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Contrasting mechanisms of non-vascular and vascular plants on spatial turnover in multifunctionality in the Antarctic continent

Hanwen Cui[1] | **Shuyan Chen**[2] | **Hongxian Song**[2] | **Ziyang Liu**[1] | **Jingwei Chen**[1] | **Anning Zhang**[2] | **Sa Xiao**[1] | **Xiaoxuan Jiang**[1] | **Zi Yang**[2] | **Xin Li**[2] | **Lizhe An**[2,3] | **Haitao Ding**[4] | **Fons van der Plas**[5]

[1]State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, College of Ecology, Lanzhou University, Lanzhou, Gansu, People's Republic of China

[2]Key Laboratory of Cell Activities and Stress Adaptations Ministry of Education, School of Life Sciences, Lanzhou University, Lanzhou, Gansu, People's Republic of China

[3]College of Forestry, Beijing Forestry University, Beijing, People's Republic of China

[4]Antarctic Great Wall Ecology National Observation and Research Station, Polar Research Institute of China, Ministry of Natural Resources, Shanghai, People's Republic of China

[5]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands

Correspondence
Sa Xiao
Email: xiaos@lzu.edu.cn

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Abstract

1. Dominant plants play crucial roles in supporting the functioning of terrestrial ecosystems. Plants can influence the spatial heterogeneity of environmental factors, as well as the spatial turnover in the composition of soil communities (i.e. β-diversity of soil communities). However, we still poorly understand how dominant plants drive the spatial turnover in multiple ecosystem functions (β-multifunctionality hereafter), and to which extent the effects of dominant plants are mediated by changes in environmental heterogeneity and the β-diversity of soil communities.
2. Antarctica supports one of the most challenging environments on the planet including low temperature and water availability. Here, we collected soil samples under three dominant plants (lichen, moss and vascular plants) and bare ground. We measured carbon storage, nutrient availability, nutrient decomposition, microbial biomass and pathogen control to calculate β-multifunctionality.
3. Both non-vascular and vascular plants were associated with increased β-multifunctionality compared to bare ground. We further showed that lichen mainly affected β-multifunctionality through soil temperature heterogeneity and β-bacterial diversity. Similarly, moss mainly affected β-multifunctionality through the spatial heterogeneity of soil water content and β-bacterial diversity. However, vascular plants did not significantly affect environmental heterogeneity. Instead, the responses of β-multifunctionality to vascular plants were mainly driven by the β-diversity of soil communities. These results indicate that environmental heterogeneity is important for turnover in multiple ecosystem functions in early successional stages (dominated by non-vascular plants), while the importance of soil communities' heterogeneity becomes more significant in late successional stages (dominated by vascular plants).
4. *Synthesis*. Our findings highlight the fundamental role of dominant plants in controlling the spatial turnover in ecosystem functions, and suggest that accelerated succession under current climate warming may increase bacterial β-diversity but

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Hanwen Cui and Shuyan Chen have contributed equally to this work.

decrease abiotic heterogeneity, thereby leading to both increases (e.g. regarding functions related to microbial biomass) and decreases (e.g. regarding functions related to nutrient availability) in β-multifunctionality and hence the spatial turnover in levels of ecosystem functioning.

KEYWORDS
Antarctica, environmental factors heterogeneity, non-vascular plants, soil communities' heterogeneity, vascular plants, β-multifunctionality

1 | INTRODUCTION

Antarctica is one of the most extreme terrestrial environments supporting cold deserts (Convey & Peck, 2019). Due to the adverse environmental conditions and isolation, plants in the Antarctic continent typically occur in patches, surrounded by bare soil (Colesie et al., 2023). Different patch types occur, characterized by the dominance of non-vascular plants (lichens and mosses) and vascular plants (*Deschampsia antarctica* and *Colobanthus quitensi*), in addition to bare, unvegetated patches (Ball et al., 2022). It has previously been shown that both non-vascular and vascular plants can contribute significantly to nutrient cycling and carbon storage in Antarctic ecosystems (Bragazza et al., 2019). Recent studies indicate that dominant plants also can influence multiple ecosystem functions simultaneously (i.e. α-multifunctionality, Hector & Bagchi, 2007; Wagg et al., 2014). However, dominant plants do not necessarily provide all ecosystem functions at their highest levels (Sasaki et al., 2022). Therefore, even if non-vascular and vascular plants can increase multiple ecosystem functions in Antarctica (Benavent-González et al., 2018), there may be contrasting responses on the spatial turnover of ecosystem multifunctionality (i.e. β-multifunctionality, Jing et al., 2021; Van der Plas et al., 2016), for example, due to the larger intraspecific variation in some specific functional traits of vascular plants compared with non-vascular plants (e.g. moss) (van Zuijlen et al., 2022).

A growing body of studies have explored the mechanisms by which plants drive ecosystem multifunctionality, including through effects of soil biodiversity. For example, soil biodiversity plays a vital role in driving relationships between above-ground plants and soil multifunctionality (Ding et al., 2021; Wang et al., 2023). Many previous studies on soil biodiversity and ecosystem multifunctionality have primarily been based on relatively small-scale manipulative experiments (Luo et al., 2018) and mainly focused on the relationships between α-diversity of soil communities and multifunctionality (Cui et al., 2022), or on the effects of the number or identity of plant species (Delgado-Baquerizo, Trivedi, et al., 2017). However, in addition to species loss or changes in the identity of dominant species (α-diversity change), the homogenization of biotic communities (also known as β-diversity loss) is also a widespread form of biodiversity loss (Sasaki et al., 2022; Zheng et al., 2021). β-diversity loss is defined as biotic communities becoming increasingly similar to each other in their species composition, causing a loss in larger scale biodiversity, and it can be driven by, for example, anthropogenic activities and climate changes. Often, different species support different ecosystem functions (Hector & Bagchi, 2007; Isbell et al., 2011), and therefore, it is expected that when different species are dominant in different sites (i.e. when β-diversity is high), different ecosystem functions are supported in different sites, causing a high spatial turnover in ecosystem functions, that is, β-multifunctionality (Van der Plas et al., 2016). Recent studies have confirmed positive relationships between soil microbial β-diversity and β-multifunctionality (Mori et al., 2016; Wang et al., 2023; Zhao et al., 2024).

In addition to β-diversity, also environmental heterogeneity can be positively related to β-multifunctionality, as sites with different abiotic conditions support different ecosystem functions (Lavorel et al., 2011). Soil heterogeneity has been considered as the basis of soil biodiversity (Nunan et al., 2020). Therefore, environmental factors varying across space directly and indirectly affect the turnover of ecosystem multifunctionality through changes in soil community composition (Martinez-Almoyna et al., 2019; Sasaki et al., 2022). For example, soil temperature heterogeneity is well known to drive heterogeneity in nutrient storage and cycling (Durán et al., 2018), and it is possible that this is mediated by soil community composition. Similarly, the spatial heterogeneity of soil water content not only affects the distribution of microbial communities but also directly influences heterogeneity in nutrient accessibility and availability (Shi et al., 2019; Wang et al., 2021). Furthermore, Wang et al. (2021) indicated that a spatial shift in soil pH is one of the drivers for the spatial variability of soil microbial community structure and enzymatic activities. Hence, both β-diversity and environmental heterogeneity can drive β-multifunctionality, but it remains unclear which of these factors is most important, and to which extent this changes with associated shifts in dominant plants.

