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Research article

Drivers and mechanisms that contribute to microbial β-diversity patterns and range sizes in mountains across a climatic variability gradient

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Microbial communities are highly diverse, yet the mechanisms underlying microbial community assembly are not well understood. Janzen's mountain passes hypothesis proposed that climatic barriers and dispersal limitation shape communities to a greater extent in mountains with lower climatic variability and overlap, permitting higher levels of species coexistence. Here, we investigate changes in microbial community dissimilarities, distributional range sizes and ecological processes along elevational gradients in three montane ecosystems representing a climatic variability gradient. We found that climate, climatic variability and spatial distance play dominating roles in affecting microbial β-diversity patterns and range sizes along elevational gradients. Janzen's mountain passes hypothesis can be applied to microbial community assembly: mountains with lower climatic variability and higher climatic difference between elevations exhibited higher β-diversity, higher endemism, lower range sizes and steeper distance–decay trends. However, microbial communities experience clear climate-driven limited range sizes and dispersal processes, and show typical endemic patterns, in all mountain ecosystems. Our results emphasize the importance of dispersal and climatic niche processes in shaping montane biodiversity. As a result, changes in climate may significantly impact soil biodiversity in montane ecosystems by altering the effects of dispersal limitation and climatic variability on bacterial and fungal community composition along elevational gradients.

Keywords: community assembly, dispersal limitation, β-diversity, montane biodiversity, microbial community

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Introduction

Over two centuries ago, Alexander von Humboldt published a series of articles that sparked scientific interest around the elevational distribution of plants and animals on mountains. This led to a long-standing ecological question: 'What drives the biogeographic patterns of mountain biodiversity?' (Lomolino 2001, McCain and Grytnes 2010, Rahbek et al. 2019). Understanding how community assembly processes shape the diversity and distribution of montane biodiversity is key to understanding the mechanisms that facilitate species coexistence and effective biodiversity conservation planning (Nemergut et al. 2013). The mechanisms that control plant and animal biogeography and community composition are relatively well understood. However, research on the mechanisms shaping microbial communities and distributions is limited (Bodelier 2011).

Microbial biogeography and diversity have been dominated by the classical microbiological tenet, 'Everything is everywhere, but the environment selects' (de Wit and Bouvier 2006). This implies that microorganisms are ubiquitous and have high distributional range sizes due to low dispersal barriers but their survival in a new locale is determined by environmental selection. However, recent studies reveal high levels of microbial endemism with widespread dispersal limitation (Talbot et al. 2014) and that taxa-area relationships of microorganisms are similar to plant and animal species (Bodelier 2011). Dispersal limitation and environmental selection may shape the microbial diversity patterns, community composition and range sizes (Zhou and Ning 2017), though their relative importance remains uncertain and may be context-dependent (Ren et al. 2018, Guerra et al. 2020, Hu et al. 2020). A deeper understanding of the ecological determinants of microbial diversity patterns and range sizes, and the relative importance of dispersal or selection, are critical to predicting microorganism responses to climate change and human disturbance (McCain and Colwell 2011, Wang and Soininen 2017).

In 1967, Daniel Janzen hypothesized that low climatic variability along elevational gradients results in greater limitations to animal migration and plant dispersal for tropical taxa compared to temperate taxa (Janzen 1967). Further, a relatively stable climate, such as that of the tropics, induces high climatic difference or low temperature overlap between elevations (Klinges and Scheffers 2020). Limited temperature variability and overlap creates a narrower distributional range of preferred environmental conditions for tropical taxa, which favors tropical species that are highly adapted to narrow thermal niches. This results in mountains with low climatic variability (e.g. tropics) experiencing greater dispersal limitation, higher community composition dissimilarity, narrower species range size and greater overall species richness. Several studies have supported Janzen's hypothesis by demonstrating greater population genetic differentiation (Eo et al. 2008, Adams and Hadly 2012), narrower thermal tolerances (Polato et al. 2018) and smaller elevational ranges (McCain 2009, Freeman et al. 2021) for tropical species. Moreover,

following Janzen's hypothesis, the elevational Rapoport's rule (ERR) suggested that species distributional range size should increase towards higher elevations, because climatic variability is typically higher at higher elevations (Stevens 1992). However, the validity of Janzen's hypothesis and ERR for microorganisms remains uncertain (but see Wang and Soininen 2017). If the mountain passes hypothesis or ERR is valid for microorganisms, the following biogeographic patterns should be evident (Ghalambor et al. 2006). First, microorganisms in mountains with lower climatic variability and overlap should have higher community composition dissimilarity along montane elevational gradients; second, microorganisms in mountains with lower climatic variability and overlap should have lower range sizes; and third, microbial range sizes should increase towards higher elevations and be driven by climatic variability.

Although microbial studies do not directly support Janzen's mountain passes hypothesis across climatic variability gradients, previous research sheds light on the dynamics of microbial β-diversity patterns and range sizes. For example, microbial survival is strongly regulated by climatic factors, such as temperature and humidity, which significantly influence microbial distributions, diversity and community composition (Wang et al. 2022, Xu et al. 2023). Climatic variability also plays an important role in driving microbial diversity and community dissimilarity and range sizes along elevational gradients (Wang and Soininen 2017, Feng et al. 2023). Moreover, in the context of climatic variability and overlap decreasing towards higher latitudes, *Streptomyces* communities have exhibited latitudinal diversity gradients and greater β-diversity at low latitudes (Andam et al. 2016), and microbial β-diversity decreases with latitude in continental paddy soils (Xiao et al. 2021). Thus, climate and climatic variability may also contribute to the microbial β-diversity patterns observed on elevational gradients of different mountains.

The mountain with lower climatic variability and overlap but higher climatic difference between elevations (e.g. tropical mountains) results in narrower thermal niches relative to those temperate mountains (Smith 2018). Species moving up or down a tropical mountain will encounter maladaptive climatic conditions, which limits their dispersal ability along elevational gradients (Huey 1978). Consequently, dispersal on tropical mountains is more restricted than on temperate mountains (Polato et al. 2018), which leads to increased endemism along elevational gradients (McCain 2009). Numerous studies have suggested that microbial community composition is influenced by dispersal limitation (Stegen et al. 2013, Stegen et al. 2015, Zhou and Ning 2017) and that microbial biogeography is governed by environmental factors such as climate, soil and plant composition (Talbot et al. 2014, Wang et al. 2022, Feng et al. 2023). However, the relative importance of dispersal versus environmental factors in structuring microbial communities remains contentious. Recently, a study conducted along a latitudinal gradient found that environment plays a more significant role than dispersal in shaping microbial communities, and that dispersal rates did

not increase with latitude (Zhang et al. 2020). However, critical gaps in our knowledge remain regarding how environmental heterogeneity and dispersal limitation affect microorganisms in montane regions.

