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Mechanisms of the Effects of Soil Amendments on Ecosystem Multifunctionality in Alpine Meadows at Different Degradation Stages

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Abstract

Currently, soil amendments are extensively employed in degraded grassland restoration research, but we know little about how soil amendments regulate degraded grassland ecosystem functions and their underlying regulatory mechanisms. We therefore conducted a field experiment across alpine meadows of varying degradation intensities on the Qinghai-Tibet Plateau, applying three soil amendments: humic acid (HA), superabsorbent resin potassium salt (K-SAP), and Bacillus subtilis (B. subtilis) at different concentration levels. Quantification of multiple ecosystem function indicators revealed pronounced stage-dependent effects of soil amendments on ecosystem multifunctionality (EMF) across the degradation gradient. In mildly degraded meadows, amendments primarily operated through optimization of dominant species performance and litter dynamics, yielding a 3.0% enhancement in EMF, whereas with increasing degradation intensity, amendment effects transitioned toward comprehensive enhancement of biomass production and α-diversity, especially in the severely degraded stage, where the EMF enhancement effect reached 31.6%. Bayesian structural equation modeling (BSEM) revealed fundamental shifts in EMF drivers across the degradation continuum: transitioning from synergistic soil nutrient-biomass coupling in mildly degraded systems (R^2=51%), to soil nutrient dominance in moderately degraded conditions (β=6.02, R^2=62%), ultimately pivoting to vegetation diversity as the primary driver in severely degraded ecosystems (β=3.32, R^2=46%). Additionally, soil nutrient pools and enzymatic activities exhibited complex trade-off relationships rather than consistent synergistic responses to amendments across the degradation spectrum. Consequently, we propose a "precision-matching" restoration framework for alpine

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grasslands: low-dose HA or B. subtilis for functional optimization in mildly degraded stages; high-dose HA or K-SAP to overcome nutrient-water dual constraints in moderately degraded systems; and high-dose B. subtilis application to reconstruct biological functionality in severely degraded ecosystems. This study provides critical scientific evidence and a theoretical framework for transitioning degraded grassland management from a "one-size-fits-all" approach toward a new "precision restoration" paradigm.

Keywords: Alpine meadow degradation; Soil amendments; Soil properties; Enzyme activity; Vegetation structure; Ecological restoration

Introduction

The Qinghai–Tibetan Plateau (QTP) encompasses the largest alpine grassland ecosystem in Eurasia (Cai et al., 2014; Dong and Sherman, 2015; Geng et al., 2012). These alpine grasslands serve as primary forage resources for livestock production (Wang et al., 2017) while delivering essential ecosystem services including climate regulation (Xu et al., 2018), biodiversity conservation (Chen et al., 2021; Jing et al., 2022), and hydrological storage (Guo et al., 2021; Li et al., 2021). However, this fragile ecosystem has undergone significant degradation since the 1950s (Shang et al., 2014), with 30% to 50% of the grasslands showing severe deterioration (Wang et al., 2022), precipitating cascading ecological crises. Converging evidence demonstrates that soil nutrient depletion and stoichiometric imbalances, exacerbated by climate warming and overgrazing, constitute the primary drivers underlying grassland degradation on the QTP (Li et al., 2014; Peng et al., 2018; Wen et al., 2013). Moreover, a comprehensive meta-analysis encompassing 3,666 experimental observations demonstrated that ecological constraints differ across degradation stages, with restoration interventions yielding heterogeneous effects on plant diversity and edaphic properties (Li et al., 2023), thus necessitating stage-specific amendment strategies.

Traditional restoration approaches implemented over the past two decades—encompassing grazing exclusion, reseeding, and chemical fertilization—have yielded notable advances in alpine meadow rehabilitation. Nevertheless, these conventional strategies have revealed critical limitations and unintended consequences. Long-term grazing exclusion, while temporally demanding, frequently fails to enhance vegetation and soil properties and paradoxically intensifies grazing pressure in adjacent non-exclosed areas (Sun et al., 2020). Furthermore, chemical fertilization of severely degraded grasslands can exacerbate nutrient leaching and contribute to aquatic eutrophication (Liu et al., 2018). These constraints underscore the urgent need for innovative restoration strategies that address stage-specific degradation mechanisms. In contrast, soil amendments offer targeted solutions by simultaneously improving multiple

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soil properties and can be tailored to address specific constraints at different degradation stages. Soil amendments refer to a class of compounds that can improve the physical, chemical and biological properties of the soil, such as lime-based materials, minerals, industrial by-products, organic materials, and biochar. These materials function through multiple mechanisms: pH modulation, structural improvement, nutrient retention enhancement, microbial community optimization, and enzyme activity stimulation, collectively establishing conducive microenvironments for plant establishment (Wallace, 2020). Contemporary applications of soil amendments in agriculture and ecological restoration have consistently demonstrated measurable improvements in soil quality metrics and ecosystem functioning. Empirical evidence confirms that soil amendments enhance plant species richness, evenness, and compositional diversity through nutrient enrichment pathways, ultimately augmenting vegetation coverage (Liu et al., 2024; Wang et al., 2025).

Drawing from ecological stoichiometry theory and the stress gradient hypothesis, we propose a conceptual framework wherein amendment efficacy is contingent upon the congruence between their functional attributes and stage-specific ecological constraints. Principal amendment categories include humic acid (HA), superabsorbent resin potassium salt (K-SAP), Bacillus subtilis (B. subtilis) and biochar. Each amendment category exhibits distinctive mechanistic pathways. HA function through: (1) root exudate stimulation, amplifying rhizosphere microbial populations by up to 256% (Sellamuthu and Govindaswamy, 2003); (2) upregulation of antioxidant enzyme systems (peroxidase, catalase, superoxide dismutase) while suppressing malondialdehyde accumulation and membrane permeability, thereby enhancing stress resilience (Akladious and Mohamed, 2018; Nikbakht et al., 2008; Suh et al., 2014); (3) pH buffering and nutrient retention enhancement via high cation exchange capacity (CEC) and acidic functional groups (Akladious and Mohamed, 2018; Nikbakht et al., 2008; Suh et al., 2014) ; and (4) phosphorus mobilization through hydroxyl-mediated complexation with ammonium phosphate, increasing P availability by 25–40% (Zhang et al., 2017). Research indicates that HA application stimulates soil metabolic enzymes—dehydrogenase and alkaline phosphatase activities increased by 31.9 % and 25.9 %, respectively (Li, 2023), consequently accelerating germination rates and seedling establishment (Bayat et al., 2021; Fahramand et al., 2014).

K-SAP constitute three-dimensional cross-linked hydrogels containing hydrophilic functional groups (hydroxyl, carboxyl) capable of absorbing water up to 400 times their mass, forming interparticle water-blocking layers that substantially reduce evaporative losses and deep percolation. This weak-bond-mediated controlled-release mechanism ensures sustained water provision during moisture deficit periods, effectively extending the plant-available water window (Cao et al., 2017; Liu et al., 2020). SAPs improve soil physical properties by optimizing pore size distribution, simultaneously enhancing water retention capacity and aeration status. Empirical evidence indicates that 0.4% SAP

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incorporation increases total porosity by 9.09% and capillary porosity by 15.26% (Sun et al., 2024), while in coarse-textured soils, water-holding capacity improvements reach 171–402% (Johnson, 1984). These structural modifications concurrently reduce soil penetration resistance and promote the formation of water-stable aggregates (WSA) >0.5 mm, thereby enhancing erosion resistance (Goebel et al., 2005; John et al., 2005). Functioning as a "retention-controlled release" matrix for water and nutrients, SAPs significantly augment soil water storage and nutrient retention, modulating nutrient release kinetics and enhancing fertilizer use efficiency, thereby establishing stable hydro-nutritional conditions for germination and seedling establishment (Liu et al., 2020; Shaji et al., 2021). The synergistic regulation of water-nutrient dynamics by SAPs cascades to plant-level responses. Illustratively, 0.45% SAP application increased saturated water content by 42.7% on level terrain and 139.4% on 60° slopes, reduced evaporative losses by 88.9%, and enhanced germination rates 2-fold for herbaceous and 3-fold for woody species (Yang et al., 2014).