Various studies demonstrated the contrasting direction and strength of relationships between different dominant plants and β-multifunctionality (Singh et al., 2018; Wang et al., 2022). The Antarctic continent is one of the most influenced areas by global warming (Li et al., 2021), with similar changes in the amount and frequency of precipitation (Bracegirdle & Stephenson, 2012). Meanwhile, the expansion of ice-free areas caused by climate changes may provide new dispersal and colonization opportunities for native species across Antarctica (Convey & Peck, 2019), which could cause the extensive expansion of vascular plants (Cannone et al., 2016). In this context, it is essential that we better understand the direct and indirect influences of dominant plants, representing different successional stages (from early to late: bare ground, lichen, moss, vascular plant), on the spatial turnover in ecosystem multifunctionality supported by Antarctic ecosystems. Compared with bare areas, non-vascular plants, such as lichens and mosses, can create heterogeneous environmental conditions (Concostrina-Zubiri et al., 2013), while it has also been indicated that vascular plants may have the ability to homogenize habitats (Ceradini & Chalfoun, 2017). Furthermore, vascular plants provide multiple microhabitats for soil communities through their complex root systems, and can thereby increase the spatial heterogeneity (i.e. β-diversity) of soil communities compared with bare ground and non-vascular plants (López-Angulo et al., 2020). Therefore, we hypothesize that non-vascular plants influence β-multifunctionality through their effects on environmental heterogeneity, while vascular plants primarily influence β-multifunctionality through their effects on β-diversity of soil communities (Durán et al., 2018; Hautier et al., 2018; Mori et al., 2018; Wang et al., 2021).

In this study, we assessed 16 functional variables beneath four specific above-ground vegetation types, including three dominant plants (lichen, moss and vascular plant) and bare ground. We classified the variables into five groups of ecosystem functions, associated with carbon storage, nutrient availability, nutrient decomposition, microbial biomass, and pathogen control (Figure 1). We applied piecewise structural equation modelling (SEM) to assess the importance of spatial heterogeneity of environmental factors and soil communities on driving relationships between dominant plants and β-multifunctionality in Antarctica. Here, we specifically assumed that: (1) dominant plants affect β-multifunctionality, due to vegetation-specific effects on environmental heterogeneity and β-diversity of soil communities; and that (2) non-vascular plants affect β-multifunctionality through environmental heterogeneity, while the effects of vascular plants on β-multifunctionality are mainly driven by the β-diversity of soil communities.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

The study was conducted on Fildes Peninsula, which is nearby the Antarctic Great Wall Ecology National Observation and Research Station (62°11′47″–62°12′42″ S, 58°56′28″–59°0′48″ W, Appendix S1: Figure S1). The mean annual temperature is −2.8°C, with the minimum mean monthly temperature −7.8°C in July and the maximum mean monthly temperature 1.5°C in January. The mean annual precipitation is 550 mm. The dominant plants in our experimental site are vascular plants (*Deschampsia antarctica*), accompanying with multiple moss and lichen species.

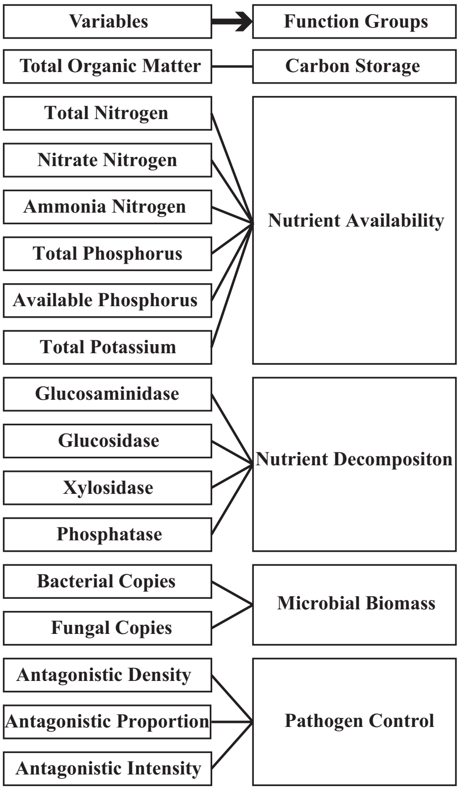

FIGURE 1 Overview of the ecosystem functions studied. Sixteen ecosystem functions beneath four specific above-ground vegetation types were classified into five ecosystem functional groups.

We selected four specific above-ground vegetation types: lichen-dominated (dominated by *Usnea antarctica*), moss-dominated (typically *Sanionia uncinata*) and vascular plant-dominated (*Deschampsia antarctica*) and bare ground. In January 2020, we selected five sites based on previous research about the distribution of *Deschampsia antarctica* on Fildes Peninsula (Yao et al., 2017), as *Deschampsia Antarctica* colonizes only a few areas on Fildes Peninsula. Every site was least 2 km apart. At each site, we established a 50 × 50 m plot and randomly chose five well-developed and single-species patches per vegetation type (>80 × 80 cm of canopy). We collected one soil sample from all patches per vegetation type within each site. To avoid excessive damage to vegetation types, we set up a 30 × 30 cm quadrat underneath each selected patch at least 5 m apart. However, not all sites harboured all above-ground vegetation types: Site 1, Site 2 and Site 3 harboured all above-ground vegetation types, while Site 4 and Site 5 did not have enough area with lichen. Therefore, we had total 90 soil samples (5 bare patches × 5 sites + 5 moss patches × 5 sites + 5 lichen patches × 3 sites + 5 vascular plant patches × 5 sites) in this study. More details about plant characteristics of our study sites can be found in Appendix S1: Section S1 and Table S1. Within each vegetation type, we collected a 200-g soil sample from the top 10–15 cm soil profile. There are previous studies that collected soil samples from the top 10 cm soil profile in Antarctica (Ferrari et al., 2021). However, there were many rocks in our soil samples, especially beneath bare patches. To have sufficiently large soil samples after removing flora residues and rocks, we dug a bit deeper in this study, nearly up to 15 cm. This research was conducted under permits from the National Natural Science Foundation of China (grant number 41830321) and the Antarctic Great Wall Ecology National Observation and Research Station.