Our study aims to examine whether Janzen's mountain passes hypothesis applies to microorganisms, which would suggest that both dispersal limitation and environmental selection drive microbial β-diversity patterns. This results from the sum of both deterministic and stochastic ecological processes, where the relative strength of microbial dispersal limitation is hypothesized to increase with decreasing climatic variability and overlap, while the strength of environmental selection is predicted to decrease. As a result, greater β-diversity and steeper distance–decay trends on mountains with lower climatic variability and overlap are expected, which would support Janzen's mountain passes hypothesis. However, recent research suggests that environmental selection may also be important and that the contributions of both dispersal limitation and environmental filtering vary across elevations and climatic zones (Zhang et al. 2020). We present an alternative hypothesis that suggests dispersal limitation and environmental selection as the core processes of Janzen's mountain passes hypothesis also play a critical role in shaping montane microbial communities in different mountains. As climate change persists, the elevational ranges of species are predicted to shift (Donhauser and Frey 2018). If dispersal limitation is common within montane microbial communities, climate change could dramatically alter microbial community composition, leading to changes in soil biogeochemical functioning.

Here, we investigate changes in microbial community dissimilarities, distributional range sizes and ecological processes along elevational gradients in three montane ecosystems representing a climatic variability gradient (Fig. 1a–b). Our study aims to uncover the mechanisms underlying microbial diversity patterns across elevational gradients in different mountains and to provide insights into how montane microorganisms may respond to climate change. Specifically, we sought to address the following questions. 1) Is the microbial β-diversity higher for mountains with lower climatic variability and overlap along elevational gradients? 2) Do mountains with lower climatic variability and communities of lower elevations have lower microbial range sizes? 3) What drivers and mechanisms contribute to microbial biogeographical and elevational patterns?

Material and methods

Study sites

This study examined three elevational gradient platforms in Yunnan Province, southwestern China. Three montane sites were included: 1) Banma Mountain in Xishuangbanna (Banna), which has a tropical montane rainforest vegetation and is situated at 21°36′N, 101°34′E; 2) Ailao Mountain in Puer, having a subtropical mid-montane moist evergreen broad-leaved forest vegetation and is located at 24°32′N, 101°01′E; and 3) Yulong Mountain in Lijiang, having a subalpine coniferous forest vegetation and situated at 27°08′N, 100°12′E (Fig. 1a). The latitudinal span of the three mountains is approximately 6° (ca 600 km). Because of huge differences in their basic/initial elevations, a complete climatic gradient is formed within the local region, which is equivalent to these climatic changes across the large-scale latitudinal gradient (Song et al. 2021, Xu et al. 2023). These three mountains represent distinct climate and climatic variability gradients (Fig. 1b), for example the intensity of climatic variability and temperature overlap: Banna < Ailao < Yulong. The Banna site was divided into distinct elevational climate zones at 800, 1000, 1200 and 1400 m a.s.l. The Ailao site had unique climate zones at 2000, 2200, 2400 and 2600 m a.s.l. The Yulong site had distinct climate zones at 3200, 3400, 3600 and 3800 m a.s.l. We selected 600 m elevational ranges in all mountains, because 1) the elevation ranges listed above for each site generally encompassed the upper and lower limits of local natural forests (Xu et al. 2023); 2) the ranges can well represent local biodiversity patterns and community variations (e.g. animal in Ashton et al. 2016, plant and microorganism in Xu et al. 2023); and 3) five plots in each elevation transect were established to contain enough environmental variations and field replicates. In 2012, we established five 20 × 20 m plots in each elevational transect of each site. The plots were spaced more than 200 m apart along the elevational transects. The consistent 200 m difference in elevation between transects at each site allowed us to conduct experiments and analyses based on a standardized procedure. In total, 60 plots were established across all three sites (i.e. five plots x four elevations x three sites). We identified, measured and tagged all trees with a diameter at breast height (DBH) in each plot of > 5 cm (Song et al. 2021, Xu et al. 2023). Detailed descriptions for the study sites' climate, geology and flora are available in Supporting information and Xu et al. (2023).

Soil sampling

During the growing season of 2021, soil samples were collected from July to October. To obtain representative soil samples, five random points were selected from each plot. At each point, 500 g of soil was collected at a depth of 10 cm after removing the litter layer. These samples were then mixed together and divided into two parts and cooled in a portable freezer before being transported to the laboratory within 4 h. Half of the soil samples were stored in a −40°C freezer for long-term storage and later used for microbial sequencing.

Half of the remaining soil samples from each plot were brought back to the laboratory for soil physicochemical property determination. The soil fresh weight was measured before drying samples in an oven to calculate the soil water content (using about 20 g of fresh soil). The remaining soil samples were air dried in cool, dry conditions and then transferred to the Public Technology Service Center (PTSC) at Xishuangbanna Tropical Botanical Garden (XTBG), which is
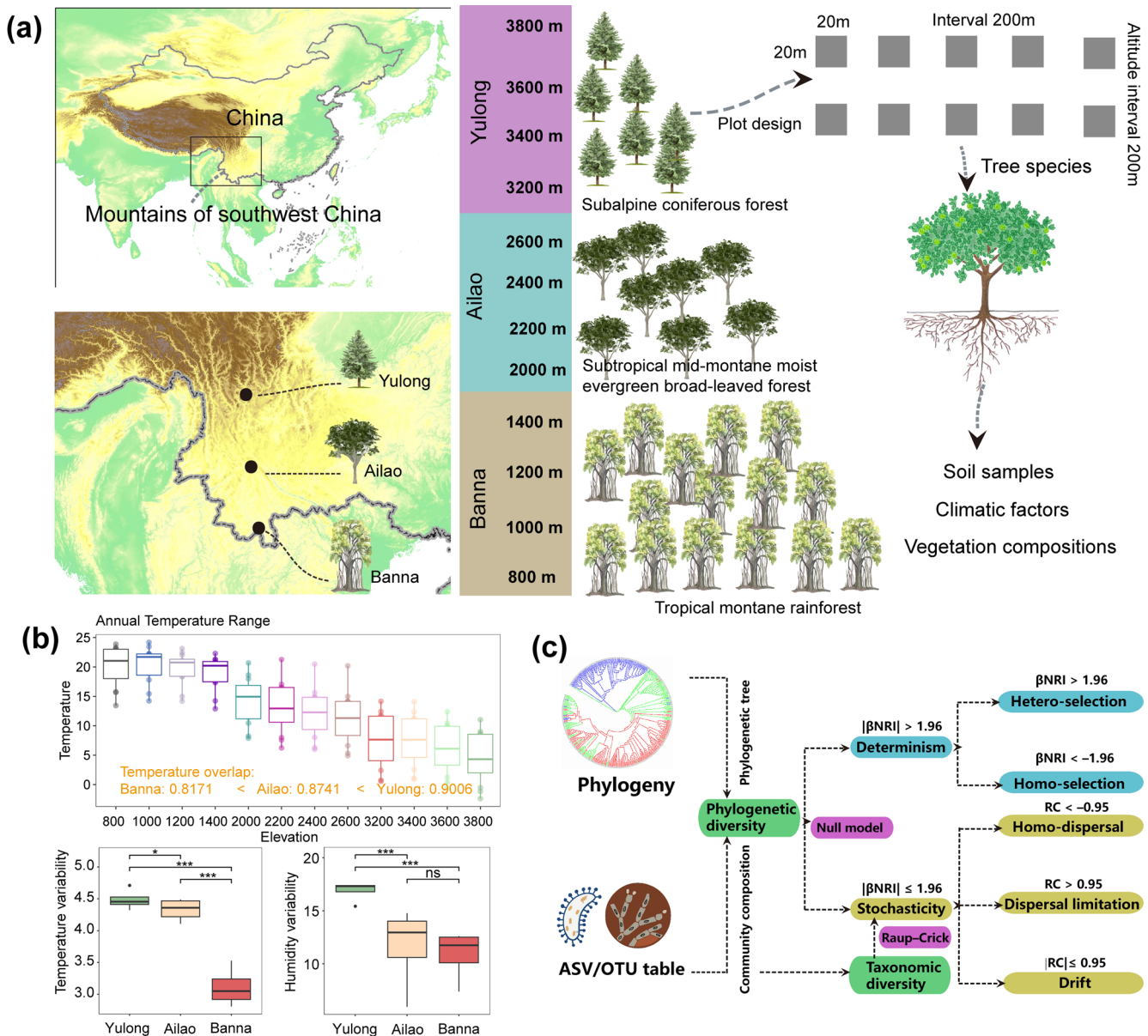
Figure 1. Study sites, experimental design and conceptual framework. (a) Schematic illustrating the location of the three study sites in southwestern China and sampling design along elevational transects at each site. (b) Annual temperature (°C) range (mean temperature of every month (January–December) and annual mean temperature), temperature and humidity (%) variability in each site shown. Temperature overlaps in three sites were calculated by kernel density coefficient of overlapping. (c) Soil microbial community assembly conceptual framework. Contemporary coexistence theory suggests that dispersal (including dispersal limitation and homogenizing dispersal), ecological drift and environmental selection (including heterogeneous and homogeneous selection) collectively determine community β-diversity. This framework can be used to determine the relative importance of different ecological processes in shaping β-diversity.

