

Changes in soil available nitrogen mediate divergent responses in plant CSR strategies with montane meadow degradation along an aridity gradient

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Abstract

Background and Aims

Grassland degradation alters plant communities and ecosystem functioning, but whether it induces predictable shifts in plant CSR (competitor-stress tolerator-ruderal) strategies, how aridity modulates these shifts, and the relative roles of soil N vs. P remain unclear. *Methods*

We investigated three montane grasslands along an aridity gradient (semi-arid alpine meadow, semi-arid marsh meadow, hyper-arid mountain steppe) using paired plots (undegraded vs. degraded). We measured community composition, above- and belowground net primary productivity (ANPP, BNPP), soil available nutrients (NH_4^+ , NO_3^- , AP), and community-weighted CSR strategies. Random forest and structural equation modelling identified drivers and pathways.

Results

Degradation triggered site-specific CSR reconfigurations. In the semi-arid alpine meadow, stress-tolerator (S) increased from 80% to 91%, while ruderal (R) decreased from 14% to 2%. In the hyper-arid steppe, S increased (78%→85%) and R decreased (20%→12%). Soil available N dominated CSR changes: ΔS positively correlated with ΔNH_4^+ (+ 30%) and ΔP (+ 265%), but negatively with ΔNO_3^- (– 64%); ΔR showed opposite patterns. Nutrient effects on CSR were fully mediated by changes in BNPP (e.g., + 439% at the alpine site, – 59% at the hyper-arid site), with no direct nutrient–CSR pathway.

Conclusion

Grassland degradation drives divergent CSR reconfigurations depending on aridity. Soil N dynamics act as a dominant biogeochemical filter, influencing CSR shifts indirectly via belowground productivity reallocation. This provides a nutrient-explicit, mechanistic framework for predicting plant community responses to degradation across climatic gradients.

Introduction

Grassland ecosystems (Lewinska et al., 2023; Parente et al., 2024) serve a pivotal role in global biogeochemical cycles, harbor substantial biodiversity, and underpin millions of livelihoods (Martins et al., 2024; Yan et al., 2025; Zhu et al., 2026). However, they are undergoing unprecedented degradation globally, driven by overgrazing and climate change (F. Cao et al., 2024; Kolluru et al., 2024; Van Wijk et al., 2003). The degradation of grasslands manifests itself not only as a loss of vegetative cover but also as a fundamental alteration of the environmental filters and disturbance. Changes in environmental filter such as nutrients shortage and water scarcity drive the community toward more highly tolerant species, and disturbances such as herbivory and trampling may favor ruderals (Dong et al., 2025; Wang et al., 2025). The consequent restructuring of plant communities would result in diminished ecosystem functionality, reduced resilience, and compromised capacity to deliver essential services (Gao et al., 2025). Effective

counteracting measures require a paradigm shift. We must move beyond descriptive accounts of degradation symptoms. Instead, we need a predictive and mechanistic understanding of how plant communities reassemble under different stress-disturbance regimes.

Grime's competitor-stress tolerator-ruderal (CSR) theory provides an integrative framework for this complexity (Grime, 1977). It posits that adaptive strategies of plants are shaped by the tension between resource capture (constrained by stress) and survival from biomass loss (imposed by disturbance) (Pierce et al., 2016). This tripartite model transcends species-specific details, translating intricate community assembly into a quantifiable CSR spectrum (McIntosh-Buday et al., 2024). This spectrum serves as a robust trait-based integrator, reflecting the collective ecological niche of a community. Empirical work has robustly validated that CSR strategies for the plant community undergo predictable shifts along natural environmental gradients, such as moisture (Yu et al., 2022) and salinity (McIntosh-Buday et al., 2024). Of profound concern, analogous strategic reorganizations are triggered by anthropogenic global change drivers. For example, atmospheric nitrogen (N) deposition often acts as a resource-based filter, favoring competitive species (Namuhan et al., 2024), while pervasive overgrazing constitutes a human-mediated intensification of the disturbance regime, frequently filtering communities toward S- or R-dominated assemblages (Zhou et al., 2021).