2.2 | Quantifying the β-diversity of soil communities

Soil DNA from 90 soil samples was extracted from 0.25 g soil using the PowerSoil® DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). We used 515F/806R (Hathaway et al., 2021) and ITS1f/ITS2 (Coince et al., 2013) to amplify the bacterial V4 region of 16S rRNA and fungal ITS1 region of 18S rRNA, respectively, while protozoan and metazoan V9 region of 18S rRNA were amplified by 1391f/EukBr (Leff et al., 2018). All PCR products were performed paired-end sequencing at Genergy Bio Technology Co., Ltd. (Shanghai, China) by Illumina Novaseq PE250 platform. In particular, sequences with any ambiguous bases or with a mismatch rate >0.2 were removed by Trimmomatic (Bolger et al., 2014). Then, double-ended sequences were denoised using dada2 of QIIME (Callahan et al., 2016). Valid sequences were classified into different operational taxonomic units (OTUs) based on 97% of similarity. Bacterial OTUs were analysed against SILVA database (Quast et al., 2013), fungal OTUs were analysed against UNITE database (Nilsson et al., 2019), while protozoan and metazoan OTUs were analysed against PR^2 database (Guillou et al., 2013) using a confidence threshold of 80%. Bacterial, fungal, protozoan and metazoan OTUs were subsequently rarefied according to the lowest number of bacterial, fungal, protozoan and metazoan sequences, respectively. Finally, we got 36,618 bacterial OTUs, 3078 fungal OTUs, 4245 protozoan OTUs and 421 metazoan OTUs. We assessed bacterial, fungal, protozoan and metazoan β-diversity at OTU levels according to the Bray–Curtis distance by comparing each pair of patches within each vegetation type within each site (Martinez-Almoyna et al., 2019).

2.3 | Measurement of each environmental factors and ecosystem functions

In total, three environmental factors and 16 ecosystem functions were measured on the location where the 90 soil samples were also collected, with one replicate per location (see for details below).

2.3.1 | Measurement of environmental factors

Soil temperature at 5 cm depth was measured with a digital thermometer (Fluke 52II, Fluke, WA, USA). Soil water content was measured by drying 10 g soil for 72 h at 105°C. The remaining soil subsample was air-dried, avoiding direct sunlight. The dried soil samples were sieved to 0.15 mm by a 100 mesh series. Soil pH was measured using a pH meter (PHSJ-3F; Shanghai INESA Scientific Instrument Co., Ltd., Shanghai, China) in a 1:2.5 soil:deionized water slurry.

2.3.2 | Measurement of carbon storage

Soil organic matter can reflect the carbon sequestration capacity of the ecosystem in the long term (Delgado-Baquerizo, Eldridge, et al., 2017). Soil total organic matter was measured using the wet oxidation method (Visconti et al., 2022).

2.3.3 | Measurement of nutrient availability

Soil total nitrogen, total phosphorus and total potassium are build-up of soil nutrient pools that most frequently limit the plant and microbial biomass (Peng et al., 2017). Soil total nitrogen and phosphorus were digested separately using concentrated H_2SO_4 at 375°C for 3 h and 45 min, followed by semi micro-Kjeldahl and Mo-Sb antispetrophotography using an auto chemistry analyser (SmartChem 200; AMS Alliance, Italy) (Tian et al., 2017). Soil total potassium was measured with the flame photometry method after melting with sodium hydroxide (Gao et al., 2017).

Soil nitrate nitrogen, ammonia nitrogen and available phosphorus can reflect important ecosystem process such as nitrification and mineralization (Kutvonen et al., 2015). Soil nitrate and ammonia were extracted by 2 M KCL and measured using the auto chemistry analyser (SmartChem 200; AMS Alliance, Italy) (Zhou et al., 2020). Soil available phosphorus was extracted by 0.5 M $NaHCO_3$ at pH 8.5 and measured using the molybdenum blue method (Zhang et al., 2023).

Since some functions were not independent, we used PC1 scores of soil total nitrogen, nitrate and ammonia to indicate soil nitrogen content, while soil phosphorus content were calculated by PC1 scores of soil total phosphorus and available phosphorus.

2.3.4 | Measurement of nutrient decomposition

Hydrolytic enzyme activities are direct measurement of the carbon, nitrogen and phosphorus cycling function of the ecosystem that is relevant to soil microbes (Gao et al., 2023), including N-acetyl-β-Glucosaminidase (NAG), β-Glucosidase (BG), β-Xylosidase (XYL) and neutral phosphatase (NP) (Liu et al., 2020), were determined by kits (Suzhou Keming Biotechnology Co., Ltd., Suzhou, China). These enzyme activities were measured by detecting colorimetrically. In brief, NAG activity was measured at 400 nm (substrates: N-acetyl-β-D-glucosaminide; product: p-nitrophenol), BG activity was measured at 400 nm (substrates: β-D-glucopyranoside; product: p-nitrophenol), XYL activity was measured at 405 nm (substrates: β-D-xylopyranoside; product: p-nitrophenol) and NP activity was measured at 660 nm (substrates: disodium phenyl phosphate; product: phenol). The enzyme activities were measured in units of μmol day^{-1} g^{-1} dry soil.

2.3.5 | Measurement of microbial biomass

Bacterial copies and fungal copies can reflect the dynamics of soil quality and microbial biomass (Drost et al., 2020). Soil DNA was extracted from 0.25 g soil using the PowerSoil® DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). Bacterial and fungal copies were quantified by the real-time quantitative PCR (qPCR) method with primers 785FL/919R (Nolvak et al., 2012) and BITS/B58S3 (Bokulich & Mills, 2013), respectively. Data were collected and analysed with an ABI Q5 real-time PCR System (Applied Biosystems; Thermo Fisher Scientific, Inc., Cleveland, OH, USA).

2.3.6 | Measurement of pathogen control

Antagonistic density, antagonistic proportion and antagonistic intensity are often used to characterize pathogen antagonism associated with different plant species (Bakker et al., 2013). For each sample, a single 5 g subsample was dried overnight under sterile cheesecloth as the first enrichment for *Streptomyces*. Dried soil samples were dispersed in 50 mL of sterile deionized water on a reciprocal shaker (175 rpm, 60 min, 4°C). Soil dilutions were spread onto 15 mL water agar plates and then covered with 5 mL of cooled, molten starch-casein agar (SCA). After 3 days of incubation (28°C), *Streptomyces* colonies were enumerated as *Streptomyces* density (CFU/g) based on morphology. These plates were also used to assess *Streptomyces* inhibitory activities using a modified Herr's assay (Valverde et al., 2014). To reveal inhibitory zones, colonies on the soil dilution plates were covered with a thin layer (10 mL) of SCA and spread with one of three indicator strains: one plant pathogen (*Streptomyces scabies ACCC 41289*) and two nonpathogenic actinomycete isolates (*Streptomyces avidini* and *Streptomyces olivochromogenes*). Plates were spread with 150 μL of a spore suspension to give approximately 1.5×10^7 colony-forming units (CFU/plate). Three soil dilution plates were spread per indicator strain. Antagonistic activity was quantified after 3 days of incubation (28°C) as antagonistic density and antagonistic proportion that produced a clear zone of inhibition against the overlay isolate. The diameter of each inhibition zone was used as a measure of antagonistic intensity. Values of antagonistic density, antagonistic proportion and antagonistic intensity were averaged across indicator strains for each sample.