part of the Chinese Academy of Sciences (CAS), for further analysis. Soil available potassium, pH, organic matter, total carbon, total nitrogen, total phosphorus and total potassium were measured for each plot (Supporting information). The protocols used for the soil measurements can be found in Supporting information and Xu et al. (2023). To reduce the physicochemical data to a few major orthogonal axes of variability, a principal component analysis (PCA) was performed using the 'FactoMineR' package in R (www.r-project.org,

Sebastien et al. 2008). The first three PCA axes accounted for over 88% of the total variation and were used to compute a distance matrix among plots.

Local-scale climatic measurements

To monitor air humidity and temperature, iButton data loggers were employed in each plot. The iButtons were placed in PVC tubes with ventilation slots to shade them from direct

sunlight. The tubes were installed at a height of 1.3 m in the center of each plot. Using another set of iButtons, soil temperature was monitored at a depth of 10 cm in each plot. Hourly measurements of air humidity, air temperature and soil temperature were recorded (Song et al. 2021). Climatic factors included 1) energy-water: annual mean air temperature and humidity, and annual mean soil temperature; 2) climatic variability: standard deviation of annual temperature and humidity (Zhang et al. 2022, Feng et al. 2023); and 3) climatic difference between elevations in each site. See the Supporting information for the corresponding air and soil measurement data. We also calculated the temperature overlap values between elevations in each site using kernel density coefficient of overlapping by the 'overlapping' package (Klinges and Scheffers 2020).

Molecular and bioinformatic analyses

See the Supporting information for detailed information about the soil DNA extractions and PCR reactions. Library preparation and paired-end Illumina MiSeq sequencing were performed using the NovaSeq 6000 SP Reagent Kit by Personal Biotechnology Co., Ltd (Shanghai, China). Bioinformatic analyses were conducted using tools from QIIME2 ver. 2.0 (Bolyen et al. 2019). Raw sequence data were processed and analyzed using the Demux plugin. Primers were clipped from reads using the Cutadapt plugin (Martin 2011). Sequences were quality filtered, denoised and merged, and sequence chimeras also removed using the DADA2 plugin (Callahan et al. 2016). Filtering was performed separately for bacterial and fungal sequences. Non-singleton amplicon sequence variants (ASVs) were aligned in MAFFT (Katoh et al. 2002). FastTree2 (Price et al. 2010) was used to infer a maximum-likelihood phylogenetic tree within QIIME (Stegen et al. 2013). Non-fungal and non-bacterial reads were removed; see Supporting information for the final taxa composition. Prior to downstream analyses, all samples were subsampled to contain the same number of reads (i.e. the lowest number of sequence reads across all samples).

Statistical analysis

To explore the effects of spatial distance, climatic factors, climatic variability and soil properties on microbial β-diversity, we first calculated β-diversity among microbial communities from the different mountain sites. Using the bacterial and fungal composition data, we computed Bray–Curtis dissimilarity matrices for each pair of samples using the 'betapart' package in R (Baselga et al. 2021). To investigate the association between microbial β-diversity (measured as Bray–Curtis dissimilarity) and geographic (latitude, longitude and elevation) or elevational distance, we employed loess regression at each site, which is well-suited for capturing distance–decay trends in microbial communities. Additionally, spatial locations, climatic factors (humidity, temperature and their variability) and edaphic properties (the first three axes of the soil

PCA) were compared across plots by calculating distance matrices for each pair of plots and each variable. These distances were later referred to as the 'elevational/geographic distance', 'climatic distance' and 'edaphic distance', respectively. To some extent, higher climatic distance/difference between elevations indicated lower climatic overlap of them.

To investigate if the relationship between climatic and edaphic distances were related to microbial community Bray–Curtis dissimilarity, Mantel tests were conducted using the 'vegan' (Oksanen et al. 2015) package in R software. Due to the high collinearity between air and soil temperatures (Pearson's r = 0.97, p < 0.001, Supporting information), only air temperature was used in the subsequent analyses. Wilcoxon tests were used to compare climatic variability, climatic distances, edaphic distances and Bray–Curtis community dissimilarity across the three study sites (Xu et al. 2021). A distance-based redundancy analysis (dbRDA) was performed to further examine the explanatory power of predictors for community dissimilarity. Generalized hierarchical variation partitioning was also carried out using the 'rdacca.hp' package to quantify the importance of predictors (Lai et al. 2022). Predictors included in the dbRDA models included climatic factors and their variability, edaphic factors (PC1-3), plant species composition and spatial distance. For plant species composition, nonmetric multidimensional scaling (NMDS) was performed for the plant species data. The first two NMDS axes were then used to represent plant composition in the dbRDA analysis (Hu et al. 2020, Zheng et al. 2021).

