler C, Classen A, Ensslin A, Ferger SW, Gebert F, Gerschlauer F, Helbig-Bonitz M *et al.* 2021. Species richness is more important for ecosystem functioning than species turnover along an elevational gradient. *Nature Ecology & Evolution* 5: 1582–1593.

Altermatt F. 2013. Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology* 47: 365–377.

Antonelli A, Kissling WD, Flantua SGA, Bermúdez MA, Mulch A, Muellner-Riehl AN, Kreft H, Linder HP, Badgley C, Fjeldså J *et al.* 2018. Geological and climatic influences on mountain biodiversity. *Nature Geoscience* 11: 718–725.

Baas Becking L, Nicolai E. 1934. On the ecology of a Sphagnum bog. *Blumea: Biodiversity, Evolution and Biogeography of Plants* 1: 10–45.

Bardgett RD, Van Der Putten WH. 2014. Belowground biodiversity and ecosystem functioning. *Nature* 515: 505–511.

Battin TJ, Besemer K, Bengtsson MM, Romani AM, Packmann AI. 2016. The ecology and biogeochemistry of stream biofilms. *Nature Reviews Microbiology* 14: 251–263.

Battin TJ, Sloan WT, Kjelleberg S, Daims H, Head IM, Curtis TP, Eberl L. 2007. Microbial landscapes: new paths to biofilm research. *Nature Reviews Microbiology* 5: 76–81.

Becker A, Bugmann H, eds. 2001. *Global change and mountain regions.* Stockholm, Sweden: IGBP.

Bertuzzo E, Carrara F, Mari L, Altermatt F, Rodriguez-Iturbe I, Rinaldo A. 2016. Geomorphic controls on elevational gradients of species richness. *Proceedings of the National Academy of Sciences, USA* 113: 1737–1742.

Blois JL, Williams JW, Fitzpatrick MC, Jackson ST, Ferrier S. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences, USA* 110: 9374–9379.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Bryant JA, Lamanna C, Morlon H, Kerkhoff AJ, Enquist BJ, Green JL. 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences, USA* 105: 11505–11511.

Cai Z, Wang X, Bhadra S, Gao Q. 2020. Distinct factors drive the assembly of quinoa-associated microbiomes along elevation. *Plant and Soil* 448: 55–69.

Cavicchioli R, Ripple WJ, Timmis KN, Azam F, Bakken LR, Baylis M, Behrenfeld MJ, Boetius A, Boyd PW, Classen AT *et al.* 2019. Scientists' warning to humanity: microorganisms and climate change. *Nature Reviews Microbiology* 17: 569–586.

Cobian GM, Egan CP, Amend AS. 2019. Plant–microbe specificity varies as a function of elevation. *The ISME Journal* 13: 2778–2788.

Colwell RK, Lees DC. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* 15: 70–76.

Dai Z, Zang H, Chen J, Fu Y, Wang X, Liu H, Shen C, Wang J, Kuzyakov Y, Becker JN *et al.* 2021. Metagenomic insights into soil microbial communities involved in carbon cycling along an elevation climosequences. *Environmental Microbiology* 23: 4631–4645.

Donhauser J, Frey B. 2018. Alpine soil microbial ecology in a changing world. *FEMS Microbiology Ecology* 94: fiy099.

Eisenhauer N, Schielzeth H, Barnes AD, Barry KE, Bonn A, Brose U, Bruelheide H, Buchmann N, Buscot F, Ebeling A. 2019. A multitrophic perspective on biodiversity–ecosystem functioning research. *Advances in Ecological Research* 61: 1–54.

Elmendorf SC, Henry GHR, Hollister RD, Fosaa AM, Gould WA, Hermanutz L, Hofgaard A, Jónsdóttir IS, Jorgenson JC, Lévesque E *et al.* 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences, USA* 112: 448–452.

Elsen PR, Monahan WB, Merenlender AM. 2020. Topography and human pressure in mountain ranges alter expected species responses to climate change. *Nature Communications* 11: 1–10.