2.4 | Quantifying turnover in environmental factors and ecosystem multifunctionality

Three environmental factors and 16 ecosystem functions potentially regulated by soil organisms were included in our study: environmental factors (soil temperature, soil pH and soil water content) and five groups of ecosystem functions related to carbon storage (soil organic matter), nutrient availability (soil nitrogen, phosphorus, and potassium contents), nutrient decomposition (N-acetyl-β-Glucosaminidase, β-Glucosidase, β-Xylosidase and neutral phosphatase), microbial biomass (bacterial copies and fungal copies) and pathogen control (antagonistic indicator, PC1 scores of antagonistic density, antagonistic proportion and antagonistic intensity) (Figure 1). Prior to the calculation of environmental and functional heterogeneity, we Z-transformed the environmental and functional variables (Kim et al., 2016). The spatial heterogeneity of environmental factors (soil temperature, soil pH and soil water content) was measured according to Euclidean distance of these variables by comparing each pair of patches within each vegetation type within each site. Spatial turnover in ecosystem multifunctionality (β-multifunctionality hereafter) and the spatial turnover in five functional groups related to carbon storage, nutrient availability, nutrient decomposition, microbial biomass and pathogen control were calculated based on (multi-dimensional) Euclidean distances of the associated ecosystem functions by comparing each pair of patches within each vegetation type within each site (Jing et al., 2021).

2.5 | Statistical analysis

We used permutation tests with 'Prob' permutation probabilities at significance level of 0.05 for ANOVA (analysis of variance) using the function 'aovp' from the 'lmPerm' package (Wheeler et al., 2022) to assess the effects of dominant plants on (i) β-multifunctionality of all ecosystem functions, (ii) β-multifunctionality of each ecosystem functional group and (iii) the spatial turnover in individual ecosystem function as well as (vi) the spatial heterogeneity of environmental factors and (v) the β-diversity of multi-trophic soil communities. Furthermore, we constructed a PCA (principal component analysis) where each data point is a plot per vegetation type, and each fitted variable is an ecosystem function, to show the differences in ecosystem function beneath four specific above-ground vegetation types among different sites. In addition, by repeating our permutation tests after systematically removing each of the ecosystem function separately, we assessed the sensitivity of β-multifunctionality patterns beneath four specific above-ground vegetation types to specific ecosystem functions. We treated 'dominant plant species' as a categorical variable with four levels representing different vegetation types in permutation tests. Mann–Whitney *U*-tests with 'Benjamini–Hochberg' corrections were performed to assess posteriori multiple pairwise comparison.

We used piecewise SEM to tease apart the relative importance of vegetation-driven heterogeneity (Euclidean distance) in environmental factors, and vegetation-driven β-diversity (Bray–Curtis distance) of bacteria, fungi, protozoa and metazoa on the spatial turnover in ecosystem multifunctionality (i.e. β-multifunctionality) following a priori developed, theoretical SEM model (Appendix S1: Figure S1). Three different SEMs were run, to compare the effects of (i) lichen patches, (ii) moss patches and (iii) vascular plant patches with those of bare ground. Within each piecewise SEM, we investigated how plant patches influenced β-multifunctionality either directly or indirectly through changes in environmental heterogeneity and/or β-diversity of soil communities. We applied the 'lme' function to take into account the effects of sites on β-multifunctionality. We treated 'dominant plant species' (converted 'bare ground' to '0', and 'plant patches' to '1') as a fixed effect and 'site' (five categorical variables representing different sites) as a random effect. Prior to running SEMs, we tested normal distribution and homogeneity of variance of the residuals of indices used in SEMs, and we sqrt-transformed the indices that did not meet these assumptions. The goodness of fit was assessed using Fisher's *C* test (Shipley, 2009). All the data were analysed with R 4.1.0. with the 'NST', 'vegan', 'lmPerm', 'multcompView', 'rcompanion', 'car', 'performance', 'nlme', 'piecewiseSEM', 'ggplot2' packages.

3 | RESULTS

3.1 | Spatial turnover in ecosystem multifunctionality and ecosystem functional groups beneath non-vascular and vascular plants

We explored the effects of three dominant plants on the turnover of ecosystem functional groups, as well as on β-multifunctionality. Overall, our results suggest that both non-vascular and vascular plants in Antarctica are associated with higher β-multifunctionality compared to bare ground, but we did not observe significant differences among the three dominant plants ($p<0.001$, Figure 2a; Appendix S1: Table S1). Furthermore, the results of PCA showed that the points representing 'bare ground' showed an aggregated distribution, while the points representing 'vascular plant' presented a more variable distribution (Figure 3), indicating that plants, and particularly vascular plants, had more differences in ecosystem function values among different sites compared to unvegetated patches. Meanwhile, we found that high values of bacterial copies, soil phosphorus and potassium contents were associated with lichen patches, and high values of soil organic matter, soil nitrogen content, N-acetyl-β-Glucosaminidase and antagonistic indicator were associated with moss patches, while high values of β-Glucosidase, β-Xylosidase, neutral phosphatase and fungal copies were associated with vascular plant patches (Figure 3). Our sensitivity analyses showed that the results of β-multifunctionality were robust to the removal of most ecosystem functions. Specifically, while removing N-acetyl-β-Glucosaminidase, caused that there were no significant differences anymore between moss and bare ground ($p=0.002$), and removing fungal copies caused that there were no significant differences anymore between vascular plants and bare ground ($p<0.001$), removing other ecosystem functions did not lead to any qualitative differences in our results (Appendix S1: Figure S1 and Table S1).

We found that the spatial turnover in carbon storage ($p<0.001$) and microbial biomass ($p<0.001$) was higher when dominant plants were present compared with bare ground (Figure 2b–e; Appendix S1: Table S1). Both non-vascular and vascular plants significantly improved the turnover of soil organic matter ($p<0.001$), bacterial copies ($p=0.035$) and fungal copies ($p<0.001$), except that moss patches had no significant effect on fungal copies heterogeneity (Appendix S2: Figure S3a,l,m and Table S3). Furthermore, lichen had significant effects on the spatial turnover in nutrient availability ($p<0.001$, Figure 2c; Appendix S1: Table S1). Specifically, lichen had a higher spatial turnover of total nitrogen compared to bare patches ($p<0.001$). Similarly, vascular plants significantly increased the heterogeneity of soil total nitrogen, while the heterogeneity of soil nitrate was lower than on non-vascular plants ($p=0.053$) (Appendix S2: Figure S3b,c,e and Table S3). Furthermore, non-vascular plants had a higher turnover of N-acetyl-β-Glucosaminidase ($p<0.001$) and β-Glucosidase activities ($p<0.001$) (Appendix S2: Figure S3h,i and Table S3).