However, emerging evidence underscores that these responses are not monolithic. Their direction and magnitude are critically mediated by the local environmental context, especially the interplay between climate (e.g. aridity) and soil resource availability. This suggests that degradation may trigger multiple, distinct ecological pathways with divergent functional outcomes (Liu et al., 2023; Nishimura et al., 2025). Despite these advances, critical mechanistic gaps persist, hindering the development of a unified predictive framework for grassland dynamics under global change. First, the interactive and potentially nonadditive effects of multiple cooccurring drivers, such as the combined impacts of intensified grazing, altered precipitation regimes, and varying nutrient inputs, on plant CSR strategies remain poorly resolved (Kong et al., 2025; Scherzinger et al., 2024). These interactions are likely to dictate critical thresholds and tipping points in ecosystem states. Second, while the general mediating role of soil resources is acknowledged, the precise causal pathways and relative importance of specific soil nutrients within the cascading “degradation soil biogeochemistry plant strategy ecosystem function” demand explicit empirical elucidation (Chen et al., 2024; Fontaine et al., 2024). Research has traditionally focused on N dynamics ($\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$), a key driver of plant productivity and competition (Lai et al., 2022). However, in many grassland systems, particularly in arid and semi-arid regions where phosphorus (P) limitations are common, soil available phosphorus (AP) may constitute an equally or more critical filter shaping plant ecological strategies (Sun et al., 2023). The role of AP as a decisive environmental sieve, operating independently or synergistically with N to filter species based on their nutrient acquisition and conservation strategies, has been conspicuously underexplored within the CSR degradation paradigm (Moenclaey et al., 2021; Sun et al., 2023). Third, there is a pressing need for a holistic framework that integrates insights from natural climatic gradients with the effects of anthropogenic disturbance to forecast ecosystem trajectories (Zhang, 2024). This framework must bridge aboveground plant strategy

theory with belowground nutrient dynamics and root functional traits to reliably predict ultimate functional outcomes, especially the fate of net primary productivity and its partitioning (J. Cao et al., 2024; Zhang et al., 2026). Therefore, this study aims to fill these gaps by comprehensively investigating the impact of grassland degradation on plant CSR strategies in the significant natural aridity gradient in the northwest of China. We employed a strictly controlled paired plot design (undegraded plots and degraded plots) and conducted research in three different locations that form a continuous aridity spectrum (semi-arid alpine meadow, semi-arid marsh meadow, and extremely arid mountain grassland) to answer the following questions: 1) How does long-term grassland degradation alter the proportional composition of plant CSR strategies, and will the aridity gradient fundamentally regulate the direction of this strategy shift, thereby revealing different degradation pathways? 2) What is the relative contribution of soil N and P availability in mediating the reorganization of plant CSR strategies after degradation? 3) How does the overall CSR strategy shift with degradation subsequently determine the net primary productivity and its partitioning, and can the changes in productivity be predicted from the corresponding changes in the CSR strategy? By systematically addressing these questions, this work aims to advance a nuanced, process-based understanding of grassland degradation.

Materials and Methods

Study area and experimental design

This study was carried out at three montane grassland sites in northwestern China, representing a strong aridity gradient from semi-arid to hyper-arid conditions (Table 1). Detailed information on the three sites was provided as follows. Eastern Qilian Mountains (EQM), located on the northeastern margin of the Qinghai-Tibet Plateau, features a semi-arid (aridity index = 0.63) alpine climate. The vegetation is classified as an alpine meadow, dominated by dense, low-growing sedges of the *genus Kobresia*, primarily *K. capillifolia* and *K. pygmaea*. Dashalong (DS), also located on the Qinghai-Tibet Plateau, is a semi-arid (aridity index = 0.68) marsh meadow. It supports a community of moisture-tolerant sedges and grasses, with dominant species including *K. capillifolia*, *K. tibetica*, and *C. moorcroftii*. Cele (CL), located in the southern Xinjiang basin, experiences a continental hyper-arid climate (aridity index = 0.025). The vegetation is a sparse mountain steppe, dominated by drought-tolerant shrubs and herbs such as *Artemisia frigida* and *Allium ramosum* in undegraded states, with significant bare ground.