Plant growth-promoting rhizobacteria (PGPR) have emerged as pivotal biological agents for reducing synthetic fertilizer dependency while enhancing soil fertility and plant stress tolerance (Ramakrishna et al., 2020). Among PGPR species, B. subtilis is particularly prominent in agricultural and restoration applications due to its environmental compatibility, broad ecological adaptability, and well-elucidated mechanistic pathways. The plant growth-promoting activities of B. subtilis operate through dual mechanistic pathways. Direct mechanisms involve the secretion of bioactive compounds including: lipopeptide antibiotics (surfactin, iturin, fengycin) (Hashem et al., 2019); hydrolytic enzymes (cellulases, proteases, β-glucanases) (Yadav et al., 2021); phytohormones (indole-3-acetic acid [IAA], gibberellins, 1-aminocyclopropane-1-carboxylate [ACC] deaminase) (Ramakrishna et al., 2020); and antioxidant enzymes (peroxidase [POD], polyphenol oxidase [PPO], superoxide dismutase [SOD]) (Chowdappa et al., 2013), collectively mitigating pathogen pressure and stress-induced growth suppression. Indirect mechanisms encompass: induced systemic resistance (ISR) activation (Gu et al., 2017; Zeriouh et al., 2011); enhancement of phosphorus solubilization and nitrogen fixation (Ahmed et al., 2022; Hayat et al., 2010); optimization of nutrient acquisition and root colonization (Xu et al., 2020); biofilm formation on root surfaces (Hashem et al., 2019); and siderophore production, cumulatively enhancing plant resilience against biotic and abiotic stressors (Mahapatra et al., 2022; Molina-Santiago et al., 2019). Sun et al. (2020) demonstrated that replacing conventional manure with a B. subtilis biofertiliser reduced NH_3 volatilisation by 44 %, while markedly enhanced seed germination of Ammopiptanthus mongolicus and Caragana korshinskii, with optimal application rates of 3 g kg^{-1} and 10 g kg^{-1}, respectively (Sun B. et al., 2020). Concurrent improvements include elevated chlorophyll content and reduced malondialdehyde and proline accumulation in seedlings (Wu et al., 2023).

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Despite these documented benefits, critical knowledge gaps persist regarding the stage-specific efficacy of soil amendments in degraded alpine meadow restoration. Specifically: (1) How do amendment responses vary across degradation gradients characterized by distinct limiting factors? (2) What interactive effects emerge between amendment type, application rate, and degradation severity? (3) Which soil-plant feedback mechanisms mediate vegetation recovery under different amendment regimes? To address these gaps, we investigated the effects of varying application rates of HA, K-SAP, and B. subtilis on soil physicochemical properties, enzymatic activities, and plant community structure across a degradation gradient in alpine meadows. Our specific objectives are to: (1) quantify the differential responses of soil properties and plant communities to amendments across degradation gradients, (2) identify the optimal amendment type and dosage for each degradation stage, and (3) elucidate the underlying soil-plant feedback mechanisms driving recovery. By elucidating the mechanisms governing amendment-mediated restoration of soil multifunctionality across degradation gradients, our findings will enable the development of precision amendment strategies tailored to stage-specific ecological constraints. These insights will inform evidence-based restoration protocols that enhance ecosystem resilience, mitigate climate change impacts, and facilitate the sustainable rehabilitation of these ecologically critical yet vulnerable systems. Moreover, our results provide essential baseline data and scientific foundations for the adaptive management of alpine meadow ecosystems on the Qinghai–Tibet Plateau, supporting their long-term ecological integrity and sustainability.

2 Materials and Methods

2.1 Site description

This study focuses on the AM ecosystem in the Sanjiangyuan National Nature Reserve located in the southwestern part of Qinghai Province. The research site is situated near National Highway 215 in Qumalai County, Yushu Tibetan Autonomous Prefecture, within the core conservation area at an elevation of 4,479 meters (Fig.1). The region experiences a plateau subarctic semi-arid climate characterized by high altitude, low oxygen levels, and strong winds with limited rainfall. The oxygen deficiency in the air can reach up to 40%, with an average temperature of approximately - 3.3°C. The warmest months, from May to September, have average temperatures ranging from 3.2°C to 9.4°C. Overall, temperatures throughout the year are relatively low, and cold weather significantly impacts the growth and development of forage grasses. The annual sunshine duration is 2,750.2 hours, peaking in spring with 715.5 hours. Average annual precipitation is 472.9 millimeters, primarily concentrated from May to September, accounting for 90% of the total, with July receiving the highest rainfall at 97.6

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millimeters, coinciding with the warm season. The sample plots were enclosed by fences and situated within a livestock grazing exclusion zone.

2.2 Criteria for degradation and Experimental methods

In April 2024, three degradation stages were identified in the study area based on vegetation cover, plant community composition, and bare soil cover (Li et al., 2014), including lightly degraded (mild), moderately degraded (moderate), and severely degraded (severe) alpine meadow (Table 1). The baseline soil nutrient status for the plots at each degradation stage is presented in Table S1 (Supplementary Material). Based on previous studies and characteristic analyses of degraded alpine meadows, 5 g/m² was determined to be the minimum effective dose, and 10 g/m² the economically optimal dose (Canellas et al., 2015b; Cao et al., 2017; Sun et al., 2020). For each degradation level, seven plots were randomly selected, establishing amendments treatments that included a control group (CK), humic acid (HA) at 5 g/m² (F5) and 10 g/m² (F10); superabsorbent resin potassium salt (K-SAP) at 5 g/m² (B5) and 10 g/m² (B10); and Bacillus subtilis (B. subtilis) at 5 g/m² (J5) and 10 g/m² (J10). This resulted in a total of seven treatments, each with three replicates, amounting to 63 plots (3 stages × 7 treatments × 3 replicates), with each plot measuring 100 × 100 cm. The amendments were applied by hand, scattering them evenly onto the soil surface of the corresponding plots. They were then incorporated into the 0-10 cm topsoil layer using shallow tillage to ensure uniform mixing (Chowdhury et al., 2015). Plot corners were marked with PVC pipes, and the entire experimental area at each degradation stage was enclosed with fencing to prevent disturbance from livestock and human activities.。 HA (a biochemical-grade [BR] blend of humic and fulvic acids, sourced from Shanghai Yuanye Bio-Technology Co., Ltd.). K-SAP (a 20-80 mesh powder of potassium polyacrylate, sourced from Shandong Yousuo Chemical Technology Co., Ltd.). B. subtilis microbial inoculant (a powdered formulation containing ≥2.0 × 10^8 colony-forming units [CFU]/g, sourced from Aosidun Bio-Technology Co., Ltd.).

Table 1 Criteria for degradation and the location of the test points

2.3 Biomass, community composition, and species diversity

We conducted the species survey in October in 2024 on the QTP. Before the survey, one of the group members has read a lot of books about the flora and consulted some plant experts to get familiar with the flora in grassland ecosystem of the QTP. During the

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survey, two flora books were frequently referred to identify the species (Editorial Committee of Flora Sinica, Chinese Academy of Sciences; Flora of Qinghai Province). The height, coverage, and frequency of each species were recorded for each species in each of the 50 cm × 50 cm sampling areas in October. To minimize edge effects, vegetation surveys and sampling were initiated 10 cm from the edges of the plots. The height recorded for each species was the average height calculated from 5 individuals of that species. Where there were fewer than 5 individuals for a given species, the recorded height was the average height calculated from all the individuals. In each plot, plants were clipped at the soil surface to obtain the aboveground biomass. Clipped plants were placed in paper bags for air drying, then weighed after 48 hours in an oven at 65 °C to obtain biomass data.