To assess whether microorganisms in the mountain with lower climatic variability have narrower distributional range sizes and higher endemism, microbial community composition was first compared among elevation transects. Bacterial and fungal community composition was examined using NMDS with Bray–Curtis dissimilarity matrices as implemented via the *metaMDS* function in the 'vegan' package. The distributions of endemic microorganisms were then calculated, i.e. Venn diagrams were created to illustrate the number of shared and unique/endemic ASVs among different sites. We calculated range size at two different scales: the ASV level and the community level (Wang and Soininen 2017). For the ASV level, the elevational range of each ASV was calculated to describe the distribution of each microbial taxon across sites. We quantified the proportion of ASVs with different elevational range sizes in each mountain. For the community level, we calculated the mean range size of all ASV in a plot (Stevens 1992). Wilcoxon tests were used to compare the difference of community-level range sizes between three sites. The relationships between elevation and community-level range sizes were fitted using linear regressions. Random forest analyses were conducted to quantify the relative importance of various predictors (climatic factors, climatic variability and soil properties) for community-level range sizes using 'rfPermute' (Eric 2022) and 'randomForest' (Liaw and Wiener 2002) packages. The relative importance of every predictor was ranked in terms of the percentage increase in mean squared error (%IncMSE) (Xu et al. 2023).

Ecological process analysis

Here, the deterministic versus stochastic framework was applied to explore soil microbial community assembly across an elevational gradient (see the Supporting information for detailed discussions). The Raup–Crick metric is a probabilistic β-diversity metric which leverages the taxonomic composition of microbial communities, as determined through null models, to remove the effect of alpha diversity (i.e. richness) from turnover estimates (Stegen et al. 2013). The βNRI is computed by rearranging species identities and abundances across the tips of a phylogeny (Stegen et al. 2013). The study framework (Fig. 1c) allows for different types of community assembly processes to be identified: |βNRI| > 1.96 indicates determinism, or environmental selection, which can be further subdivided based on βNRI values with βNRI > 1.96 indicating heterogeneous selection and βNRI < −1.96 indicating homogeneous selection. A |βNRI| ≤ 1.96 indicates stochasticity, which can be further subdivided, with RC_{bray} > 0.95 indicating dispersal limitation, RC_{bray} < −0.95 homogenizing dispersal and |RC_{bray}| ≤ 0.95 indicating ecological drift (Stegen et al. 2013, Zhou and Ning 2017).

Homogenizing dispersal occurs when high dispersal rates lead to decreases in community dissimilarity and a lower β-diversity. Conversely, dispersal limitation reduces the exchange of species among communities, typically increasing community dissimilarity and β-diversity (Stegen et al. 2013). To evaluate the importance of these processes, we used iCAMP to conduct a phylogenetic bin-based null model analysis (Ning et al. 2020). The iCAMP approach demonstrated high accuracy, precision, sensitivity and specificity when applied to simulated communities, outperforming entire community-based approaches like those used in Stegen et al. (2013). We estimated the relative importance of each ecological process separately for the tropical, subtropical and subalpine sites. The effects of dispersal limitation and environmental selection were estimated with all other ecological processes categorized as 'ecological drift and others'. All statistical analyses were conducted in R ver. 4.1.2 (www.r-project.org).

Results

Microbial β-diversity patterns and distributional range sizes along elevational gradients

Community composition dissimilarity was examined within the study sites (Fig. 2a–d). Bray–Curtis dissimilarity was found to increase sharply with elevation/geographic distance from 0 m to 200 m for both bacteria and fungi. This suggests substantial microbial community dissimilarity between adjacent elevational transects. The Banna site had greater microorganismal dissimilarities than the Ailao and Yulong sites from 200 to 600 m (Fig. 2a–d). Significant differences in β-diversity were observed among the three study sites for both bacteria and fungi (Fig. 3). The Banna site had the highest dissimilarity values for fungal communities (n = 190, p <

0.001), while the Ailao and Yulong sites showed similar dissimilarity values (n = 190, p > 0.05, Fig. 3c). For bacteria, the Bray–Curtis dissimilarity was higher in the Banna than in the Ailao site (n = 190, p < 0.05), which had higher dissimilarity again than the Yulong site (n = 190, p < 0.001, Fig. 3d).

In common with the NMDS analyses, microbial community composition varied with elevation within all study sites (Supporting information). For both bacteria and fungi, the Banna site had the highest number of unique ASVs, and the Ailao site had more unique ASVs than the Yulong site (Supporting information). In addition, lower elevations often had more unique ASVs than higher elevations within each study site (Supporting information). At the ASV level, more than 80% of ASVs were identified from only a single elevation across all study sites (Fig. 2e). At the community level, Banna had lower distributional range sizes of fungi than those of Yulong (p < 0.05, Fig. 4a); and Banna had lower distributional range sizes of bacteria than those of Ailao and Yulong (p < 0.05, Fig. 4b). In each study site and microbial taxon, lower elevation always had lower distributional range sizes than those at higher elevation (Fig. 4a–b).

Drivers of β-diversity patterns and distributional rang sizes in microbial communities