3.2 | Contrasting mechanisms of non-vascular and vascular plants on β-multifunctionality

We observed that non-vascular plants had significant effects on the spatial heterogeneity of environmental factors. Specifically, lichen positively influenced soil temperature heterogeneity ($p<0.001$), while lichen and moss significantly improved soil water content heterogeneity ($p<0.001$). However, there were no significant differences in environmental heterogeneity between bare ground and vascular plants (Appendix S2: Figure S4 and Table S4).

We found that non-vascular and vascular plants significantly improved β-bacterial diversity compared with bare ground, and bacterial β-diversity was higher on vascular plants than on other plant types ($p<0.001$). Moreover, moss and vascular plants significantly decreased β-metazoan diversity ($p<0.001$). However, we did not observe significant differences of β-fungal diversity ($p=0.016$) and β-protozoan diversity ($p=0.123$) beneath four specific vegetation types, except that moss patches decreased β-fungal diversity (Figure 4; Appendix S2: Table S5).

The results of piecewise SEM models showed that lichen had significantly positive effects on β-multifunctionality through the spatial heterogeneity of soil temperature and β-bacterial diversity (Figure 5a; Appendix S2: Tables S6 and S7). Similarly, moss indirectly affected β-multifunctionality through soil water content heterogeneity and β-bacterial diversity (Figure 5b; Appendix S2: Tables S8 and S9). Furthermore, β-multifunctionality was significantly positively related to the heterogeneity of soil pH within vascular plants, but vascular plants did not significantly affect environmental heterogeneity. Instead, vascular plants affected β-multifunctionality mainly by biotic pathways. Specifically, vascular plants had significantly positive effects on β-multifunctionality through β-bacterial diversity. Moreover, vascular plants directly and indirectly affected β-protozoan diversity through β-diversity of bacteria, fungi and metazoa, further influencing β-multifunctionality (Figure 5c; Appendix S2: Tables S10 and S11).

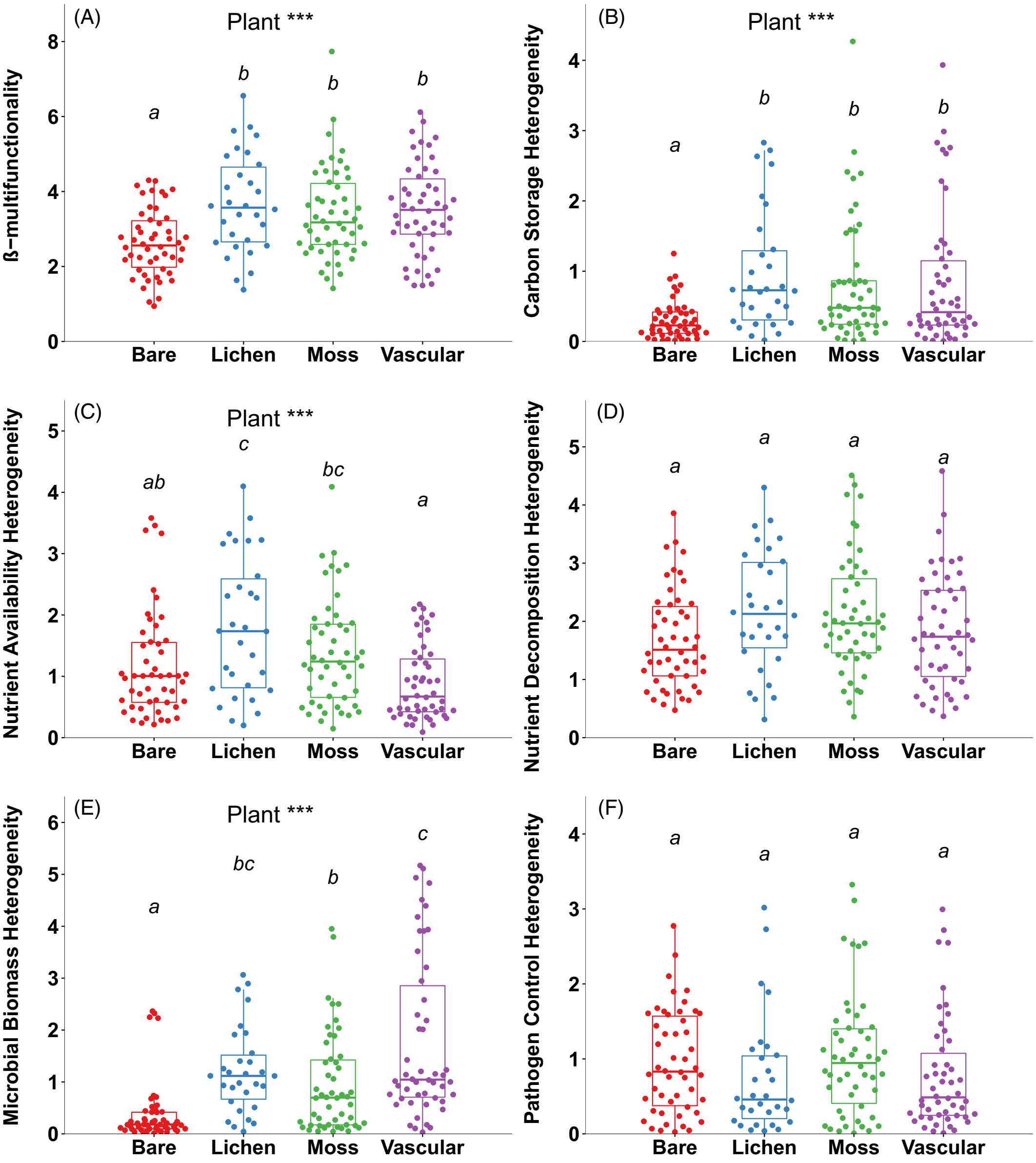

FIGURE 2 Boxplots show the spatial turnover in ecosystem multifunctionality and functional groups (A, β-multifunctionality; B, carbon storage heterogeneity; C, nutrient availability heterogeneity; D, nutrient decomposition heterogeneity; E, microbial biomass heterogeneity; F, pathogen control heterogeneity) beneath four specific above-ground vegetation types. Points represent Euclidean distances of ecosystem functional groups by comparing each pair of patches within each vegetation type within each site. Results of permutation test are shown above. Lowercases adjacent to boxplot indicate significant differences between treatments according to the Mann–Whitney *U*-tests with 'Benjamini–Hochberg' corrections at $p < 0.05$. ***, $p < 0.001$.