Three indices were chosen as proxies for diversity:

(1) Importance of the species: Si = (relative height + relative frequency + relative coverage)/3

(2) Species richness index: S=n

(3) Shannon-Wiener diversity index :

(4) Pielou evenness index: J = H/lnS

(5) Simpson diversity index:

(6) Fisher's alpha index: $S=\alpha \ln(1+N/\alpha)$

(7) Margalef's Richness Index: R = (S-1)/lnN

In the above equations, n is the number of species recorded in each sampling area; p_i is the relative abundance of the species, defined as the proportion of individuals of that species to the total number of individuals; S is the species number of the sampling area; N is the total number of individuals; α is the Fisher's α index.

2.4 Soil sampling and soil properties measurement

After species identification and biomass collection, soil cores at depths of 0 – 5 cm (Top) and 5 – 10 cm (Sup) were extracted at the center of each plot using an auger. The auger is cylinder-shaped with an internal diameter of 7 cm (Xu et al., 2015). The soil samples were crumbled by hand and passed through a 2 mm diameter sieve to remove large particles such as roots, dead roots, gravel, and plant debris from the finer soil (Peng et al., 2018, 2020). Sieved samples were sealed in sterile bags, maintained at 4 °C in a vehicle-mounted refrigerator, and transported to the laboratory for analysis of soil physicochemical properties and enzymatic activities.

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pH was measured using the acidimeter (FE28K, Mettler Toledo, Shanghai). Soil organic matter (SOM) was obtained by the K2Cr2O7 - H2SO4 oxidation method. The content of available potassium (AK) was assayed using flame atomic absorption spectrophotometry (Sims, 1989). The Olsen's method was used for colorimetric determination of the content of available phosphorus (AP) in 0.5 mol NaHCO3 (pH 8.5) (Horta and Torrent, 2007). Soil ammonium nitrogen (NH4+) concentration was measured by using the indophenol blue colorimetric method. Soil nitrate nitrogen (NO3−) concentration was measured by using the ultraviolet Spectrophotometry method. Urease (UR) was measured by using the Phenol Sodium - Hypochlorite Colorimetric Method. Catalase (CAT) was determined by the Potassium Permanganate Titration Method. Alkaline Phosphatase (ALP) was assessed through the Disodium Phenyl Phosphate Colorimetric Method. Dehydrogenase (DH) was quantified via the TTC Colorimetric Method. Cellulase (CEL) was evaluated with the 3,5 - Dinitrosalicylic Acid Colorimetric Method.

2.5 Data analysis Methods

Prior to statistical analysis, all raw data from measurements and surveys were standardized and compiled. All datasets were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test). For data that met these assumptions, parametric tests were used. For data that violated these assumptions, we employed non-parametric tests based on 9999 permutations for group comparisons. The data are presented as mean ± standard error. Various biodiversity indices were calculated using the Vegan package in RStudio, and phylogenetic trees of plant species were constructed using the V.PhyloMaker and picante packages to compute phylogenetic diversity. Before further analysis, the heterogeneity of variance among different groups was tested. The differences in diversity indices between different treatment groups and varying degrees of degradation exhibited heterogeneity; thus, a non-parametric test was employed to assess the impact of degradation and experimental treatment on diversity indices in RStudio using the Kruskal-Wallis Test. Post-hoc analysis of the differences between paired degradation groups was conducted using the pairwise.wilcox.test in RStudio. To calculate ecosystem multifunctionality (EMF), all individual function indicators were first standardized to a [0, 1] scale. A specific standardization was applied to pH, where values within the optimal range of 6.5–7.8 (determined from literature) were scored as Wang et al., (2022a), Ma et al., (2002) and Wei et al., 2022), with scores decreasing as values moved away from this range. Subsequently, we performed collinearity diagnostics on all candidate indicators. To prevent the over-representation of any single functional dimension, we calculated the Variance Inflation Factor (VIF) using the 'car' package and excluded any indicator with a VIF > 5. The final EMF index for each plot was calculated using the averaging method on the remaining, independent indicators. Following the

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collinearity analysis, we used Principal Component Analysis (PCA) to create composite variables from the remaining indicators. The first principal component (PC1) was extracted to represent three latent dimensions: 'biodiversity', 'soil properties', and 'soil enzyme activity'. Aboveground biomass and litter mass were combined to represent 'biomass'. We then constructed a Bayesian structural equation model (BSEM) using the 'brms' package to test the causal relationships among these variables. Weakly informative priors were set for the model parameters. After optimization, the parameters of the best-fit model were reported. All data analyses and visualizations were performed in R (version 4.4.2) and Rstudio (version 2025.05.0 Build 496), and the resulting plots were refined and adjusted in Adobe Illustrator CC 2018.

3 Results

3.1 Plant communities response to soil amendments across degradation gradients

Our study revealed that the responses of aboveground biomass and litter to soil amendments were pronounced only at the mild and severe degradation stages. In mildly degraded meadows, compared with the control group, F5 treatment exhibited the strongest positive effect on litter production (33.52% increase, Cohen's d = 1.58), followed by B10 (11.20% increase, Cohen's d = 0.95). In contrast, aboveground biomass responses were minimal, with only F5 and B10 inducing marginal increases of 1.89% and 0.26%, respectively. In moderately degraded meadows, some soil amendments treatments (F5, B5, J10) exhibited opposing effects, reducing litter while increasing aboveground biomass, specifically, treatments F5, F10, B5, and J10 increased biomass by 17.28%, 36.53%, 0.73%, and 4.72%, respectively. In severely degraded meadows, F5 and F10 treatments had a slight positive effect on litter, while for biomass, only the F5 treatment induced a substantial increase (25.86%) (Fig. 2a).

Soil amendments significantly affected plant Importance Values (IV): in mildly degraded meadows, J5 treatment increased Poaceae IV 5.99-fold and J10 treatment increased Kobresia IV 1.04-fold than the control group; in moderately degraded meadows, F5 treatment enhanced Kobresia IV 1.16-fold; in severely degraded meadows, J10 treatment elevated Kobresia IV 2.80-fold (Fig.2b).

Alpha diversity indices responded differentially across degradation stages. In mildly degraded meadows, F5 treatment significantly enhanced multiple diversity metrics: abundance index (30.80%, Cohen's d = 1.84), Shannon-Wiener index (34.14%, Cohen's d = 2.33), Pielou evenness (22.01%, Cohen's d = 1.68), and phylogenetic diversity (10.20%, Cohen's d = 0.91). In moderately degraded meadows, F10, B5, B10, and J10 treatments strongly enhanced most diversity metrics, B5 treatment enhanced abundance index by 60.62% (Cohen's d = 1.16), Shannon-Wiener index by 10.15% (Cohen's d = 1.20), Phylogenetic diversity index by 15.11% (Cohen's d = 0.84). F5, B10 and J10 treatments

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significantly increased abundance index by 91.67%, 64.05%, 56.21% ($P < 0.05$). In severely degraded meadows, except for the K-SAPs treatments, other treatments all showed a strong enhancing effect on the diversity index. J10 treatment demonstrated optimal effects, enhancing Shannon-Wiener index by 47.68% (Cohen's d = 1.96), Pielou evenness by 23.65% (Cohen's d = 1.89) and Phylogenetic diversity index by 22.07% (Cohen's d = 0.87) (Fig.2c).

3.2 Soil nutrients and enzyme activity response to soil amendments across degradation gradients

The effects of soil amendments on soil physicochemical properties were indicator-specific, similar to the biomass response pattern: effects were more pronounced at the mild and severe degradation stages, with a muted response in the moderate stage.