We explored the effects of predictors (such as climatic factors and their variability, edaphic variables, host plant species composition and spatial distance) on microbial community dissimilarity. Results revealed that climatic factors, climatic variability and spatial distance showed high importance in all three study sites for both bacteria and fungi (Fig. 3, 5). Mantel tests identified stronger correlations (higher R^2 values) between microbial dissimilarity and climatic distance versus edaphic properties (Fig. 3). For example, in fungal communities, Bray–Curtis dissimilarity was strongly and positively related to climatic distance (r = 0.6–0.8 in Mantel tests) (Fig. 3e). This relationship was also observed for bacteria (Fig. 3f) and was stronger at the Banna site (r = 0.6–0.8) versus the other two study sites (r = 0.45–0.6). In contrast, for both bacteria and fungi, Bray–Curtis dissimilarity was only weakly and positively related to edaphic distance (r < 0.5 (Fig. 3g–h). In all cases (bacteria, fungi and all study sites), the spatial distance, temperature, humidity, temperature variability and humidity variability were most important factors (~ 15%) in driving community dissimilarity (Fig. 5a–f). Host plant species composition had less importance than spatial distance or climatic factors. Edaphic factors were the least important in driving soil bacterial and fungal community assembly (Fig. 5a–f). Community-level distributional range sizes had significant positive relationships with elevations in all cases (bacteria, fungi and all study sites), but the R^2 decreased from Banna to Ailao and Yulong (Fig. 5a–b). Random forest analyses revealed that elevation, annual mean air temperature, temperature variability and humidity variability showed consistently high and significant importance that affected distributional range sizes of fungi and bacteria in all models (Fig. 4c–f).
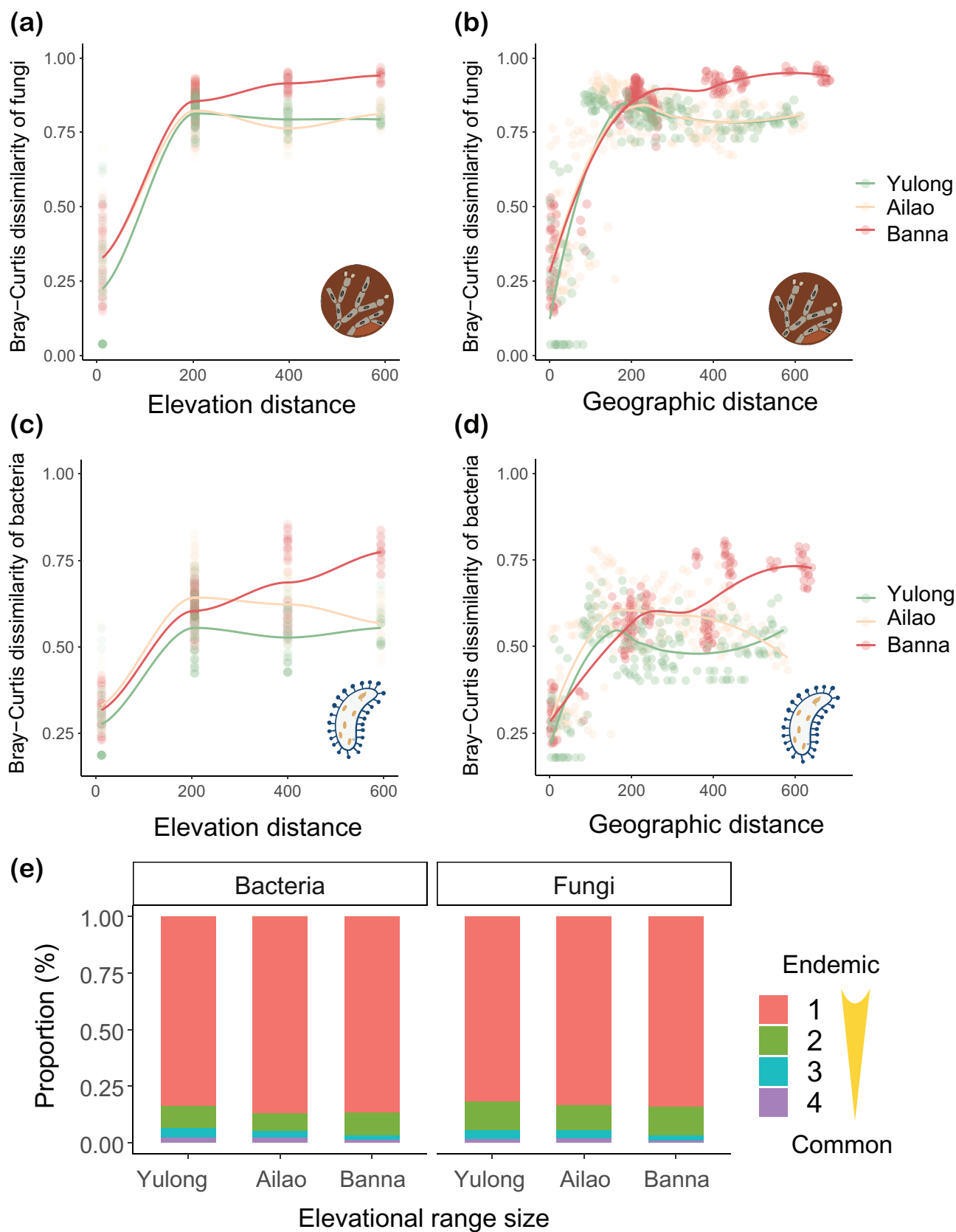