Escalas A, Hale L, Voordeckers JW, Yang Y, Firestone MK, Alvarez-Cohen L, Zhou J. 2019. Microbial functional diversity: from concepts to applications. *Ecology and Evolution* 9: 12000–12016.

Ferreira V, Canhoto C. 2015. Future increase in temperature may stimulate litter decomposition in temperate mountain streams: evidence from a stream manipulation experiment. *Freshwater Biology* 60: 881–892.

Ferrier S, Manion G, Elith J, Richardson K. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions* 13: 252–264.

Fierer N, Bradford MA, Jackson RB. 2007. Toward an ecological classification of soil bacteria. *Ecology* 88: 1354–1364.

Fierer N, McCain CM, Meir P, Zimmermann M, Rapp JM, Silman MR, Knight R. 2011. Microbes do not follow the elevational diversity patterns of plants and animals. *Ecology* 92: 797–804.

Frindte K, Pape R, Werner K, Löffler J, Knief C. 2019. Temperature and soil moisture control microbial community composition in an arctic–alpine ecosystem along elevational and micro-topographic gradients. *The ISME Journal* 13: 2031–2043.

Glassman SI, Weihe C, Li JH, Albright MBN, Looby CI, Martiny AC, Treseder KK, Allison SD, Martiny JBH. 2018. Decomposition responses to climate depend on microbial community composition. *Proceedings of the National Academy of Sciences, USA* 115: 11994–11999.

Gray M. 2004. *Geodiversity: valuing and conserving abiotic nature.* Chichester, UK: John Wiley & Sons.

Grytnes J-A, McCain CM. 2007. Elevational trends in biodiversity. *Encyclopedia of Biodiversity* 2: 1–8.

Hoorn C, Mosbrugger V, Mulch A, Antonelli A. 2013. Biodiversity from mountain building. *Nature Geoscience* 6: 154.

Hu A, Choi M, Tanentzap AJ, Liu J, Jang K-S, Lennon JT, Liu Y, Soininen J, Lu X, Zhang Y. 2021a. Quantifying microbial associations of dissolved organic matter under global change. *bioRxiv.* doi: 10.1101/2021.1108.1112.456177.

Hu A, Ren M, Wang J. 2021b. Microbial species performance responses to environmental changes: genomic traits and nutrient availability. *Ecology* 102: e03382.

Hu A, Wang J, Sun H, Niu B, Si G, Wang J, Yeh C-F, Zhu X, Lu X, Zhou J *et al.* 2020. Mountain biodiversity and ecosystem functions: interplay between geology and contemporary environments. *The ISME Journal* 14: 931–944.

Hungate BA, Mau RL, Schwartz E, Caporaso JG, Dijkstra P, van Gestel N, Koch BJ, Liu CM, McHugh TA, Marks JC *et al.* 2015. Quantitative microbial ecology through stable isotope probing. *Applied and Environmental Microbiology* 81: 7570–7581.

Kapos V, Rhind J, Edwards M, Price M, Ravilious C. 2000. Developing a map of the world's mountain forests. In: Price MF, Butt N, eds. *Forests in sustainable mountain development: a state of knowledge report for 2000. Task force on forests in sustainable mountain development.* Wallingford, UK: CAB International.

Kärnä O-M, Heino J, Laamanen T, Jyrkänkallio-Mikkola J, Pajunen V, Soininen J, Tolonen KT, Tukiainen H, Hjort J. 2019. Does catchment geodiversity foster stream biodiversity? *Landscape Ecology* 34: 2469–2485.

Knudson C, Kay K, Fisher S. 2018. Appraising geodiversity and cultural diversity approaches to building resilience through conservation. *Nature Climate Change* 8: 678–685.

Körner C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution* 22: 569–574.