In mildly degraded meadows, soil pH significantly increased across all treatments (from 7.43 to 7.87, $P < 0.05$), accompanied by an enhancement in nitrogen availability. For instance, the F5 treatment increased available phosphorus (AP) and nitrate nitrogen (NO_3^--N) contents by 1.01% and 10.76%, respectively, J10 treatment elevated ammonium nitrogen (NH_4-N) and NO_3^--N by 15.69% and 91.36% respectively, with NO_3^--N reaching 7.41 mg kg^{-1} ($P < 0.05$). In moderately degraded meadows, nutrient responses diverged: the F5 treatment enhanced Available potassium (AK), AP, and soil organic matter (SOM) by 12.14%, 10.10%, and 14.22%, respectively, while the B10 treatment increased AK and SOM contents by 47.11% ($P < 0.05$) and 8.76%, respectively. Conversely, J10 reduced all measured nutrients. Severely degraded meadows exhibited the most pronounced nutrient responses. B10 treatment significantly increased the AK content by 104.58%, reaching 92.60 mg kg^{-1} ($P < 0.05$). Furthermore, AP content increased by 17.40–24.17% across the F5, B5, and B10 treatments ($P < 0.05$). J5 and J10 treatments dramatically enhanced NO_3^--N by 168.99% and 159.80% respectively ($P < 0.05$), while reducing pH and SOM (Fig.3a).

Soil enzyme activities also showed clear stage-dependent responses. In mildly degraded meadows, catalase (CAT) activity was universally enhanced, with the J10 treatment achieving the maximum increase of 114.00% ($P < 0.05$). In moderately degraded meadows, urease (URE) activity was enhanced across all treatments, peaking at 1.24 mg g^{-1} with the B10 treatment (+36.90% vs. control). And the J5 treatment significantly increased both CAT (+25.97%, $P < 0.05$) and cellulase (CEL) (+23.95%) activities. Furthermore, F5 increased CEL activity by 17.43%, F10 increased CAT activity by 17.94%, and B10 increased dehydrogenase (DH) activity by 22.76%. In severely degraded meadows, the J5 and J10 treatments enhanced both CAT (by 8.03% and 11.11%, respectively) and CEL activities (by 32.21% and 18.27%, respectively) (Fig. 3b).

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3.3 Ecosystem multifunctionality (EMF) responses to soil amendments across degradation gradients

The ability of soil amendments to restore ecosystem multifunctionality (EMF) is highly dependent on the initial degradation state, with their effectiveness increasing as the severity of degradation intensifies. In mildly degraded meadows, only the F5 and J5 treatments induced a modest enhancement in EMF (+2.54% and +3.00%, respectively). In the moderate degradation stage, a broader range of amendments (F5, F10, B10, and J5) proved effective, with the F10 treatment delivering the greatest EMF increase (+7.88%). The restorative effect was most pronounced in severely degraded meadows, where F5, F10, J5, and J10 all enhanced EMF; the J10 treatment was optimal, yielding a significant 31.56% increase relative to the control ($P < 0.05$). Furthermore, amendment efficacy was governed by clear dose-response relationships that shifted with degradation severity. For instance, high-dose humic acid (F10) suppressed EMF in the mild stage but became beneficial under moderate and severe conditions. K-SAP effectiveness increased with dosage across all stages. Conversely, the optimal dosage for microbial amendments inverted with degradation severity: low doses were more effective in mild-to-moderate stages, while high doses were superior in the severe stage.

3.4 Bayesian structural equation modeling reveals degradation-dependent pathways to ecosystem multifunctionality

Bayesian Structural Equation Model (BSEM) revealed the response mechanisms of ecosystem multifunctionality (EMF) to soil amendments across the different degradation stages. The BSEM explained 51%, 62%, and 46% of the variance in EMF within the mild, moderate, and severe degradation stages, respectively (Fig. 5). In mildly degraded meadows, EMF was directly and significantly positively influenced by soil nutrients (β = 2.70, 95% Credible Interval [CI]: 0.73–4.63) and biomass (β = 2.54, 95% CI: 0.23–4.89). The B5 treatment had an indirect negative effect on EMF mediated by a reduction in soil nutrients, whereas all amendments indirectly promoted EMF via positive effects on soil enzyme activity. In moderately degraded meadows, EMF was predominantly and directly driven by soil nutrients (β = 6.02, 95% CI: 3.74–8.38), a pathway that was strongly enhanced by the J5 treatment. In severely degraded meadows, EMF was directly and significantly positively influenced by vegetation diversity (β = 3.32, 95% CI: 0.38–6.10). Correspondingly, the indirect amendment strategies bifurcated but followed two distinct pathways: the F5, K-SAPs (B5, B10), and B. subtilis (J5, J10) treatments all indirectly enhanced EMF by increasing soil nutrients, whereas the F10 and J10 treatments operated by increasing soil enzyme activity.

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4 Discussion

4.1 Stage-specific amendment effectiveness reflects shifting ecological constraints

By employing a systematic degradation gradient and a rigorous multifunctionality assessment, we demonstrate that the optimal restoration strategy fundamentally shifts with the ecosystem's degradation state. Consequently, effective restoration of alpine meadows requires tailoring interventions to match the specific ecological limiting factors of each degradation stage. Specifically, the response of EMF to amendments was minimal in mildly degraded meadows (F5: +2.54%, J5: +3.00%), showed a moderate increase in the moderate degradation stage (F10: +7.88%), and had a significant improvement under severe degradation (J10: +31.56%, $P < 0.05$). These responses are consistent with the theory of threshold dynamics in restoration ecology (Suding et al., 2004), indicating that degraded ecosystems require state-specific interventions. Our findings, consistent with other studies, demonstrate the broad effectiveness of HA under various environmental conditions (Ali and Mindari, 2016; Ampong et al., 2022; Fahramand et al., 2014; Gumus and Seker, 2015). However, inconsistent with other research (Saha et al., 2020; Mahapatra et al., 2022; Rillig et al., 2019), we found that K-SAP and B. subtilis did not have universal effectiveness. This discrepancy arises because other studies have often overlooked the shifts in nutrient limiting factors across degradation stages. These factors, however, fundamentally determine amendment efficacy. Our gradient-based experimental design captured these ecological thresholds, revealing that the success of soil amendments in degraded grasslands depends not only on the intrinsic properties of the amendment but also on the match between its mechanism of action and the specific nutrient limitations of a given degradation stage.

Moreover, the varying dose-response patterns of soil amendments observed in this study provide powerful mechanistic insights for heterogeneous ecosystem restoration. For example, the effects of HA dosage reversed along the degradation gradient: high-dose HA (F10) reduced EMF in mildly degraded conditions but became the optimal choice in moderately degraded conditions. These findings strongly support the "Subsidy-Stress Gradient" hypothesis (Odum et al., 1979), which predicts that excessive resource inputs can destabilize systems with established competitive equilibria (mild degradation), yet become beneficial when systems experience intensified stress and resource constraints (moderate degradation). Similarly, the dose effect of B. subtilis shifted from a preference for low doses in mild/moderate stages (J5>J10) to a requirement for high doses in the severely degraded stage (J10>J5). These dose-dependent responses suggest that minimal microbial inoculation suffices to catalyze native processes in functionally intact or partially compromised ecosystems; however, biologically depleted systems require

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substantial nutrient and microbial inputs to reconstruct functional microbial communities capable of crossing critical restoration thresholds.

The vegetation and soil data analyses in our study confirm that the EMF response patterns at these specific stages are inextricably linked to soil biogeochemical cycling. Soil in mildly degraded meadows retained relatively high soil organic matter (SOM) (41.38 $g \cdot kg^{-1} \pm 0.24$) and nutrient levels, while aboveground vegetation also remained relatively intact (Supplementary Table 1), resulting in intense competition for nutrients among plants and showing initial signs of stress, particularly in nitrogen-limited alpine regions (Midolo et al., 2019). Under these conditions, the beneficial effects of low-dose HA and B. subtilis (F5, J5) demonstrate that minimal interventions suffice to enhance ecosystem function, whereas higher input intensities proved counterproductive. HA and B. subtilis enhanced EMF through multiple pathways: increasing nutrient mobility, facilitating nutrient acquisition by competitive vegetation, and stimulating the production of soil enzymes critical for ecosystem stability (Ampong et al., 2022; Mahapatra et al., 2022). This mechanistic pathway was evidenced by significant increases in litter production, biomass accumulation (Fig. 2a), vegetation diversity (Fig. 2c), NO_3^--N availability (Fig. 3a), and catalase (CAT) activity (Fig. 3b). These responses align with established mechanisms by which ha and B. subtilis enhance soil physicochemical properties and stimulate microbial activity (Ampong et al., 2022; Mahapatra et al., 2022; Rasool et al., 2021).