At each site, we employed a paired-plot design with five replicates. For each grassland type, we carefully selected one undegraded (UD) plot and one degraded (D) plot in close proximity to ensure similar macroclimatic and geological conditions. UD plots were characterized by stable high-coverage vegetation, representing the potential natural state with minimal anthropogenic disturbance. The D plots exhibited clear visual signs of degradation, including reduced vegetation cover, soil erosion, and a shift in species composition toward less palatable or invasive species, primarily as a result of long-term overgrazing. Detailed criteria for classifying undegraded (UD) and degraded (D) plots are provided in the Supporting Information.

Plant productivity measurement

At the peak of the growing season (August 2024), within each large sampling plot (20 m × 20 m), we established five randomly placed independent 50 cm × 50 cm quadrats for the above-ground biomass harvest plot. All living plant material (growth for the current year) was separated from the litter. Within each quadrat, living biomass was further sorted into four primary functional groups: sedges, legumes, grasses and forbs. All samples were placed in paper bags, oven dried at 65°C for 48 hours to a constant weight, and then weighed with a precision of 0.01 g. ANPP for each plot and functional group was calculated as the mean dry mass per square meter per year ($\text{g m}^{-2} \text{yr}^{-1}$).

Net below-ground primary production (BNPP) was estimated using the highest standing root biomass method, a common approach in grassland ecosystems where root turnover within a single growing season is assumed to be minimal (Milchunas, 1992). During the biomass harvest, three soil cores (7 cm in diameter) were randomly taken from each plot to a depth of 30 cm. Each core was immediately separated into three depth segments: 0–10 cm, 10–20 cm, and 20–30 cm. The soil samples were placed in sealed plastic bags and stored at 4°C. In the laboratory, the roots were carefully washed free of soil over a 0.5 mm sieve. Live roots (distinguished by color, elasticity and the presence of stele) were collected, oven dried at 65°C for 72 hours and weighed. The total BNPP for each plot and for each soil layer was expressed as root biomass per square meter (g m^{-2}).

Soil nutrient analysis

Five soil samples (0–30 cm depth) were randomly collected from each plot using a soil auger. The five subsamples of the same plot were thoroughly mixed to form a composite sample, which was intended to represent the average soil condition of that plot. Visible roots and stones were removed. The soil was then sieved through a 2 mm mesh. A portion of fresh soil was stored at 4°C for immediate analysis of inorganic nitrogen. Soil ammonium ($\text{NH}_4^+\text{-N}$) and nitrate ($\text{NO}_3^-\text{-N}$) were extracted with 2M KCl (soil: solution ratio of 1:5) by shaking for 1 h. The extracts were filtered, $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were determined using a continuous-flow autoanalyzer (SEAL Analytical AutoAnalyzer 3, Northern Ireland, UK). Soil-available phosphorus (AP) was extracted with 0.5 M NaHCO_3 (Olsen method) and colorimetrically quantified via the molybdenum blue reaction, measuring absorbance at 880 nm. Results were calculated against a standard curve of KH_2PO_4 and expressed as mg P kg^{-1} dry soil.

Plant functional traits and CSR strategy calculation

Adjacent to the quadrants used for community surveys, a dedicated 50 cm × 50 cm functional trait measurement quadrat was established for each species within each plot. Within each trait measurement quadrant, at least 15 groups of healthy mature leaves exposed to the sun were selected per species (for species with small leaves, 10 leaves per group were collected to reduce the measurement error). According to the standardized procedures, the following characteristics were measured. Fresh leaf

weight (LFW) and leaf area (LA) were measured immediately after collection using a portable leaf area meter (LI-3000C, LI-COR Biosciences). The leaves were then oven dried at 70°C for 72 h to determine the dry weight of the leaf (LDW). The CSR strategy for each species was determined using the "StrateFy" algorithm (Pierce et al., 2017). The community-weighted mean (CWM) CSR coordinates for each plot were then calculated by averaging the CSR scores of all species present, weighted by their relative percent cover.