Kou Y, Liu Y, Li J, Li C, Tu B, Yao M, Li X. 2021. Patterns and drivers of nirK-Type and nirS-Type denitrifier community assembly along an elevation gradient. *mSystems* 6: e00667-00621.

Krause S, Le Roux X, Niklaus PA, Van Bodegom PM, Lennon JT, Bertilsson S, Grossart H-P, Philippot L, Bodelier PL. 2014. Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. *Frontiers in Microbiology* 5: 251.

Lear G, Lau K, Perchec AM, Buckley HL, Case BS, Neale M, Fierer N, Leff JW, Handley KM, Lewis G. 2017. Following Rapoport's Rule: the geographic range and genome size of bacterial taxa decline at warmer latitudes. *Environmental Microbiology* 19: 3152–3162.

Legendre P, Borcard D, Peres-Neto PR. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75: 435–450.

Li G, Xu G, Shen C, Tang Y, Zhang Y, Ma K. 2016. Contrasting elevational diversity patterns for soil bacteria between two ecosystems divided by the treeline. *Science China-Life Sciences* 59: 1177–1186.

Li H, Zeng J, Ren L, Wang J, Xing P, Wu Q. 2017. Contrasting patterns of diversity of abundant and rare bacterioplankton in freshwater lakes along an elevation gradient. *Limnology and Oceanography* 62: 1570–1585.

Li J, Mau RL, Dijkstra P, Koch BJ, Schwartz E, Liu X-J, Morrissey EM, Blazewicz SJ, Pett-Ridge J, Stone BW *et al.* 2019. Predictive genomic traits for bacterial growth in culture versus actual growth in soil. *The ISME Journal* 13: 2162–2172.

**Li J, Shen Z, Li C, Kou Y, Wang Y, Tu B, Zhang S, Li X. 2018.** Stair-step pattern of soil bacterial diversity mainly driven by pH and vegetation types along the elevational gradients of Gongga Mountain, China. *Frontiers in Microbiology* **9**: 569.

**Liboriussen L, Landkildehus F, Meerhoff M, Bramm ME, Søndergaard M, Christoffersen K, Richardson K, Søndergaard M, Lauridsen TL, Jeppesen E. 2005.** Global warming: design of a flow-through shallow lake mesocosm climate experiment. *Limnology and Oceanography: Methods* **3**: 1–9.

**Linnaeus C. 1781.** On the increase of the habitable earth. *Amoenitates Academicae* **2**: 17–27.

**Liu L, Zhu K, Krause SMB, Li S, Wang X, Zhang Z, Shen M, Yang Q, Lian J, Wang X et al. 2021.** Changes in assembly processes of soil microbial communities during secondary succession in two subtropical forests. *Soil Biology and Biochemistry* **154**: 108144.

**Lomolino MV. 2001.** Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**: 3–13.

**Looby CI, Martin PH. 2020.** Diversity and function of soil microbes on montane gradients: the state of knowledge in a changing world. *FEMS Microbiology Ecology* **96**: 13.

**Loreau M, Mouquet N, Holt RD. 2003.** Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* **6**: 673–679.

**Malik AA, Martiny JB, Brodie EL, Martiny AC, Treseder KK, Allison SD. 2020.** Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *The ISME Journal* **14**: 1–9.

**McCain CM. 2007.** Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**: 1–13.

**McCain CM, Bracy Knight K. 2013.** Elevational Rapoport's rule is not pervasive on mountains. *Global Ecology and Biogeography* **22**: 750–759.

**Miyamoto Y, Nakano T, Hattori M, Nara K. 2014.** The mid-domain effect in ectomycorrhizal fungi: range overlap along an elevation gradient on Mount Fuji, Japan. *The ISME Journal* **8**: 1739–1746.

**Miyamoto Y, Sakai A, Hattori M, Nara K. 2015.** Strong effect of climate on ectomycorrhizal fungal composition: evidence from range overlap between two mountains. *The ISME Journal* **9**: 1870–1879.