The moderately degraded stage constitutes a critical transition zone in ecosystem succession, characterized by emergent water stress coupled with accelerated nutrient depletion (Xu et al., 2025; Deng et al., 2021) (Supplementary Table 1). This "dual stress" of nutrients and water makes the ecosystem more sensitive to external inputs. High-dose humic acid (F10) enhanced EMF by 7.88% in moderately degraded systems (Fig. 4), corresponding with its synchronized aboveground effects: a 25.86% increase in litter production and 36.53% enhancement in biomass accumulation (Fig. 2A). Simultaneously, HA as an efficient biostimulant and soil conditioner acts on both physical and chemical levels. Physically, it enhances water retention and drought resistance through improved soil aggregate formation (Muscolo et al., 2007); chemically, it adsorbs and mobilizes soil nutrients via its high cation exchange capacity (Ali and Mindari, 2016), while creating favorable rhizosphere conditions for root proliferation and nutrient conservation through enzymatic regulation. Accordingly, our F10 treatment significantly elevated activities of the stress-resistance enzyme catalase (CAT), nitrogen-cycling urease (URE), and carbon-cycling cellulase (CEL) (Fig. 3b). Consequently, F10 treatment emergences as the optimal treatment for moderately degraded systems stems from HA's tripartite mechanism—"structural improvement + nutrient mobilization + stress resistance induction"—which simultaneously enhances productivity while activating key stress-response and decomposition pathways in the soil matrix, achieving synergy between "top-down" productivity drivers and "bottom-up" biogeochemical function optimization,

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which is conducive to breaking through the complex ecological limiting factors of the moderate degradation stage. Additionally, K-SAP directly mitigated the stage-critical water stress constraint, emerging as a key diversity driver with substantial EMF enhancement effects. In our study, B10 treatment strengthened total biomass, litter mass, and diversity indices (abundance index, Shannon-Wiener index, phylogenetic diversity), and as a potassium-containing polymer, K-SAP directly released large amounts of K+, significantly increasing AK content by 47.11% ($P < 0.05$) and greatly stimulating the activity of URE and DH, which are closely related to the nitrogen cycle. Therefore, the pathway of K-SAP is "water promoting enzymes, water releasing potassium," which indirectly promotes nutrient cycling and EMF by precisely addressing the main contradiction of water stress in the moderate degradation stage.

In severely degraded meadows, high-dose B. subtilis (J10) demonstrated excellent restoration capability, significantly increasing EMF by 31.56% ($P < 0.05$), far exceeding other treatments, while HA (F5, F10) treatments had positive effects but limited improvement, and K-SAP was almost ineffective. This finding is consistent with previous studies on the generally positive role of B. subtilis in promoting soil health (Kim et al., 2019; Mahapatra et al., 2022; Ng et al., 2022), but our study is the first to quantitatively demonstrate that under severely degraded conditions, high-dose B. subtilis (J10) has more significant advantages compared to low-dose (J5), which forms a stark contrast with the "low-dose superior to high-dose" trend observed in mild and moderate degradation stages. The function of severely degraded ecosystems has nearly collapsed, requiring large-scale "biological reconstruction" rather than simple "functional activation." Our data robustly support this mechanistic model: J10 treatment significantly enhanced the Shannon-Wiener diversity index by 47.68% (Cohen's $d = 1.96$) and phylogenetic diversity by 22.07% (Fig. 2C), increased the importance value of the foundation species Kobresia by 2.80-fold (Fig. 2B), and dramatically elevated nitrate nitrogen (NO_3^--N) concentrations by 159.80% ($P < 0.05$) (Fig. 3A), while simultaneously upregulating catalase activity (CAT, +11.10%) and cellulase activity (CEL, +18.27%, $P < 0.05$) (Fig. 3B). These coordinated responses indicate concurrent enhancement of species diversity, community structural reorganization, and nutrient mobilization. This tripartite mechanism of "nitrogen activation + stress resistance enhancement + carbon decomposition stimulation" suggests that exogenous microbial inoculation not only compensates for depleted native microbial communities but, crucially, reinitializes stagnant biogeochemical cycling processes. In contrast, although K-SAP treatments (B5, B10) significantly increased AK (B10 increased AK by 104.58%, $P < 0.05$) and AP (increases of 17.40%-24.17%), they failed to translate into improvements in diversity and EMF, indicating that in the absence of biological function, mere nutrient supplementation or water improvement can no longer drive the restoration of degraded grasslands.

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4.2 Mechanistic pathways of soil amendment effects on ecosystem multifunctionality

Our Bayesian structural equation modeling (BSEM) analysis revealed pronounced stage-specific shifts in both the drivers of EMF and functional trade-offs along the degradation gradient. In mildly degraded systems, EMF was synergistically driven by soil nutrient-biomass coupling, while moderately degraded systems transitioned to nutrient-dominated control, and severely degraded systems pivoted to vegetation diversity as the primary driver, with soil functions assuming a subordinate role (Fig. 5). This stage-dependent functional trade-off pattern corroborates ecosystem threshold theory Berdugo et al. (2020), which posits that ecosystems respond to stress not through linear degradation but undergo abrupt changes in structure and function once critical thresholds are traversed.

The mechanisms by which soil amendments influence EMF fundamentally transform across degradation stages. In mildly degraded stage, EMF was predominantly regulated by soil nutrients and aboveground biomass. All amendments indirectly modified EMF by simultaneously negatively affecting soil nutrient pools while significantly enhancing soil enzymatic activities. These results suggest that mildly degraded grasslands maintain relatively intact functioning regarding soil nutrition, biodiversity, and productivity, existing in a quasi-saturated state where microbial community functions remain largely uninhibited (Steinauer et al., 2015; Wang et al., 2020). Consequently, all amendments (HA, K-SAP, B. subtilis) could indirectly influence EMF through significant positive effects on soil enzyme activities, with soil nutrient cycling and productivity functions constituting the primary contributors to overall EMF.

As degradation intensified, a critical state transition emerged in moderately degraded systems, where EMF became almost exclusively controlled by soil nutrients (β=6.02), indicating that the grassland ecosystem enters a nutrient-limited state characterized by depleted labile organic matter fractions and relative enrichment of recalcitrant organic compounds (Lützow et al., 2006), a pattern consistent with research identifying nutrient availability as a primary constraint in global terrestrial ecosystems (Berdugo et al., 2020). Consequently, nutrient supplementation emerges as the critical restoration intervention at this stage, with our data demonstrating that EMF primarily responded to direct enhancement of soil nutrient content through J5 treatment (Fig. 5), indicating a fundamental transformation in nutrient acquisition strategies—shifting from enzyme-mediated endogenous organic matter mineralization toward immediate utilization of directly available inorganic nutrients. According to microbial life history strategy theory, microbial communities under intensifying environmental stress (nutrient scarcity, water limitation) typically reallocate finite resources from high-cost growth-related functions (extracellular enzyme synthesis) toward survival-maintenance mechanisms (osmolyte production, cellular repair) (Malik et al., 2020). At the severely degraded stage, where system functionality has effectively collapsed, plant diversity emerges as the predominant

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direct driver of EMF (β=3.32), with diversity significantly enhancing biomass production (β=3.15), supporting the biodiversity-ecosystem function hypothesis that in highly stressed or species-depauperate systems, species richness and composition become foundational determinants of ecosystem functionality (Loreau and Mazancourt, 2013). At this stage, exogenous amendments (especially F10 and J10) can quickly alleviate microbial substrate limitations and stress states by introducing organic substrates and exogenous microorganisms (Heijboer et al., 2016; Reynolds et al., 2003; Zhang et al., 2018), establishing soil enzymatic activity as the crucial mediator converting resource inputs into biogeochemical functionality, which subsequently facilitated vegetation diversity reconstruction — the core EMF driver, through indirect regulation of soil nutrient pools.