Statistical analyses

All statistical analyses were performed in the R software (v4.2.0). Significance was accepted at $\alpha = 0.05$. We used a two-way analysis of variance (ANOVA) to test the fixed effects of site (EQM, DS, CL), degradation (UD, D) and their interaction with ecosystem properties and diversity, including ANPP, BNPP (total and by layer), α -diversity indices, and soil nutrients. When the interaction was significant, simple effects analyses were conducted. Data were checked for normality (Shapiro-Wilk test) and homoscedasticity (Levene test). BNPP data were logarithmically transformed to meet the ANOVA assumptions. Post hoc comparisons were performed using Tukey's Honest Significant Difference (HSD) test. The results are presented as mean $\pm$ standard error. Shifts in community-weighted C, S, and R scores were visualized on ternary plots using the *ggtern* package. The statistical significance of the difference in the overall composition of the CSR strategy between UD and D at each site was tested using PERMANOVA on a Euclidean distance matrix of the C-S-R coordinates. For each model, the percentage increase in the mean squared error (% IncMSE) when a given variable was permuted was used as the metric for the importance of the variable. To identify the drivers of the community-weighted CSR strategies, we constructed three separate random forest models (for CWM_C, CWM_S, and CWM_R) with the following predictor groups: a) Plant Community Structure: Shannon index (H'), Simpson index (D), species richness (S), and the β -diversity turnover component (β_{sim}) between UD and D; b) soil nutrients: NH_4^+ -N, NO_3^- -N, and AP concentrations; c) Climate: Aridity Index and Mean Annual Precipitation (MAP). The relative importance of each predictor variable and each group was assessed based on the %IncMSE. The explanatory power of the model was evaluated using pseudo- R^2 ($1 - [MSE / \text{variance of the response variable}]$).

Results

Plant productivity and community diversity along grassland degradation

The three sites exhibited markedly different trajectories in above-ground –below-ground biomass allocation after degradation (Fig. 2). At EQM, a pronounced belowground compensation occurred: ANPP decreased by 84% while BNPP increased by 439%, driving the root-to-shoot ratio from 1.7 to 56.4. This massive root proliferation was concentrated in the surface layer (0–10 cm), whose proportion of total BNPP rose from 76% to 89% and was accompanied by a collapse of sedge dominance aboveground. At

DS, a coordinated decline in both ANPP and BNPP was observed, with reductions of 37% and 78%, respectively. The loss of root biomass was evenly distributed across all soil layers. At CL, functional group reorganization rather than major ANPP change characterized the response. ANPP decreased only marginally (12%, not significant), while BNPP declined substantially by 59%. In particular, ANPP of legumes increased threefold, greatly enhancing their relative importance in the degraded community.

Drought-dependent effects of grassland degradation on soil nutrients

Soil nutrient responses to degradation exhibited strong site-specific patterns along the aridity gradient (Fig. 3). At EQM, degradation triggered divergent N responses: NO_3^- decreased by 64%, while NH_4^+ and AP increased by 30% and 265%, respectively. In DS, NO_3^- more than doubled (158% increase), while NH_4^+ remained stable and AP increased by 95%. On the contrary, at the hyperacid CL site, degradation led to consistent declines in all measured nutrients: NH_4^+ , NO_3^- and AP decreased by 39%, 42% and 28%, respectively. Collectively, these results reveal that degradation does not uniformly deplete soil nutrients, but triggers site-specific biogeochemical responses modulated by baseline aridity, with contrasting patterns in N form availability across the gradient.