**Mod HK, Buri A, Yashiro E, Guex N, Malard L, Pinto-Figueroa E, Pagni M, Niculita-Hirzel H, van der Meer JR, Guisan A. 2021.** Predicting spatial patterns of soil bacteria under current and future environmental conditions. *The ISME Journal* **15**: 2547–2560.

**Morrissey EM, Mau RL, Hayer M, Liu X-J, Schwartz E, Dijkstra P, Koch BJ, Allen K, Blazewicz SJ, Hofmockel K et al. 2019.** Evolutionary history constrains microbial traits across environmental variation. *Nature Ecology & Evolution* **3**: 1064–1069.

**Morueta-Holme N, Engemann K, Sandoval-Acuña P, Jonas JD, Segnitz RM, Svenning J-C. 2015.** Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences, USA* **112**: 12741–12745.

**Mouillot D, Loiseau N, Grenié M, Algar AC, Allegra M, Cadotte MW, Casajus N, Denelle P, Guéguen M, Maire A et al. 2021.** The dimensionality and structure of species trait spaces. *Ecology Letters* **24**: 1988–2009.

**Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000.** Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

**Norberg A, Abrego N, Blanchet FG, Adler FR, Anderson BJ, Anttila J, Araújo MB, Dallas T, Dunson D, Elith J et al. 2019.** A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. *Ecological Monographs* **89**: e01370.

**Nottingham AT, Fierer N, Turner BL, Whitaker J, Ostle NJ, McNamara NP, Bardgett RD, Leff JW, Salinas N, Silman MR et al. 2018.** Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes. *Ecology* **99**: 2455–2466.

**Nottingham AT, Whitaker J, Ostle NJ, Bardgett RD, McNamara NP, Fierer N, Salinas N, Ccahuana AJ, Turner BL, Meir P. 2019.** Microbial responses to warming enhance soil carbon loss following translocation across a tropical forest elevation gradient. *Ecology Letters* **22**: 1889–1899.

**O'Malley MA. 2007.** The nineteenth century roots of 'everything is everywhere'. *Nature Reviews Microbiology* **5**: 647–651.

**Peters MK, Hemp A, Appelhans T, Becker JN, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB et al. 2019.** Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature* **568**: 88–92.

**Picazo F, Vilmi A, Aalto J, Soininen J, Casamayor EO, Liu Y, Wu Q, Ren L, Zhou J, Shen JI et al. 2020.** Climate mediates continental scale patterns of stream microbial functional diversity. *Microbiome* **8**: 1–14.

**Purcell AM, Hayer M, Koch BJ, Mau RL, Blazewicz SJ, Dijkstra P, Mack MC, Marks JC, Morrissey EM, Pett-Ridge J. 2022.** Decreased growth of wild soil microbes after 15 years of transplant-induced warming in a montane meadow. *Global Change Biology* **28**: 128–139.

**Qi Q, Zhao M, Wang S, Ma X, Wang Y, Gao Y, Lin Q, Li X, Gu B, Li G et al. 2017.** The biogeographic pattern of microbial functional genes along an altitudinal gradient of the Tibetan Pasture. *Frontiers in Microbiology* **8**: 976.

**Rahbek C. 1995.** The elevational gradient of species richness: a uniform pattern? *Ecography* **18**: 200–205.

**Rahbek C. 2005.** The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**: 224–239.

**Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, Nogues-Bravo D, Rasmussen CMØ, Richardson K, Rosing MT, Whittaker RJ et al. 2019a.** Building mountain biodiversity: geological and evolutionary processes. *Science* **365**: 1114–1119.

**Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J. 2019b.** Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* **365**: 1108–1113.

**Ren M, Wang J. 2021.** A few dominant bacteria and their genomic basis in mediating distinct ecosystem functions. *Environmental Microbiology* **23**: 4478–4488.

**Ren M, Wang J. 2022.** Phylogenetic divergence and adaptation of *Nitrososphaeria* across lake depths and freshwater ecosystems. *The ISME Journal.* doi: 10.1038/s41396-41022-01199-41397.