Despite yielding significant insights, our investigation was constrained by its short-term experimental design spanning only a single growing season in the high-altitude Qinghai-Tibet Plateau ecosystem. This limitation precludes comprehensive assessment of amendment effect temporal dynamics, persistence, and cross-ecosystem applicability—particularly regarding the colonization persistence and functional stability of microbial inoculants under variable environmental conditions. Consequently, we propose two critical directions for future research: (1) establishment of long-term monitoring platforms with permanently marked plots to capture interannual variations and cumulative effects of soil amendments, with particular emphasis on restoration stability during extreme climate perturbations; (2) conduct controlled experiments across different ecosystems to test the universality of stage-specific mechanisms revealed in our study across diverse ecosystems. These improvements will help build a more complete theoretical system for degraded ecosystem restoration and provide scientific support for sustainable management of global grasslands.

5 Conclusions

Overall, our findings demonstrate that the mechanistic pathways through which soil amendments modulate EMF in alpine meadows fundamentally transform across the degradation gradient: transitioning from a synergistic soil nutrient-biomass coupling in mildly degraded systems (R^2=51%), to soil nutrient-dominated control in moderately degraded systems (β=6.02, R^2=62%), culminating in vegetation diversity becoming the primary driver in severely degraded conditions (β=3.32, R^2=46%). Additionally, the intensity of EMF response to soil amendments exhibited a linear increase with degradation severity, progressing from minimal responses in mildly degraded systems (2.54%-3.00%), to moderate enhancement in moderately degraded stage (7.88%), reaching maximum efficacy in severely degraded conditions (31.56%, $P<0.05$). Traditional soil amendment applications may underestimate the improvement effects of soil amendments due to neglecting the continuously changing ecological functional bottlenecks along the degradation gradient. Based on our findings, we propose a

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"precision-matching" restoration framework: applying low-dose HA (5 g m^{-2}) or B.subtulis (5 g m^{-2}) for functional optimization in mildly degraded stages; implementing high-dose HA or K-SAP (10 g m^{-2}) to overcome nutrient-water dual constraints in moderately degraded stages; deploying high-dose B.subtulis (10 g m^{-2}) to reconstruct biological functionality in severely degraded systems. This framework provides a scientific foundation for hierarchical, classification-based management of degraded alpine grasslands across the Qinghai-Tibet Plateau and globally, while challenging the prevailing "one-size-fits-all" restoration paradigm that dominates current ecological practice.

Author Contributions

Conceptualization, N.W., Z.Z. and Y.D.; methodology, N.W., Z.Z., H.Z. and Y.D.; software, N.W. and Z.Z.; validation, N.W., Z.Z., Y.W. and X.W.; formal analysis, N.W. and Z.Z.; investigation, N.W., Z.Z., Y.W., X.W. and H.S.; resources, H.Z. and Y.D.; data curation, N.W. and Z.Z.; writing—original draft preparation, N.W. and Z.Z.; writing—review and editing, N.W., Z.Z., H.Z. and Y.D.; visualization, N.W. and Z.Z.; supervision, H.Z. and Y.D.; project administration, Y.D.; funding acquisition, Y.D. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

The data presented in this study are available on request from the corresponding author. The data are not publicly available due to restrictions related to ongoing long-term monitoring at the study site.

Code Availability

The custom R code used for statistical analysis and Bayesian structural equation modeling in this study is available from the corresponding author upon reasonable request. The code includes scripts for data preprocessing, diversity index calculation, ecosystem multifunctionality quantification, and BSEM implementation using the brms and piecewiseSEM packages.

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Conflicts of Interest

The authors declare no conflicts of interest.

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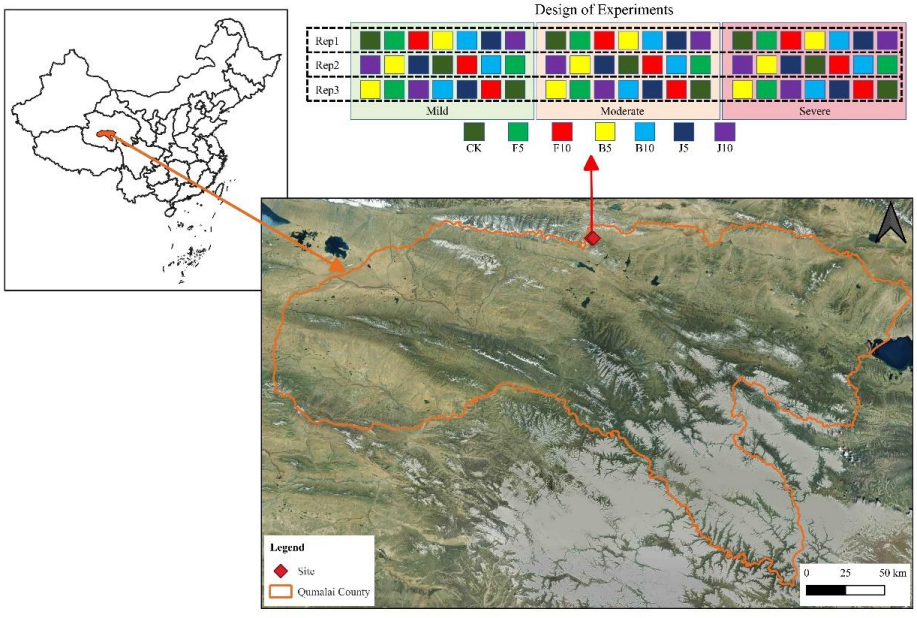
Tables

Table 1. Criteria for degradation and the location of the test points.

Degradation Stages	Plant coverage (%)	Bare ground coverage (%)	Sedge and grass (%)	Latitude / Longitude	Altitude / m
Mild	>80	<5	50-80	34°94'18"N 94°70'47"E	4471
Moderate	50-80	5-20	30-50	34°94'20"N 94°70'01"E	4472
Severe	<30	>50	<10	34°94'19"N 94°70'59"E	4467

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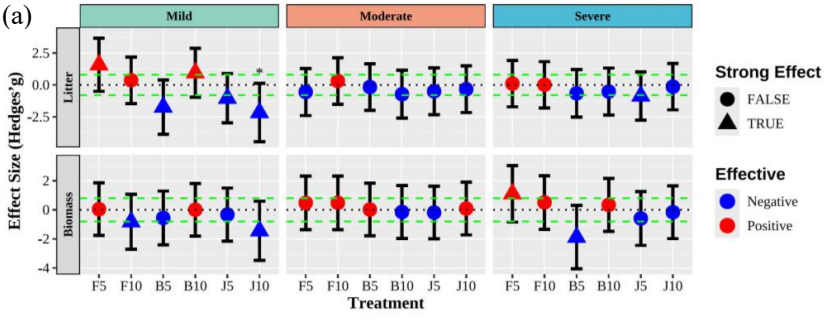
914 # Figures



915

916 **Fig.** 1 Map of the research sampling sites. “Mild,” “Moderate,” and “Severe” correspond to slightly,
917 moderately, and severely degraded stages, respectively. “AM” represents alpine meadow. “CK” represents
918 the control group. “F” represents humic acid; “F5” denotes 5 g of humic acid applied per m², and “F10”
919 denotes 10 g of humic acid applied per m². “J” represents Bacillus subtilis; “J5” and “J10” denote 5 g and
920 10 g applied per m², respectively. “B” represents the potassium salt of polyacrylamide; “B5” and “B10”
921 denote 5 g and 10 g applied per m², respectively.