4 | DISCUSSION

4.1 | Similarities and differences between effects of non-vascular and vascular plants on β-multifunctionality

Our results provided evidence that both non-vascular and vascular plants had the potential to enhance the spatial turnover in ecosystem multifunctionality (Figure 2a). A few previous studies have also shown greater overall β-multifunctionality beneath plants than beneath bare ground (Legay et al., 2016; Zuo et al., 2009), although these did not further investigate which mediating factors were driving this. Furthermore, we observed similarities and differences between effects of non-vascular and vascular plants on the spatial heterogeneity of different ecosystem functional groups (Figure 2b–f).

We found that both non-vascular and vascular plants significantly increased the spatial turnover in carbon storage and microbial biomass (Figure 2b,e). The positive associations of dominant plants with greater spatial heterogeneity of soil carbon storage and microbial biomass are similar to patterns previously observed in other studies (Koteen et al., 2015; Štursová et al., 2016; Zhou et al., 2017). Compared to bare ground, plants are expected to have higher spatial turnover in soil organic matter and total nitrogen content due to large differences among plants in nutrient input and decomposition rates of litter (Bambrick et al., 2010;

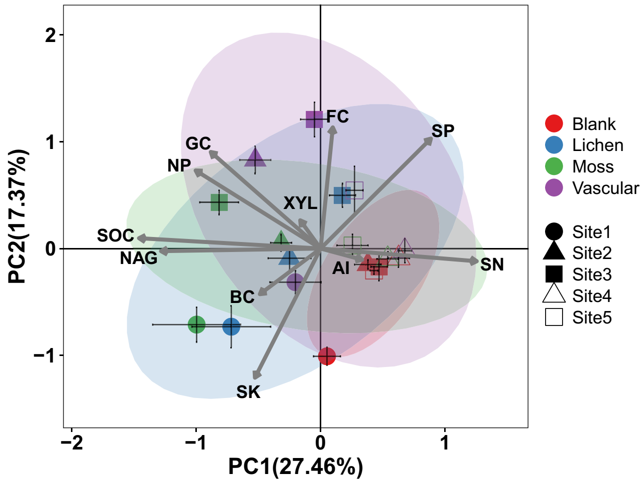

FIGURE 3 Loading of ecosystem functions along the first two axes derived from a principal component analysis (PCA) beneath four specific above-ground vegetation types in five sites of Fildes Peninsula in Antarctica. Each data point is a plot per vegetation type, and each fitted variable is an ecosystem function (grey arrows). Shaded areas show 95% confidence interval. AI, antagonistic indicator; BC, bacterial copies; FC, fungal copies; GC, β-Glucosidase; NAG, N-acetyl-β-Glucosaminidase; NP, neutral phosphatase; SK, soil potassium content; SN, soil nitrogen content; SOC, soil organic matter; SP, soil potassium content; XYL, β-Xylosidase.

Benavent-González et al., 2018). Furthermore, the increased litter nutrient heterogeneity induced by dominant plants promotes more varied resource niches (Santonja et al., 2017), thus improving the levels of microbial abundance heterogeneity (Xiao et al., 2020).

Our PCA and sensitivity analyses showed that N-acetyl-β-Glucosaminidase was a driver of the relationship between non-vascular plants (moss) and β-multifunctionality, while fungal copies played an important role on the response of β-multifunctionality to vascular plants (Figure 3). In contrast to vascular plants, non-vascular plants increased spatial heterogeneity in N-acetyl-β-Glucosaminidase and β-Glucosidase activities (Figure S3h,i), which is in line with previous studies (Sedia & Ehrenfeld, 2006). Benavent-González et al. (2018) showed that enzyme activities are highly related to soil temperature and soil water content, which explains our finding that increased spatial heterogeneity in these abiotic factors under non-vascular plants led to a higher β-multifunctionality. Furthermore, we found the turnover of fungal copies was higher on vascular plants than on other plant types (Figure S3m). Fungal abundance is related to plant functional traits (Ochoa-Hueso et al., 2018), and therefore, higher intraspecific variation in functional traits in, for example, specific leaf area in vascular plants than in non-vascular plants (van Zuijlen et al., 2022), is a potential explanation for increased heterogeneity in fungal abundance under vascular plants.

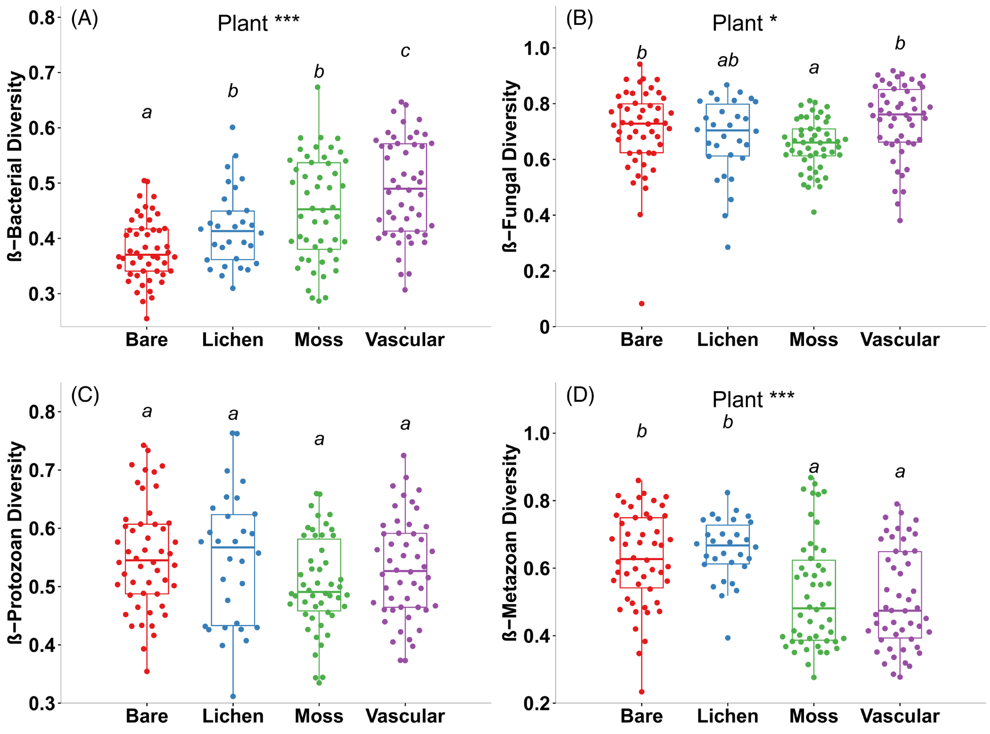

FIGURE 4 Boxplots show the β-diversity of multi-trophic soil communities (A, β-bacterial diversity; B, β-fungal diversity; C, β-protozoan diversity; D, β-metazoan diversity) beneath four specific above-ground vegetation types according to Bray–Curtis distance. Points represent Bray–Curtis distances of multi-trophic soil communities by comparing each pair of patches within each vegetation type within each site. Results of permutation test are shown above. Lowercases adjacent to boxplot indicate significant differences between treatments according to the Mann–Whitney *U*-tests with 'Benjamini–Hochberg' corrections at $p < 0.05$. *, $p < 0.05$; ***, $p < 0.001$.