**Rofner C, Peter H, Catalan N, Drewes F, Sommaruga R, Perez MT. 2017.** Climate-related changes of soil characteristics affect bacterial community composition and function of high altitude and latitude lakes. *Global Change Biology* **23**: 2331–2344.

**Roller BR, Stoddard SF, Schmidt TM. 2016.** Exploiting rRNA operon copy number to investigate bacterial reproductive strategies. *Nature Microbiology* **1**: 1–7.

**Rousk J, Bååth E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, Knight R, Fierer N. 2010.** Soil bacterial and fungal communities across a pH gradient in an arable soil. *The ISME Journal* **4**: 1340–1351.

**Ruiz-González C, Niño-García JP, Del Giorgio PA. 2015.** Terrestrial origin of bacterial communities in complex boreal freshwater networks. *Ecology Letters* **18**: 1198–1206.

**Rumpf SB, Hülber K, Klonner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger S. 2018.** Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences, USA* **115**: 1848–1853.

**Salinas N, Malhi Y, Meir P, Silman M, Roman Cuesta R, Huaman J, Salinas D, Huaman V, Gibaja A, Mamani M et al. 2011.** The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist* **189**: 967–977.

**Scherer-Lorenzen M, Gessner MO, Beisner BE, Messier C, Paquette A, Petermann JS, Soininen J, Nock CA. 2022.** Pathways for cross-boundary effects of biodiversity on ecosystem functioning. *Trends in Ecology & Evolution.* doi: 10.1016/j.tree.2021.1012.1009.

**Schrodt F, Bailey JJ, Kissling WD, Rijsdijk KF, Seijmonsbergen AC, van Ree D, Hjort J, Lawley RS, Williams CN, Anderson MG et al. 2019.** Opinion: to advance sustainable stewardship, we must document not only biodiversity but geodiversity. *Proceedings of the National Academy of Sciences, USA* **116**: 16155–16158.

**Seddon AW, Macias-Fauria M, Long PR, Benz D, Willis KJ. 2016.** Sensitivity of global terrestrial ecosystems to climate variability. *Nature* **531**: 229–232.

**Shen C, Shi Y, Ni Y, Deng Y, Van Nostrand JD, He Z, Zhou J, Chu H. 2016.** Dramatic increases of soil microbial functional gene diversity at the treeline ecotone of Changbai Mountain. *Frontiers in Microbiology* **7**: 1184.

Shen C, Xiong J, Zhang H, Feng Y, Lin X, Li X, Liang W, Chu H. 2013. Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. *Soil Biology and Biochemistry* 57: 204–211.

Singh D, Takahashi K, Kim M, Chun J, Adams JM. 2012. A hump-backed trend in bacterial diversity with elevation on Mount Fuji, Japan. *Microbial Ecology* 63: 429–437.

Soininen J, Bartels P, Heino J, Luoto M, Hillebrand H. 2015. Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience* 65: 174–182.

Soininen J, McDonald R, Hillebrand H. 2007. The distance decay of similarity in ecological communities. *Ecography* 30: 3–12.

Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J et al. 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* 536: 456–459.

Stegen JC, Lin X, Fredrickson JK, Chen X, Kennedy DW, Murray CJ, Rockhold ML, Konopka A. 2013. Quantifying community assembly processes and identifying features that impose them. *The ISME Journal* 7: 2069–2079.

Stevens GC. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist* 140: 893–911.

Teittinen A, Wang J, Strömgård S, Soininen J. 2017. Local and geographical factors jointly drive elevational patterns in three microbial groups across subarctic ponds. *Global Ecology and Biogeography* 26: 973–982.

Thornton JM, Palazzi E, Pepin NC, Cristofanelli P, Essery R, Kotlarski S, Giuliani G, Guigoz Y, Kulonen A, Pritchard D et al. 2021. Toward a definition of essential mountain climate variables. *One Earth* 4: 805–827.