Figure 2. The distance–decay relationships and elevational range sizes of microorganisms in different study sites. Fungal (a–b) and bacterial (c–d) distance–decay relationships for β-diversity (Bray–Curtis dissimilarity), shown for elevational (a, c) and geographic (b, d) distance. (e) The proportion of amplicon sequence variants (ASVs) with different elevational range sizes in different sites. 1/2/3/4: species distributed in one/two/three/four elevational transects.
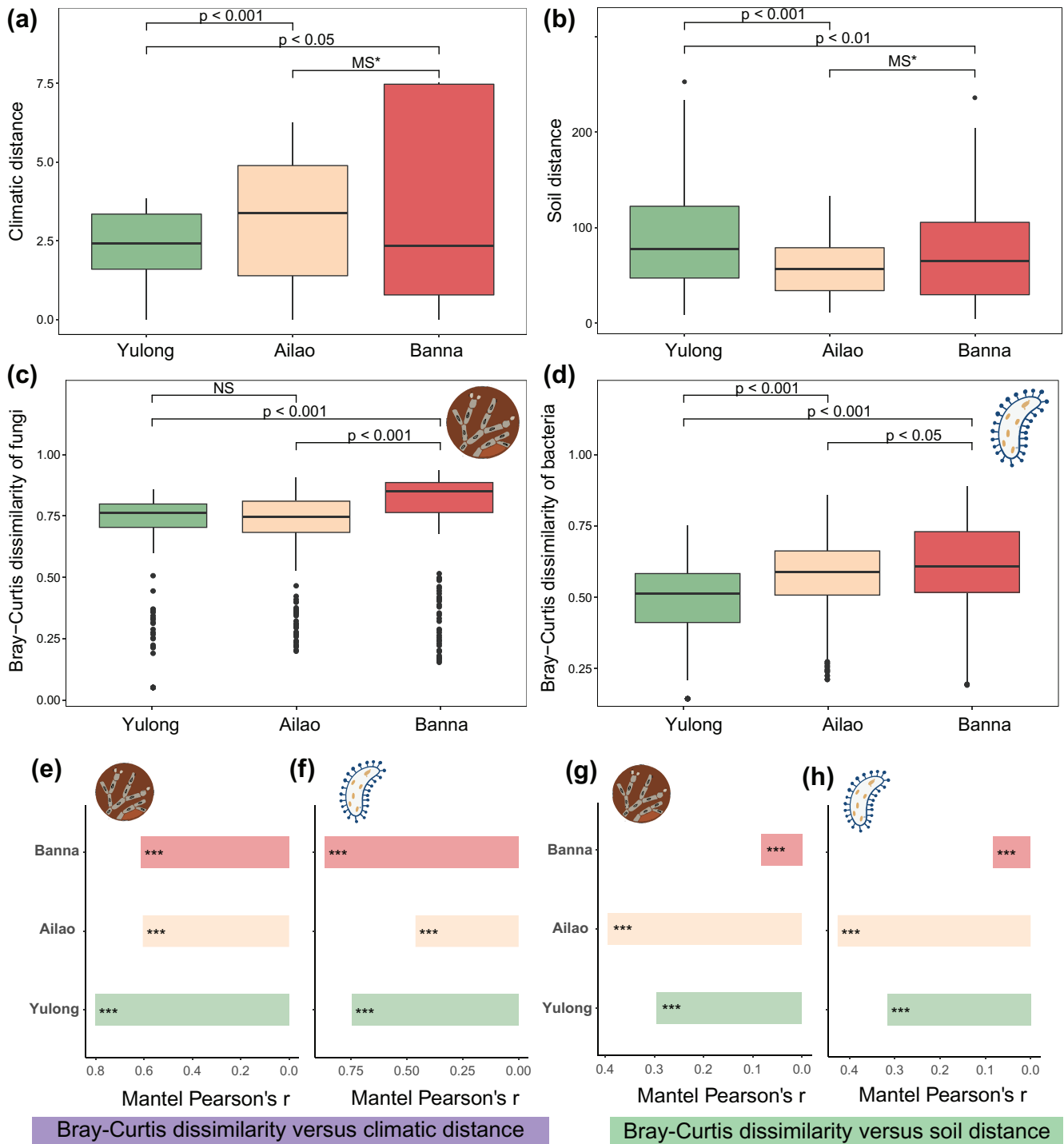
Figure 3. Comparisons of environmental distance and β-diversity between three climatic zones and the relationships between them. (a) Differences in climatic factors between all paired plots. (b) Differences in soil factors between all paired plots. (c) Bray–Curtis dissimilarity of fungi. (d) Bray–Curtis dissimilarity of bacteria. NS: not significant, MS*: marginally significant ($0.05 < p < 0.08$). Correlation between β-diversity (as Bray–Curtis dissimilarity) and either climatic (a–d) or edaphic (e–h) distance as determined using Mantel tests. Analyses were performed separately for fungal (e, f) and bacterial (g, h) communities. NS: not significant, **$p < 0.01$, ***$p < 0.001$.
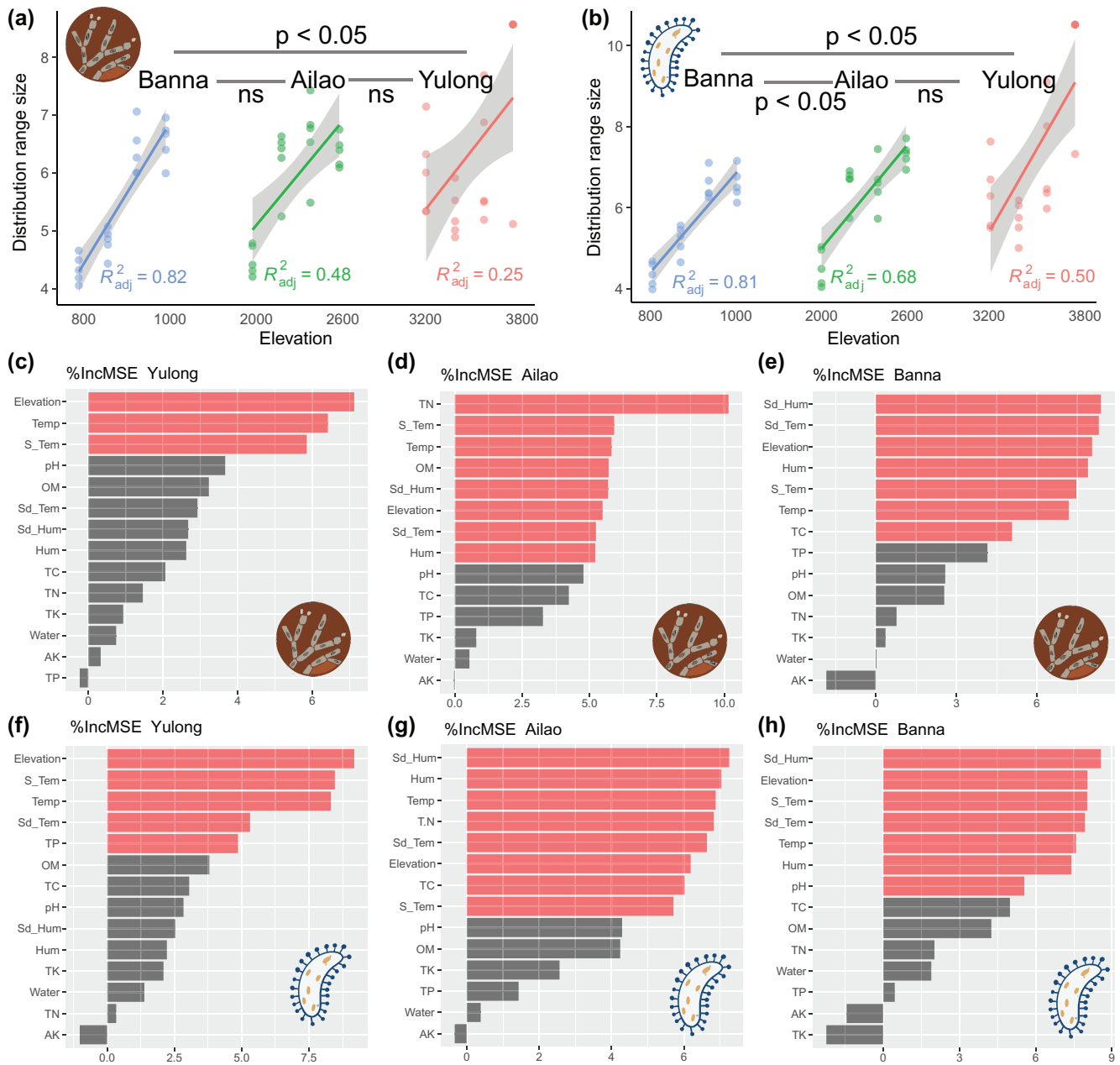
Figure 4. Community-level range sizes of fungi and bacteria and their drivers. (a–b) The relationships between range sizes and elevation in different sites. (c–h) The relative importance of predictors that affect range sizes for different sites and microbial taxa. Annual mean air temperature (Temp), temperature variability (Sd_Tem), annual mean air humidity (Hum), humidity variability (Sd_Hum), annual mean soil temperature (S_Tem), soil organic matter (OM), total carbon (TC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available potassium (AK), soil water content (Water) and soil pH (pH). Red bars indicate significant predictors and gray bars indicate non-significant predictors.