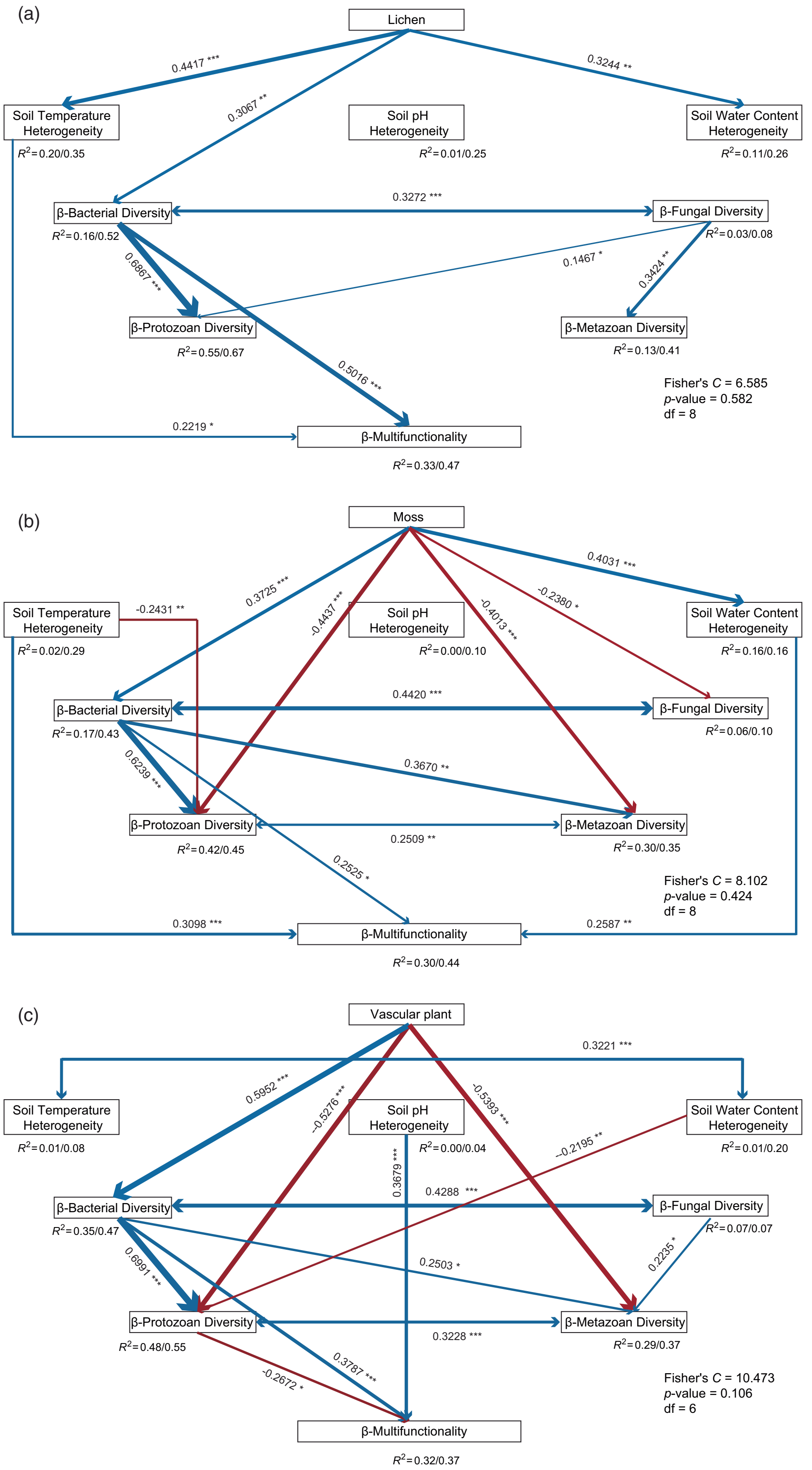

FIGURE 5 Standardized effects of dominant plants (a, lichen; b moss; c, vascular plant) on β-multifunctionality compared to bare ground through the spatial heterogeneity of environmental factors and the β-diversity of multi-trophic soil communities. Positive effects are revealed by blue solid arrows, while negative effects are shown by red solid arrows. R^2 accompanied with response variables indicates the proportion of explained variation (Marginal R^2/Conditional R^2). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

4.2 | Relative importance of environmental heterogeneity and β-diversity of soil communities in mediating dominant plant effects on β-multifunctionality

We found that non-vascular plants affected the turnover of ecosystem multifunctionality through environmental heterogeneity (Figure 5a,b), as environmental heterogeneity was relatively high beneath non-vascular plants and promoted the spatial turnover in multiple ecosystem functions (Martinez-Almoyna et al., 2019). Specifically, lichen positively affected β-multifunctionality through increasing the spatial turnover in soil temperature (Figure 5a; Figure S4a). Previous studies have shown that soil temperature beneath lichen is negatively related to its mat density (Ellis et al., 2021; van Zuijlen et al., 2020), although it is possible that these effects vary among lichen species. There were multiple lichen species with different mat densities in our study, which may have caused the greater soil temperature heterogeneity beneath lichen. Furthermore, mosses had positive effects on β-multifunctionality through increasing heterogeneity of soil water content (Figure 5b; Figure S4c), which is line with previous studies (Benavent-González et al., 2018; Sedia & Ehrenfeld, 2005). Compared with bare ground, mosses have greater surface roughness and soil porosity (Chamizo et al., 2016), which can increase their ability to absorb soil water (Sun et al., 2021) and increase soil water retention. Differences among moss species in their ability to improve water retention may have caused increased heterogeneity in soil water content, with consequences for the spatial turnover in ecosystem functioning.