Site-specific shifts in CSR strategies induced by degradation

The impact of degradation on plant CSR strategies was site-specific, leading to a different restructuring of CSR proportions throughout the aridity gradient (Fig. 4). In EQM, degradation intensified the dominance of stress-tolerators: S strategy increased from ~ 80% to ~ 91%, while R strategy declined sharply from ~ 14% to ~ 2%, with C strategy remaining a minor and stable component. At DS, degradation promoted a shift toward a more ruderal stress-tolerant mixture: the R strategy more than doubled (from ~ 5% to ~ 14%), accompanied by a modest decline in the dominant S strategy (from ~ 89% to ~ 84%) and a halving of the already low C strategy. At CL, degradation rebalanced the community towards greater tolerance to stress: the R strategy decreased from ~ 20% to ~ 12%, while the S strategy increased from ~ 78% to ~ 85%, with the C strategy showing only a marginal change.

The environmental drivers of the CSR change along degradation

Random forest analysis identified soil properties as the dominant drivers of CSR changes, accounting for 49%, 66%, and 75% of the variance in ΔC , ΔS , and ΔR , respectively. Climatic factors explained 27% of ΔS and 17% of ΔR , but had negligible influence on ΔC , while the diversity metrics of the plant community contributed less than 11% in all strategies. For individual variables, ΔNO_3^- was the most influential predictor of ΔC (8.5% importance), whereas ΔNH_4^+ was the main driver for both ΔS (33.2%) and ΔR (39.8%), followed by ΔAP and ΔNO_3^- .

The correlation analysis confirmed these patterns: ΔS was positively correlated with ΔNH_4^+ and ΔP , and negatively with ΔNO_3^- . ΔR exhibited opposite relationships, negatively correlating with ΔNH_4^+ and ΔP , and positively with ΔNO_3^- . ΔC showed no significant correlations with soil nutrients. Among nutrients, ΔNO_3^- was negatively correlated with ΔP , while ΔNH_4^+ and ΔP were positively correlated.

Structural equation model linking soil nutrients, productivity, and CSR strategies

We constructed a structural equation model to examine pathways linking soil nutrient changes to CSR changes (Fig. 7). Soil nutrients ($\Delta \text{Nutrients}$) were positively associated with ΔANPP and negatively with ΔBNPP . ΔBNPP negatively predicted ΔCSR . These results demonstrate that the effects of nutrients on the CSR strategy operate indirectly through altered subsurface productivity allocation.

Discussion

The aridity-dependent restructuring of plant strategies reveals divergent ecological pathways in degraded grasslands

This study provides empirical evidence that long-term grassland degradation induces distinct and context-dependent changes in plant CSR strategies, and aridity serves as a critical modulator of these trajectories (J. Cao et al., 2024). In line with our first research question, we found that degradation did not produce a uniform directional change in CSR profiles, but instead triggered divergent strategic reassemblies across the aridity gradient (Kim et al., 2023). In the semiarid alpine meadow (EQM), degradation intensified the existing S dominance while nearly eliminating R species (Fig. 4) (Bricca et al., 2022). This response likely stems from synergistic mechanisms that include soil compaction, reduced water infiltration, and nitrate depletion, which collectively strengthen abiotic filters that favor conservative traits such as a high content of dry matter in leaves and a low specific area of leaves. On the contrary, at the hyperarid site (CL), degradation attenuated R and reinforced S (Fig. 4), reflecting a strategic rebalancing toward a more stress-adapted community. Here, extreme baseline aridity may restrict further abiotic stress amplification, causing chronic overgrazing to operate primarily through disturbance-mediated biotic filtering that favors persistence traits over ruderal opportunism. This mechanism is consistent with observations from long-grazed arid systems, where millennia of pastoral history have already filtered out disturbance-sensitive species, leaving stress-tolerant dominants that respond to increased grazing primarily through selective herbivory effects rather than additional abiotic stress (Jauffret & Visser, 2003). The semi-arid marsh meadow (DS) exhibited an intermediate yet distinct response, with a marked increase in R-strategy contribution (Fig. 4), suggesting a disturbance-amplification pathway wherein waterlogging stress and grazing jointly create microsites for ruderal species. This pattern aligns with findings from semi-arid depressional wetlands, where heavy livestock