Community assembly mechanisms

In the ecological process analysis, dispersal limitation (bacteria: 20–27%, fungi: 34–41%) and environmental selection (bacteria: 30–50%, fungi: 19–25%,) dominated microbial community assembly across study sites and for both bacteria and fungi (Fig. 6a–f). Dispersal limitation and environmental selection often showed high total importance for all

sites (53–70%, Fig. 6a–f). For fungi, dispersal limitation and environmental selection had the highest importance (38 and 25%, respectively) in the Banna site. Similarly, dispersal limitation had the highest importance in the Ailao (41%) and Yulong (34%) sites, followed by environmental selection (Ailao: 25%, Yulong: 19%) (Fig. 6a–c). For bacteria, a different pattern emerged where environmental selection was the most important process (Banna: 30%, Ailao: 36%, Yulong:
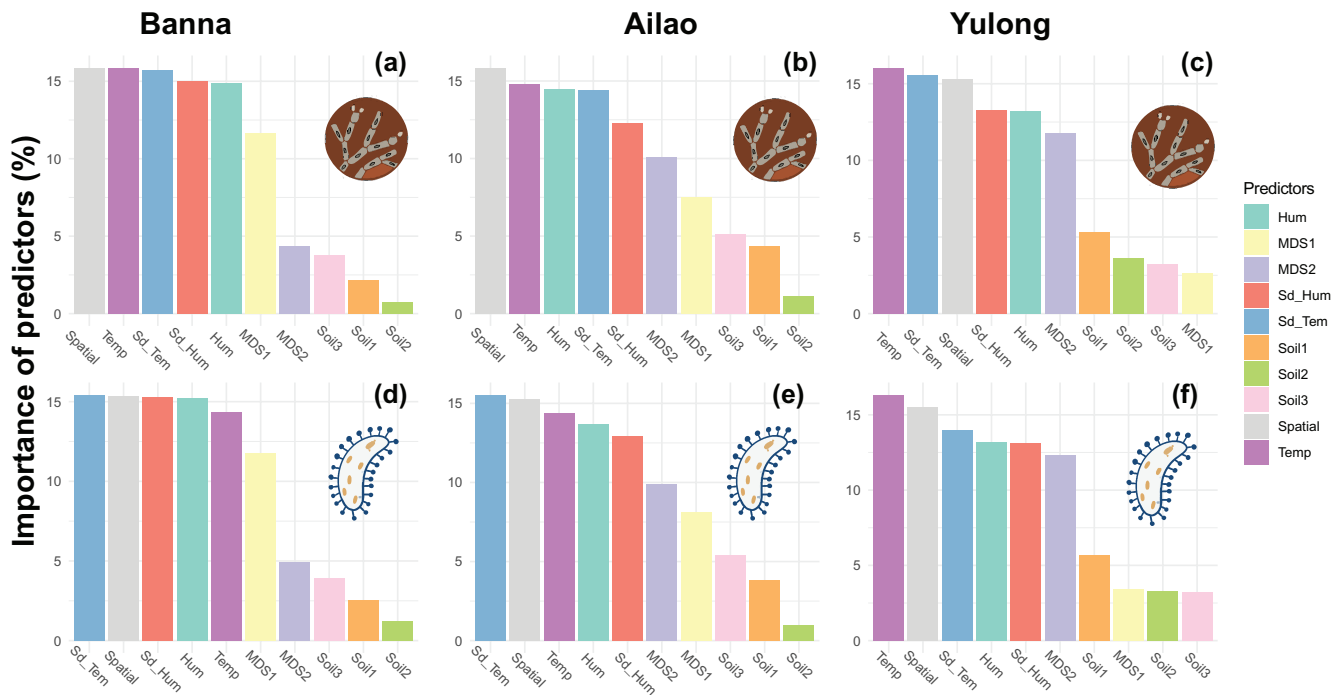
Figure 5. The relative importance of predictors as determined in distance-based redundancy analyses (dbRDA) performed separately for fungal (a–c) and bacterial (d–f) communities. For both bacteria and fungi, the data were analyzed separately for each study site. Spatial: spatial distance, Temp: temperature, Sd_Tem: temperature variability, Hum: air humidity, SD_Hum: humidity variability, Soil1-3: the first three axes of a PCA of soil properties, MDS1-2: the first two axes of a nonmetric multidimensional scaling (NMDS) of plant community composition.

50%), followed by dispersal limitation (Banna: 27%, Ailao: 24%, Yulong: 20%) (Fig. 6d–f).

Discussion

Climate-dominated microbial biogeography in mountains

Since the first study about microbial diversity patterns along an elevation gradient (Bryant et al. 2008), microbial community differences were often best explained by soil properties in mountains, e.g. pH, carbon and nitrogen (Shen et al. 2013, Ren et al. 2018). Only a few studies revealed the dominating drivers of climatic variables on microbial diversity (Wang and Soininen 2017, Xu et al. 2023), which may be caused by the low-resolution macroclimate data (e.g. a raster map resulting from grid-based interpolations) used by previous studies (Feng et al. 2023). In recent years, increasing numbers of studies have supported the view that microclimates are ecologically important in shaping microbial biogeography in mountains (Ma et al. 2022, Xu et al. 2023). We found that local climate and climatic variability play more important roles in affecting microbial β-diversity patterns and range sizes along elevational gradients in three different mountains compared with soil properties and plant compositions. This does not negate the role of soil properties in regulating microbial diversity, but emphasizes that high soil heterogeneity can shape complex patterns of microbial diversity at various

climatic scales (Xu et al. 2023). The weaker importance of plant compositions suggested that soil microbial communities have independent diversity patterns and may be less affected by host plants at regional scales (see Supporting information for detailed discussion). Revealing the role of climate in microbial biogeography along montane gradients is essential for predicting the consequences of climate change.

Testing Janzen's mountain passes hypothesis

Janzen's mountain passes hypothesis and niche theory, in relation to environmental heterogeneity, can potentially explain the sustained high levels of montane biodiversity (Rahbek et al. 2019), especially in tropical regions (Ghalambor et al. 2006). Although empirical testing of Janzen's mountain passes hypothesis has been carried out in various studies (Polato et al. 2018), the regulation of community assembly along montane elevational gradients remains elusive, especially for soil microorganisms. Janzen's hypothesis indicates that low climatic variability and overlap (or higher climatic difference between elevations) creates a narrower distributional range of preferred environmental conditions and favors species with limited dispersal ability that are highly adapted to narrow thermal niches (Janzen 1967). To some extent, Wang and Soininen (2017) and Feng et al. (2023) supported Janzen's hypothesis, i.e. climatic variability shapes microbial range sizes and has a strong influence on the distribution of soil bacteria and fungi, but studies conducted along a climatic variability gradient are still lacking.

Here, we focused on soil bacterial and fungal communities along elevational gradients in three montane ecosystems representing a climatic variability/overlap gradient (i.e. Banna < Ailao < Yulong). Our study addresses an important premise of Janzen's mountain passes hypothesis, which states that climatic differences over a given distance along an elevational gradient are greatest or climatic overlaps are lowest in Banna; and hence that climatic barriers to dispersal are more severe (Janzen 1967). By analyzing bacterial and fungal communities across elevational gradients, we provide direct evidence that Banna has higher β-diversity than Ailao or Yulong mountains (Fig. 3). Distance–decay analysis also reveals that community dissimilarity increased more steeply for Banna than for Ailao or Yulong mountains over elevational distances ranging from 200 to 600 m (Fig. 2a–d). Microorganisms in Banna have lower distributional range sizes than those in Ailao or Yulong. The above biogeographic patterns are significantly affected by climatic variability, climatic difference and spatial distance. Spatial distance is the fundamental unit of species dispersal (Chave 2004). The importance of spatial distance may reflect the crucial role of dispersal limitations in community assembly, which will be linked to the predictions of Janzen's hypothesis. Moreover, the importance of dispersal limitation for microbial community assembly decreased from the site with lower climatic variability and overlap to that with higher climatic variability and overlap, while the importance of environmental selection increased (Fig. 6). These findings suggest that 'mountain passes' in regions with lower climatic variability and overlap are indeed more difficult for microorganisms to cross (Feng et al. 2023), even within the same elevational distance compared with other mountains. Thus, mountains with lower climatic variability and overlap exhibit greater β-diversity, higher endemism, lower range sizes, steeper distance–decay trends and more dispersal limitation over comparable elevational gradients, which ultimately promotes species coexistence and facilitates biodiversity (Huey 1978, Ghalambor et al. 2006).