Similar to non-vascular plants, there was still strong drivers of the spatial heterogeneity of environmental factors on β-multifunctionality beneath vascular plants, as a high environmental heterogeneity could provide different levels of nutrient storage and availability at different locations (Qiao et al., 2023). However, despite significant responses of β-multifunctionality to heterogeneity of soil pH, vascular plants had non-significant effects on soil pH heterogeneity (Figure 5c; Figure S4). Compared to rootless, poikilohydric and poikilothermic non-vascular plants such as mosses and lichens, vascular plants could create a stable, enclave-like environment (Casanova-Katny et al., 2014), which non-vascular plants cannot. Meanwhile, rather than only one vascular species, there were multiple non-vascular species in our study. Different species may adapt to different habitats, leading to the greater environmental heterogeneity beneath non-vascular plants. Our results showed that vascular plants affected β-multifunctionality mainly by the β-diversity of soil communities (Figure 5c). The importance of the β-diversity of soil communities on the turnover of ecosystem multifunctionality has been shown by previous studies (Jing et al., 2021; Mori et al., 2016; Wang et al., 2023) that show that soil communities can mediate effects of dominant plants on β-multifunctionality, especially through bacterial pathways (Figures 4a and 5c) (Zhao et al., 2024). This is in line with our results (Figure 5), where spatial variation in bacterial community composition (β-diversity) mediates effects of dominant plants on β-multifunctionality. Therefore, while in young successional stages, the dominant (non-vascular) plants affect β-multifunctionality through heterogeneity in environmental factors, by ameliorating microclimatic conditions in some, but not across all sites (Concostrina-Zubiri et al., 2013); the importance of soil β-diversity in mediating effects of dominant (vascular) plants on spatial turnover in ecosystem functioning becomes greater in late successional stages (Bu et al., 2014), particularly the cascading effects among soil communities.

While ecosystem multifunctionality has received increased attention recently, it remains relatively poorly understudied in the Antarctic ecosystem due to the adverse environmental conditions and isolation (Ball et al., 2022). This is particularly the case for spatial turnover in ecosystem multifunctionality (i.e. β-multifunctionality), which is still highly understudied. Yet, the contrasting mechanisms by which β-multifunctionality responds to different dominant plants highlight changes in the relative importance of vegetation-driven heterogeneity in environmental factors, versus vegetation-driven β-diversity of soil communities, over succession. Our results showed that non-vascular plants affected β-multifunctionality through increasing environmental heterogeneity, while the effects of vascular plants on β-multifunctionality were mainly driven by increases in the β-diversity of soil communities. Thus, the 'greening' of Antarctica in response to climate change, particularly the extensive expansion of vascular plants (Cannone et al., 2016; Convey & Peck, 2019) will likely result in increased heterogeneity of bacterial communities in the soils (but decreased abiotic heterogeneity), with important consequences for spatial turnover in the provision of multiple ecosystem functions. While the spatial turnover of some ecosystem functions is expected to increase (e.g. those related to microbial biomass), heterogeneity of others may decrease (e.g. functions related to nutrient availability). At the same time, exact changes are challenging to predict, due to, for example, the possibility of the arrival and spread of exotic (vascular) plant species following climate change, which may have different effects on abiotic heterogeneity and microbial communities than the current dominant plants. Consequently, further research on the links between plants, microbial communities, abiotic conditions and ecosystem multifunctionality is direly needed to accurately predict the potentially strong, but largely unknown consequences of changing species distribution for soil and ecosystem functioning in Antarctica.

5 | CONCLUSIONS

Altogether, our findings provide strong empirical evidence that (i) both non-vascular and vascular plants promote spatial turnover in ecosystem multifunctionality in Antarctician terrestrial ecosystems, and that (ii) Antarctic dominant plants differ in the mechanisms by which they promote spatial turnover in ecosystem multifunctionality. By increasing β-multifunctionality, both vascular and non-vascular plants also have the ability to promote larger scale ecosystem multifunctionality in Antarctica, as a high spatial turnover in ecosystem functioning allows multiple ecosystem functions to be provided at high levels in at least some patches within larger landscapes (Van der Plas et al., 2016). We also observed that heterogeneity in environmental factors is important for spatial turnover in multiple ecosystem functions in early successional stages, while the importance of soil communities' heterogeneity becomes more significant in late successional stages. Hence, the accelerated vegetation succession on the Antarctic continent in response to current climate change projections will result in altered soil function heterogeneity, and may cause that soil community composition, that is, β-diversity will become increasingly important in driving future ecosystem function heterogeneity.

AUTHOR CONTRIBUTIONS

Ziyang Liu and Lizhe An designed the study; Shuyan Chen, Haitao Ding and Sa Xiao performed the field measurement, while Hongxian Song, Jingwei Chen, Xin Li and Anning Zhang performed the laboratorial measurement. Xiaoxuan Jiang and Zi Yang performed statistical analysis and made the figures. Hanwen Cui and Fons van der Plas drafted the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14346.

DATA AVAILABILITY STATEMENT

The data supporting the results in this paper are available from the Figshare: https://doi.org/10.6084/m9.figshare.25303873 (Cui et al., 2024). Codes are available from the corresponding author upon request (the codes are not for novel analyses and are based on existing r packages).

ORCID

Hanwen Cui https://orcid.org/0000-0002-3126-811X
Shuyan Chen https://orcid.org/0009-0001-2281-7674
Sa Xiao https://orcid.org/0000-0002-8427-752X
Fons van der Plas https://orcid.org/0000-0003-4680-543X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Plant characteristics of our study sites.

Figure S1: A priori model of piecewise structural equation modelling showing how dominant plants may impact the spatial turnover in ecosystem multifunctionality (i.e. β-multifunctionality) through the spatial heterogeneity of environmental factors and the β-diversity of multi-trophic soil communities.

Figure S2: Boxplots show the sensitivity of β-multifunctionality patterns beneath four specific aboveground vegetation types by removing each of the ecosystem function separately.

Figure S3: Boxplots show the spatial turnover in individual ecosystem function beneath four specific aboveground vegetation types.

Figure S4: Boxplots show the spatial heterogeneity of environmental factors beneath four specific aboveground vegetation types.

Table S1: Permutation tests show the spatial turnover in ecosystem multifunctionality and functional groups beneath four specific aboveground vegetation types.

Table S2: Permutation tests show the sensitivity of β-multifunctionality patterns beneath four specific aboveground vegetation types by removing each of the ecosystem function separately.

Table S3: Permutation tests show the spatial turnover in individual ecosystem function beneath four specific aboveground vegetation types.

Table S4: Permutation tests show the spatial heterogeneity of environmental factors beneath four specific aboveground vegetation types.

Table S5: Permutation tests show the β-diversity of multi-trophic soil communities beneath four specific aboveground vegetation types according to Bray–Curtis distances.

Table S6: Normal distribution and homogeneity of variance of the residuals of indices used in SEM model, which is compared between bare ground and lichen.

Table S7: Standardized coefficients of all hypothesized causal relationships and their significance levels for SEM model which is compared between bare ground and lichen.

Table S8: Normal distribution and homogeneity of variance of the residuals of indices used in SEM model, which is compared between bare ground and moss.

Table S9: Standardized coefficients of all hypothesized causal relationships and their significance levels for SEM model which is compared between bare ground and moss.

Table S10: Normal distribution and homogeneity of variance of the residuals of indices used in SEM model, which is compared between bare ground and vascular plant.

Table S11: Standardized coefficients of all hypothesized causal relationships and their significance levels for SEM model which is compared between bare ground and vascular plant.

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