use was positively correlated with ruderal abundance, and grazing-induced soil disturbance was identified as the primary driver of plant strategy shifts (Teuber et al., 2013). The study further demonstrated that in wetland systems, background stress from waterlogging interacts with grazing disturbance to alter competitive hierarchies and create colonization niches, thus promoting ruderal establishment despite prevailing stress conditions. These findings collectively demonstrate that aridity regulates not only the magnitude but also the direction of CSR reorganization (J. Cao et al., 2024), thereby revealing multiple degradation pathways that diverge along a climatic continuum.

The availability of available soil emerges as the predominant biogeochemical filter that governs the reorganization of CSRs along degradation.

Our results reveal that soil N dynamics, particularly the distinct roles of ammonium and nitrate, plays a dominant role in mediating CSR reorganization, while P availability plays a secondary but synergistic role. Random forest models (Fig. 5) showed that changes in available N in the soil accounted for the majority of the explained variance in the shifts of the stress tolerator (S) and ruderal (R) strategies. On the contrary, available P contributed substantially but to a lesser degree. Correlation analyses further clarified the directionality (Fig. 6): The increase in strategy S was associated with an increase in NH_4^+ and P but a decrease in NO_3^- , while the increase in strategy R was related to an increase in NO_3^- but a decrease in NH_4^+ and P. These contrasting patterns indicate that the N forms act as distinct biogeochemical filters: NH_4^+ enrichment favors strategies of S, while accumulation of NO_3^- favors strategies of R. NH_4^+ dominated conditions often occur under low soil disturbance and high organic matter accumulation, favoring conservative resource use traits typical of stress-tolerators (Ashton et al., 2010). In contrast, NO_3^- is more mobile and typically increases under moderate disturbance or nitrification promoting conditions, which can benefit fast-growing ruderal species with higher nitrogen demand (Grassein et al., 2015). Our site-specific patterns align with these mechanisms: for instance, the pronounced depletion of NO_3^- in degraded EQM plots likely filtered out competitor-leaning species and reinforced stress-tolerator dominance. Similarly, at the CL site, concurrent declines in both NH_4^+ -N and NO_3^- -N may have further constrained ruderal species with high nutritional demands, explaining the observed reduction in the proportion of R strategy. This interpretation is supported by evidence that ruderal species typically exhibit lower nitrogen use efficiency (NUE), meaning they require greater soil N availability to sustain growth and competition (Ding, 2024), and that high N inputs are positively correlated with the abundance of ruderal strategies in grassland communities (Leslie Mauchamp, 2016). Although P limitation is often highlighted in arid and semi-arid grasslands, our results indicate that within the timeframe and degradation stages examined, N availability acts as a more sensitive and immediate regulator of plant strategic trade-offs. This may be attributed to the central role of N in controlling photosynthetic capacity, growth rates, and competitive hierarchies, key traits differentiating C-, S-, and R-strategists (Ding, 2024; T. Zhou et al., 2021). The stronger explanatory power of the N metrics does not imply that P is irrelevant but rather suggests that the dynamics of N represents a faster-responding filter in the initial to midphases of degradation, possibly due to its high mobility and susceptibility to grazing-

induced alterations in mineralization and uptake. Our structural equation model further elucidated the pathway underlying this nutrient-strategy link (Fig. 7). Changes in available nutrients in the soil were associated with a pronounced reallocation of productivity from the belowground to the aboveground components, and the resulting decrease in belowground productivity was in turn associated with changes toward more stress-tolerant CSR strategies. In particular, the direct path from soil nutrients to CSR was not statistically significant, suggesting that the influence of soil biogeochemistry on plant strategy reorganization may be primarily indirect, operating through changes in biomass allocation.