According to Finlay and Clarke (1999), microorganisms are typically dispersed more variably than larger organisms, with some bacterial and fungal species having diverse distribution patterns over very large distances. This suggests that microbial endemism is not commonly observed at fine taxonomic scales, such as genus or species (Louca 2022). However, we found clear patterns of endemism and constrained range sizes among ASVs (amplicons). The number of endemic ASVs decreased and microbial range sizes increased from Banna to Yulong. This finding suggests that the process of dispersal limitation was more important in Banna than in Ailao and Yulong, supporting Janzen's mountain passes hypothesis. The endemism also decreased and range sizes increased towards high elevations, which can be explained by increasing climatic variability in higher elevations, as theorized by the elevational Rapoport's rule (Stevens 1992) and also represents an extension of the latitudinal Janzen's hypothesis (Polato et al. 2018, Smith 2018).

How do microorganisms in mountains respond to climate change?

We also found some shared microbial biogeographic patterns and mechanisms in three mountains. For example, we found strong microbial community dissimilarity (Supporting
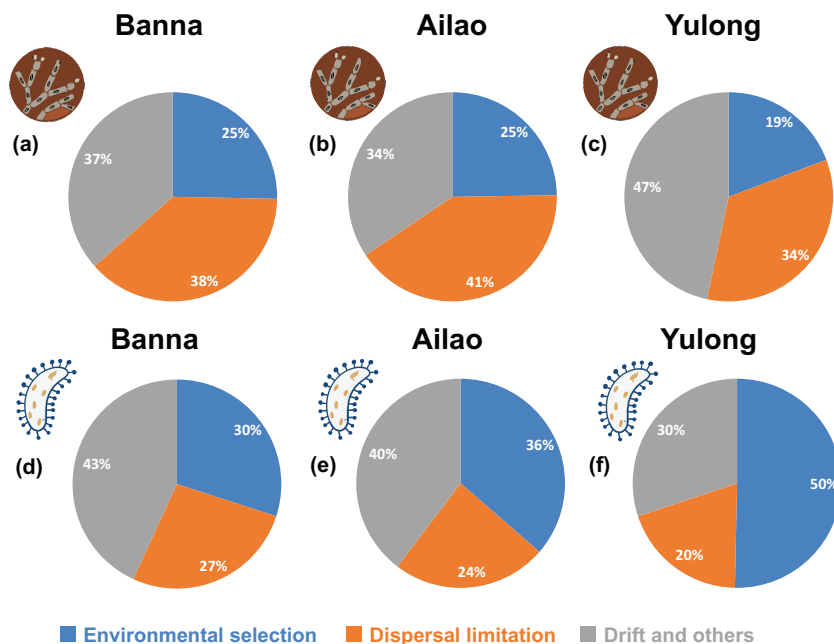

Figure 6. Ecological processes of microbial communities in different sites. The relative importance of dispersal limitation, drift and environmental selection for community assembly as assessed for fungal (a–c) and bacterial (d–f) communities and for each study site individually: (a, d) Banna, (b, e) Ailao and (c, f) Yulong.

information) as well as steep distance–decay relationships in community dissimilarity (Fig. 2) between adjacent elevations (200 m apart) for all study sites. Additionally, more than 80% of ASVs at each site were found only within a single elevational transect (Fig. 2). These results suggest that montane microorganisms' dispersal across elevational gradients may be widely limited by climatic barriers. This study's three montane sites possessed very different environmental conditions (Supporting information) yet showed similar biogeographic patterns. This suggests that a common mechanism may regulate montane microbial diversity across regions. This may explain why many low-latitude mountains exhibit high levels of biodiversity across elevational climate zones (Zhang et al. 2021). Dispersal limitation and environmental selection (based on climatic niches) along elevational gradients are the core ecological processes revealed in this study. We found that spatial distance and climatic factors, particularly climatic variability, were the most important drivers of microbial community composition in all study sites (Fig. 5). Spatial distance can affect stochastic dispersal processes, while climate represents a deterministic environmental filtering (Stegen et al. 2013, 2015). Our community assembly analyses further supported this understanding, as dispersal limitation and environmental selection consistently contributed to shaping microbial community composition across study sites (Fig. 6). These results support the key role of climatic niche processes and dispersal processes driving microbial community dissimilarity at regional scales.

Geographic isolation caused by dispersal limitation can be a significant factor driving biogeographic patterns and evolutionary dynamics (Mueller et al. 2007). Previous research has suggested that dispersal limitation is strongest when geographic distances exceed species dispersal thresholds (Wang et al. 2017). However, our findings reveal that absolute spatial distance is not the only cause of dispersal limitation (all elevational transects were spaced 200 m apart). While greater climatic barriers lead to more significant dispersal limitation, endemism and community dissimilarity, the increased importance of climate-dependent dispersal limitation may contribute to their high levels of species coexistence and biodiversity (Rahbek et al. 2019, Zhang et al. 2021). Overall, climatic barriers coupled with dispersal limitation may be the primary drivers of montane microbial community assembly, particularly for low-latitude mountains with dramatic vertical landscape changes. An important extension of Janzen's hypothesis and our findings considers how montane species may respond to climate change (Smith 2018). As temperatures rise and precipitation patterns shift, the elevational ranges of species may also shift (Donhauser and Frey 2018). The ability of species to disperse or adapt to these changes will determine whether they can survive or not. Some species may be able to expand their ranges into new elevational zones, while others may be pushed to extinction if suitable habitat disappears. Our study provides evidence for extensive dispersal limitation in montane microorganisms, indicating that the survival of many microorganisms will be challenged by climate change, especially for microorganisms in low elevations.

Conclusions

Our current understanding of the maintenance mechanism and diversity of microbial communities is not well understood compared to those of plant and animal species. This has resulted in a dearth of conservation efforts for microbial diversity despite the existing risks (Guerra et al. 2020). Our limited understanding of microbial biogeography makes it difficult to determine what should be conserved and what has already been lost (Bodelier 2011). Here, we show that: 1) climate (e.g. climatic differences or overlap between elevations), climatic variability and spatial distance play dominating roles in affecting microbial β-diversity patterns and range sizes along elevational gradients in mountain ecosystems; 2) Janzen's mountain passes hypothesis can be applied for microbial community assembly: mountains with lower climatic variability and overlap exhibited higher β-diversity, higher endemism, lower range sizes, steeper distance–decay trends and more dispersal limitation; 3) both dispersal limitation and environmental selection were dominant processes shaping montane microbial biodiversity; and 4) ubiquitous dispersal limitations and constrained range sizes were identified for montane microorganisms, suggesting that microorganisms face significant risks from climate change. Improving our understanding of the ecological mechanisms shaping microbial biogeography may be invaluable for conservation decision making to protect and restore biodiversity at regional to global scales.

Author contributions

Yazhou Zhang: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (lead); Software (lead); Supervision (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal).
J. Aaron Hogan: Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing

(equal). **Thomas W. Crowther**: Conceptualization (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Shijia Xu**: Investigation (equal); Methodology (equal); Visualization (equal). **Rensheng Zhao**: Investigation (equal); Methodology (equal). **Pengfei Song**: Investigation (equal). **Mufeng Cui**: Investigation (equal); Methodology (equal). **Xiaoyang Song**: Investigation (equal). **Min Cao**: Investigation (equal). **Jie Yang**: Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Writing – original draft (lead); Writing – review and editing (lead).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4b8gthtk2 (Zhang et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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