Tito R, Vasconcelos HL, Feeley KJ. 2020. Mountain ecosystems as natural laboratories for climate change experiments. *Frontiers in Forests and Global Change* 3: 38.

Tonkin JD, Altermatt F, Finn DS, Heino J, Olden JD, Pauls SU, Lytle DA. 2018. The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshwater Biology* 63: 141–163.

Treseder KK, Kivlin SN, Hawkes CV. 2011. Evolutionary trade-offs among decomposers determine responses to nitrogen enrichment. *Ecology Letters* 14: 933–938.

Vacher C, Cordier T, Vallance J. 2016. Phyllosphere fungal communities differentiate more thoroughly than bacterial communities along an elevation gradient. *Microbial Ecology* 72: 1–3.

Wang J, Cao P, Hu H, Li J, Han L, Zhang L, Zheng Y, He J. 2015. Altitudinal distribution patterns of soil bacterial and archaeal communities along Mt. Shegyla on the Tibetan Plateau. *Microbial Ecology* 69: 135–145.

Wang J, Legendre P, Soininen J, Yeh CF, Graham E, Stegen J, Casamayor EO, Zhou J, Shen J, Pan F. 2020. Temperature drives local contributions to beta diversity in mountain streams: stochastic and deterministic processes. *Global Ecology and Biogeography* 29: 420–432.

Wang J, Meier S, Soininen J, Casamayor EO, Pan F, Tang X, Yang X, Zhang Y, Wu Q, Zhou J et al. 2017. Regional and global elevational patterns of microbial species richness and evenness. *Ecography* 40: 393–402.

Wang J, Pan F, Soininen J, Heino J, Shen J. 2016. Nutrient enrichment modifies temperature-biodiversity relationships in large-scale field experiments. *Nature Communications* 7: 1–9.

Wang J, Shen J, Wu Y, Tu C, Soininen J, Stegen JC, He J, Liu X, Zhang L, Zhang E. 2013a. Phylogenetic beta diversity in bacterial assemblages across ecosystems: deterministic versus stochastic processes. *The ISME Journal* 7: 1310–1321.

Wang J, Soininen J. 2017. Thermal barriers constrain microbial elevational range size via climate variability. *Environmental Microbiology* 19: 3283–3296.

Wang J, Soininen J, He J, Shen J. 2012a. Phylogenetic clustering increases with elevation for microbes. *Environmental Microbiology Reports* 4: 217–226.

Wang J, Soininen J, Shen J. 2013b. Habitat species pools for phylogenetic structure in microbes. *Environmental Microbiology Reports* 5: 464–467.

Wang J, Soininen J, Zhang Y, Wang B, Yang X, Shen J. 2011. Contrasting patterns in elevational diversity between microorganisms and macroorganisms. *Journal of Biogeography* 38: 595–603.

Wang J, Soininen J, Zhang Y, Wang B, Yang X, Shen J. 2012b. Patterns of elevational beta diversity in micro-and macroorganisms. *Global Ecology and Biogeography* 21: 743–750.

Warton DI, Blanchet FG, O'Hara RB, Ovaskainen O, Taskinen S, Walker SC, Hui FKC. 2015. So many variables: joint modeling in community ecology. *Trends in Ecology & Evolution* 30: 766–779.

Westoby M, Gillings MR, Madin JS, Nielsen DA, Paulsen IT, Tetu SG. 2021. Trait dimensions in bacteria and archaea compared to vascular plants. *Ecology Letters* 24: 1487–1504.

Wilhelm L, Singer GA, Fasching C, Battin TJ, Besemer K. 2013. Microbial biodiversity in glacier-fed streams. *The ISME Journal* 7: 1651–1660.

Yang T, Tedersoo L, Soltis PS, Soltis DE, Gilbert JA, Sun M, Shi YU, Wang H, Li Y, Zhang J et al. 2019. Phylogenetic imprint of woody plants on the soil mycobiome in natural mountain forests of eastern China. *The ISME Journal* 13: 686–697.