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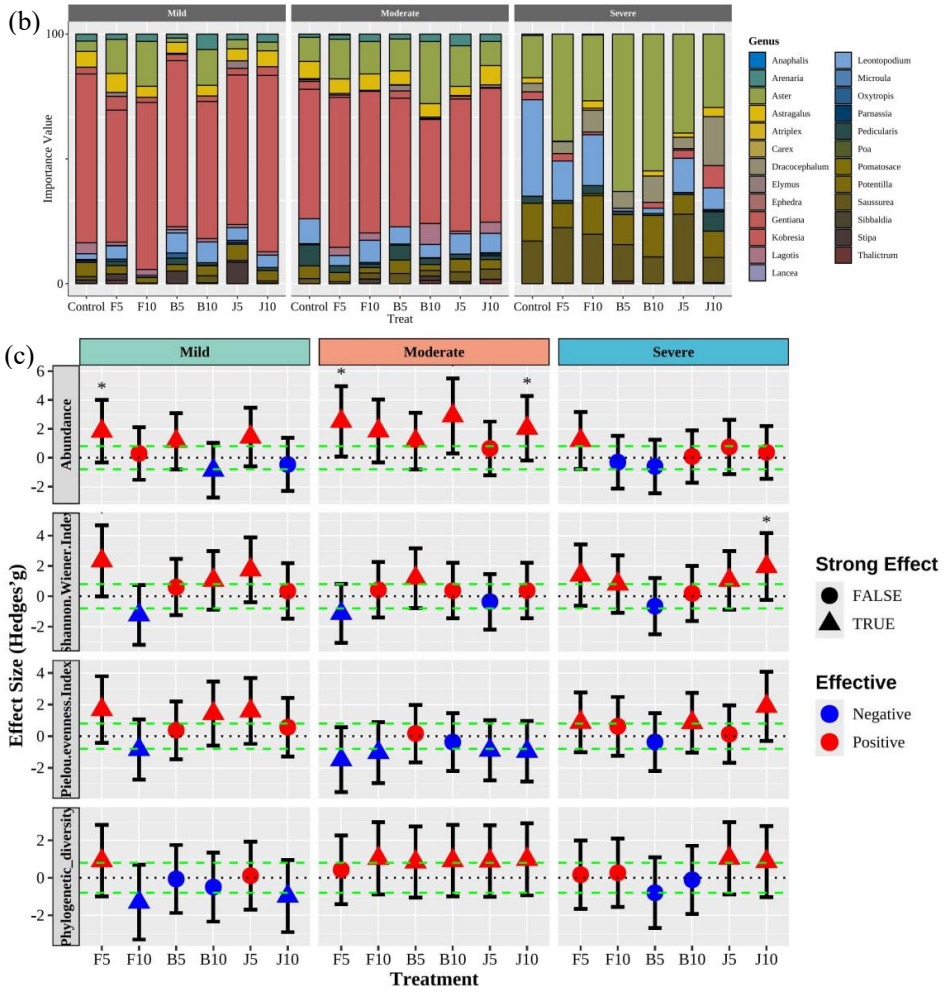
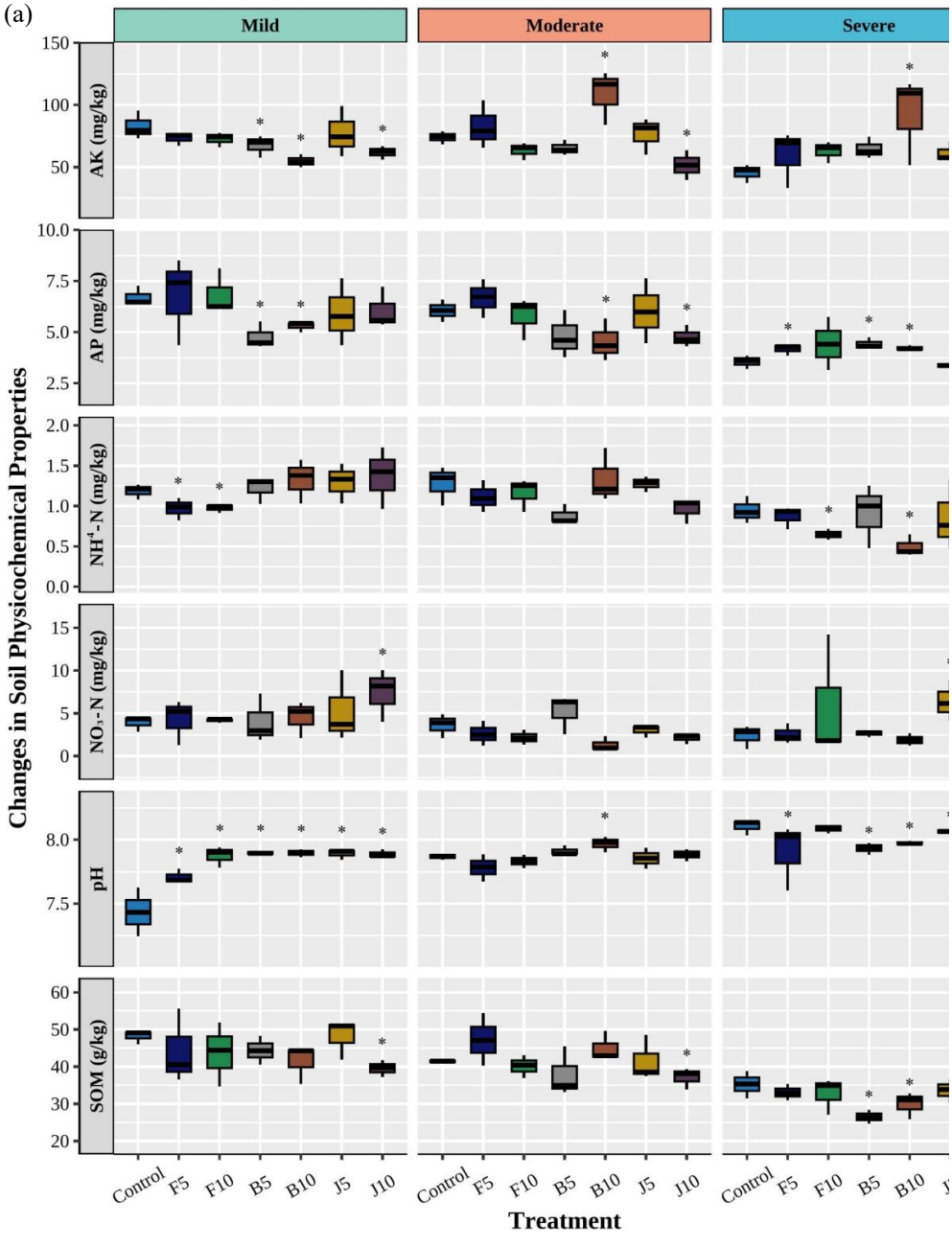


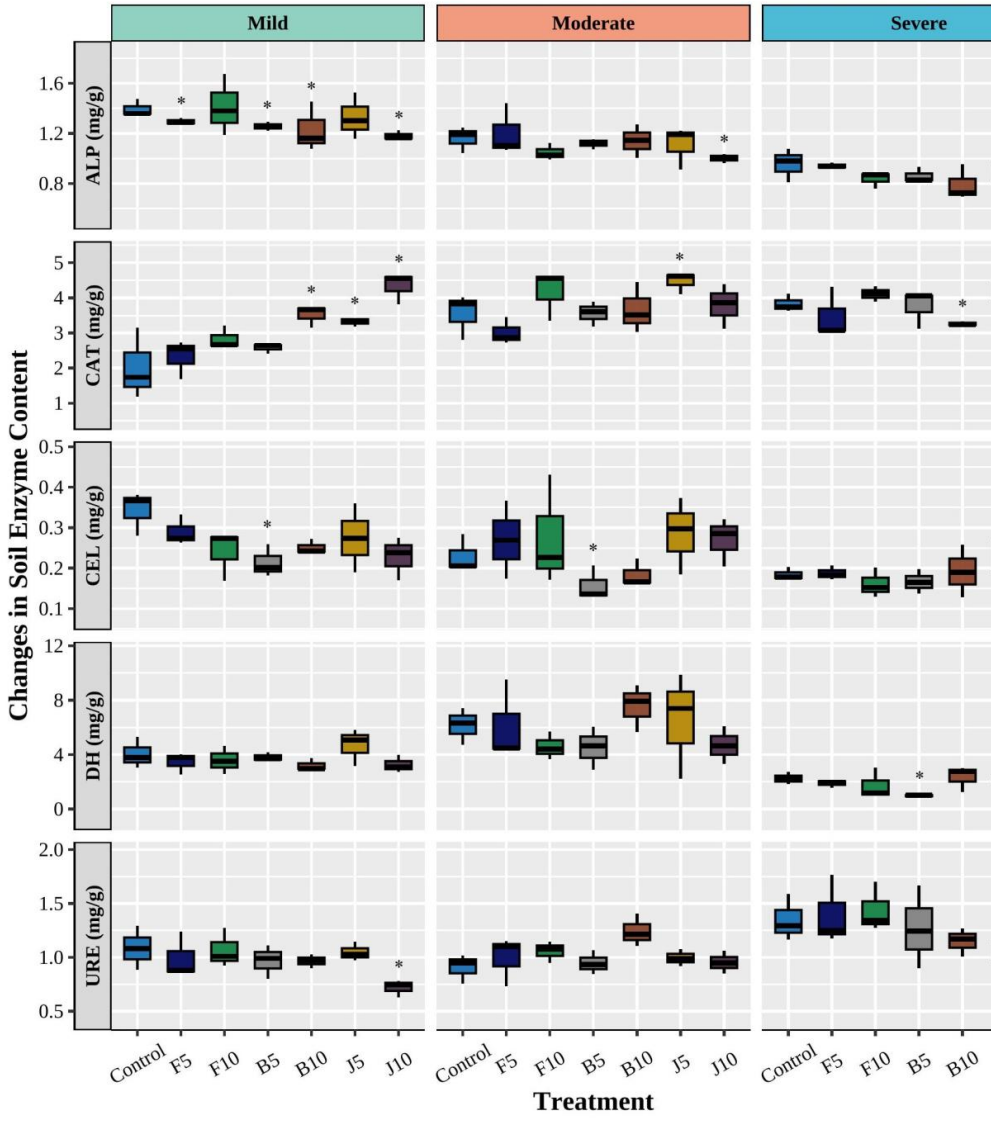
Fig. 2 Changes in aboveground biomass, litter, plant composition, and diversity under different degradation levels. Aboveground biomass and litter (a), the percent of plant community families (b), the abundance index, Shannon.Wiener. diversity index, Pielou.evenness.index, Phylogenetic diversity index (c) under different degradation levels (mean ± SD). "*" in the panel indicate significant differences between the treatment and the control group at a significance level of 0.05.

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(a)



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930

931 **Fig.** 3 Variation in soil nutrients and enzyme activity at different treatments under different degradation
932 levels. Available potassium (AK), available phosphorus (AP), ammonium nitrogen (NH_4-N), nitrate
933 nitrogen (NO_3-N), pH, soil organic matter (SOM) (a), alkaline phosphatase (ALP), catalase (CAT),
934 cellulase (CEL), dehydrogenase (DH), urease (UR) (b) under different degradation levels (mean ± SD). "*"
935 in the panel indicate significant differences between the treatment and the control group at a significance
936 level of 0.05.

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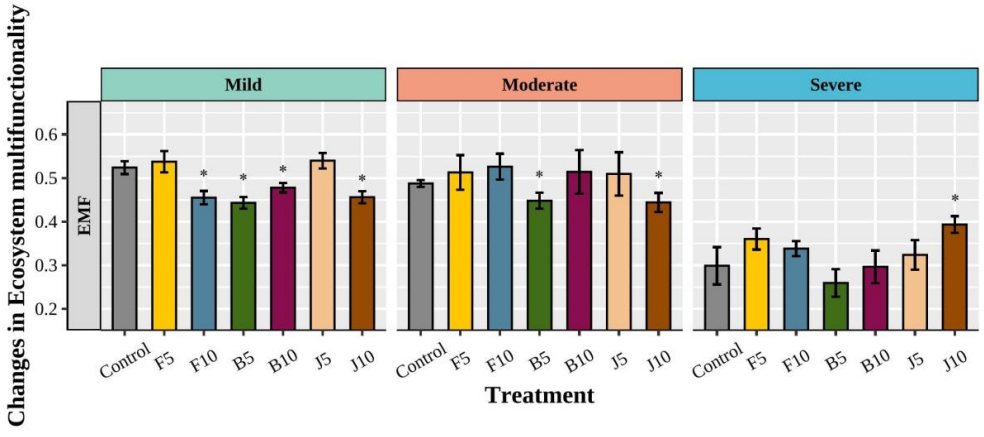
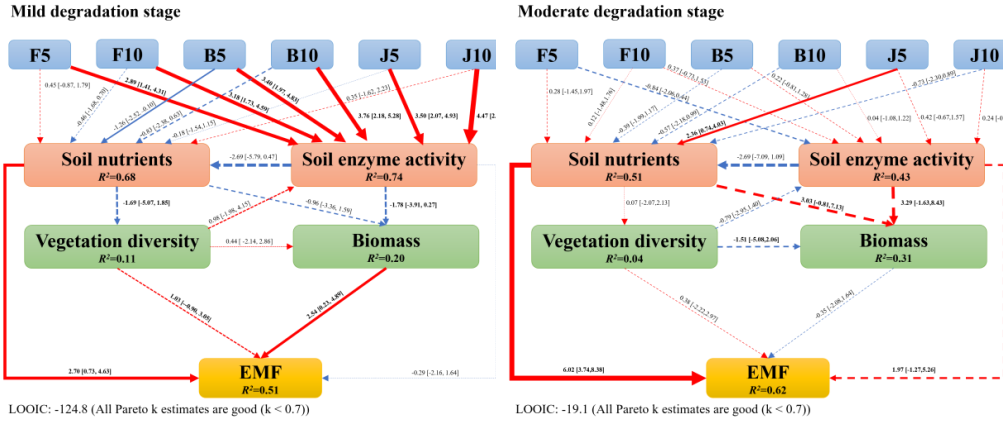


Fig. 4 Variation in ecosystem multifunctionality (EMF) at different treatments under different degradation levels. "*" in the panel indicate significant differences between the treatment and the control group at a significance level of 0.05.



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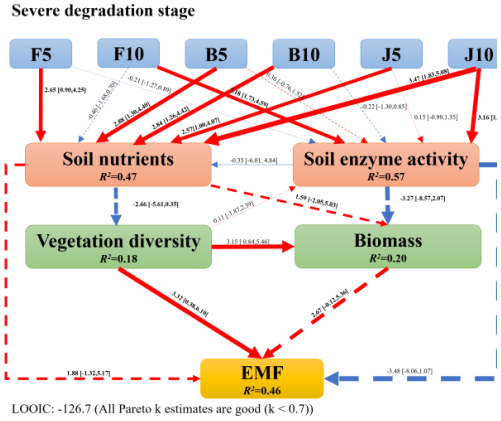


Fig. 5. Response pathways of ecosystem multifunctionality (EMF) to soil amendments in the mild, moderate, and severe degradation stages. (a) Bayesian structural equation model (BSEM) under the mild degradation stage, (b) BSEM under the moderate degradation stage, (c) BSEM under the severe degradation stage. R2 represents the degree of explanation of the endogenous variable. Red and blue arrows indicate positive and negative effects, respectively. Solid and dashed lines indicate significant and non-significant path coefficients, respectively. The width of the arrows in the connecting line is proportional to the magnitude of the path coefficients with the text indicating the mean and 95% credible intervals (CIs) of the standardised path coefficients.