Yang Y. 2021. Emerging patterns of microbial functional traits. *Trends in Microbiology* 29: 874–882.

Yang Y, Gao Y, Wang S, Xu D, Yu H, Wu L, Lin Q, Hu Y, Li X, He Z et al. 2014. The microbial gene diversity along an elevation gradient of the Tibetan grassland. *The ISME Journal* 8: 430–440.

Yeh CF, Soininen J, Teittinen A, Wang J. 2019. Elevational patterns and hierarchical determinants of biodiversity across microbial taxonomic scales. *Molecular Ecology* 28: 86–99.

Yuan Y, Si G, Wang J, Luo T, Zhang G. 2014. Bacterial community in alpine grasslands along an altitudinal gradient on the Tibetan Plateau. *FEMS Microbiology Ecology* 87: 121–132.

Zhang Y, Cong J, Lu H, Li G, Xue Y, Deng Y, Li H, Zhou J, Li D. 2015. Soil bacterial diversity patterns and drivers along an elevational gradient on Shennongjia Mountain, China. *Microbial Biotechnology* 8: 739–746.

Zhao K, Kong WD, Khan A, Liu JB, Guo GX, Muhanmmad S, Zhang XZ, Dong XB. 2017. Elevational diversity and distribution of ammonia-oxidizing archaea community in meadow soils on the Tibetan Plateau. *Applied Microbiology and Biotechnology* 101: 7065–7074.

Zhou J, Deng Y, Zhang P, Xue K, Liang Y, Van Nostrand JD, Yang Y, He Z, Wu L, Stahl DA. 2014. Stochasticity, succession, and environmental perturbations in a fluidic ecosystem. *Proceedings of the National Academy of Sciences, USA* 111: E836–E845.

Zhou J, Deng YE, Shen L, Wen C, Yan Q, Ning D, Qin Y, Xue K, Wu L, He Z et al. 2016. Temperature mediates continental-scale diversity of microbes in forest soils. *Nature Communications* 7: 1–10.

Zhou J, He Z, Yang Y, Deng Y, Tringe SG, Alvarez-Cohen L. 2015. High-throughput metagenomic technologies for complex microbial community analysis: open and closed formats. *mBio* 6: e02288-02214.

Zhou J, Liu W, Deng Y, Jiang Y-H, Xue K, He Z, Van Nostrand JD, Wu L, Yang Y, Wang A. 2013. Stochastic assembly leads to alternative communities with distinct functions in a bioreactor microbial community. *mBio* 4: e00584-00512.

Zhou J, Ning D. 2017. Stochastic community assembly: does it matter in microbial ecology? *Microbiology and Molecular Biology Reviews* 81: e00002-00017.

Zhu Y, Xiong C, Wei Z, Chen Q, Ma B, Zhou S, Tan J, Zhang L, Cui H, Duan G. 2021. Impacts of global change on phyllosphere microbiome. *New Phytologist*. doi: 10.1111/nph.17928.

## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Radar plot for the percentages of data sets with typical elevational patterns in alpha diversity.

**Fig. S2** The strength of elevational distance–decay patterns of microbial communities across taxonomic groups and habitat types, and their relationships with elevational ranges.

**Table S1** Summary of our literature review on elevational diversity patterns of microorganisms across global mountains.

**Table S2** Summary of the references for meta-analysis of the strength of the elevational distance–decay pattern.

**Table S3** Summary of the categorised terms of different abiotic and biotic variables in shaping microbial elevational patterns for terrestrial or aquatic ecosystems.

**Table S4** Reference list for the relative importance of deterministic vs stochastic processes underlying microbial communities.

**Table S5** Detailed key questions for the proposed seven perspectives.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

---

## About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Foundation, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews and Tansley insights.

- Regular papers, Letters, Viewpoints, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <23 days. There are **no page or colour charges** and a PDF version will be provided for each article.

- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.

- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)

- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**