Linking CSR strategy shifts to ecosystem functional outcomes: predictive insights for productivity partitioning along degradation

How does the overall CSR reorganization of the community determine the magnitude and distribution of net primary productivity (NPP), as well as whether the distribution on the aboveground (ANPP) and underground (BNPP) can be predicted from the dominant strategies? Although the SEM above examined how soil nutrients affect CSR via BNPP, the reverse direction, how CSR shifts in turn constrain productivity allocation, is equally important for ecosystem functioning. Our results established a clear mechanistic link between the composition of the CSR and functional responses of the ecosystem, supporting a trait-based framework for forecasting productivity patterns (Liu et al., 2025). At EQM, the extreme S dominance after degradation (Fig. 4) and associated with a belowground compensation response (Fig. 2) reflects a resource allocation strategy in which plants under heightened stress invest disproportionately in root systems to improve soil foraging and persistence, a functional signature of stress-tolerator communities (Moeneclaey et al., 2021). In contrast, in DS, the profile of the mixed R-S strategy coincided with a systemic decline in both ANPP and BNPP (Fig. 2), suggesting that the conjunction of water limitation and disturbance exceeded the compensatory capacity of the community, leading to broad reductions in metabolic activity. At CL, the shift toward S-strategy dominance accompanied a functional reassembly pattern, wherein ANPP remained stable despite a 59% decline in BNPP, alongside a notable increase in legume contribution (Fig. 2). This indicates that in extremely arid systems, productivity is maintained not through biomass accumulation but through functional group turnover and symbiotic nitrogen fixation - a strategy consistent with stress-adapted communities optimizing limited resources (Li et al., 2024; Wei et al., 2019). These patterns collectively indicate that the CSR composition serves as a diagnostic indicator of the allocation of carbon in the ecosystem. S-dominated systems favor below-ground sinks, R-influenced systems emphasize above-ground turnover, and mixed strategies reflect unstable or transitional functional states (J. Cao et al., 2024). Although the predictive power of CSR shifts for productivity outcomes is supported by the consistent associations observed across divergent aridity contexts, further validation through independent datasets or experimental manipulations would be valuable to establish causality and quantify prediction uncertainty. However, our findings collectively demonstrate that the CSR composition of a community, particularly the balance between the S and R strategies, offers a predictive lens for the allocation of above-ground versus below-ground productivity.

Conclusions

Grassland degradation restructures plant communities, but the direction and magnitude of this restructuring are not uniform. Our study demonstrates that aridity critically modulates the ecological outcomes of degradation, leading to divergent shifts in plant CSR strategies along a climatic continuum. Among the drivers examined, the available nitrogen in the soil, particularly the contrasting roles of ammonium and nitrate, became the predominant biogeochemical filter that governs the reorganization of the CSR. The structural equation model further revealed that the influence of soil nutrients on CSR is not direct but is fully mediated by changes in bottom productivity. By linking CSR shifts to changes in productivity allocation, our results offer predictive insights for ecosystem functioning: stress-tolerator dominance was consistently associated with belowground biomass compensation, while ruderal increases coincided with aboveground turnover or systemic productivity decline. Collectively, this work advances a nutrient-explicit mechanism-based understanding of plant community reassembly under grassland degradation, highlighting the need for context-dependent, trait-based frameworks to anticipate ecosystem trajectories and guide resilience-oriented management.

Declarations

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Author contributions

Jun Zhou, Hongtao Zhong, Benfeng Yin and Fei Peng conceived the ideas and designed methodology; **Jianbo Sun, Xiaolong Li, Lin Wu, Yuan Liu, Xingzhi Xu and Feifei Wang** collected the data; **Jianbo Sun, Mingting Hu, Xiaojie Chen and Ben Chen** analysed the data; **Jianbo Sun** led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests None declared.

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Table 1

Table 1 is available in the Supplementary Files section.

Figures

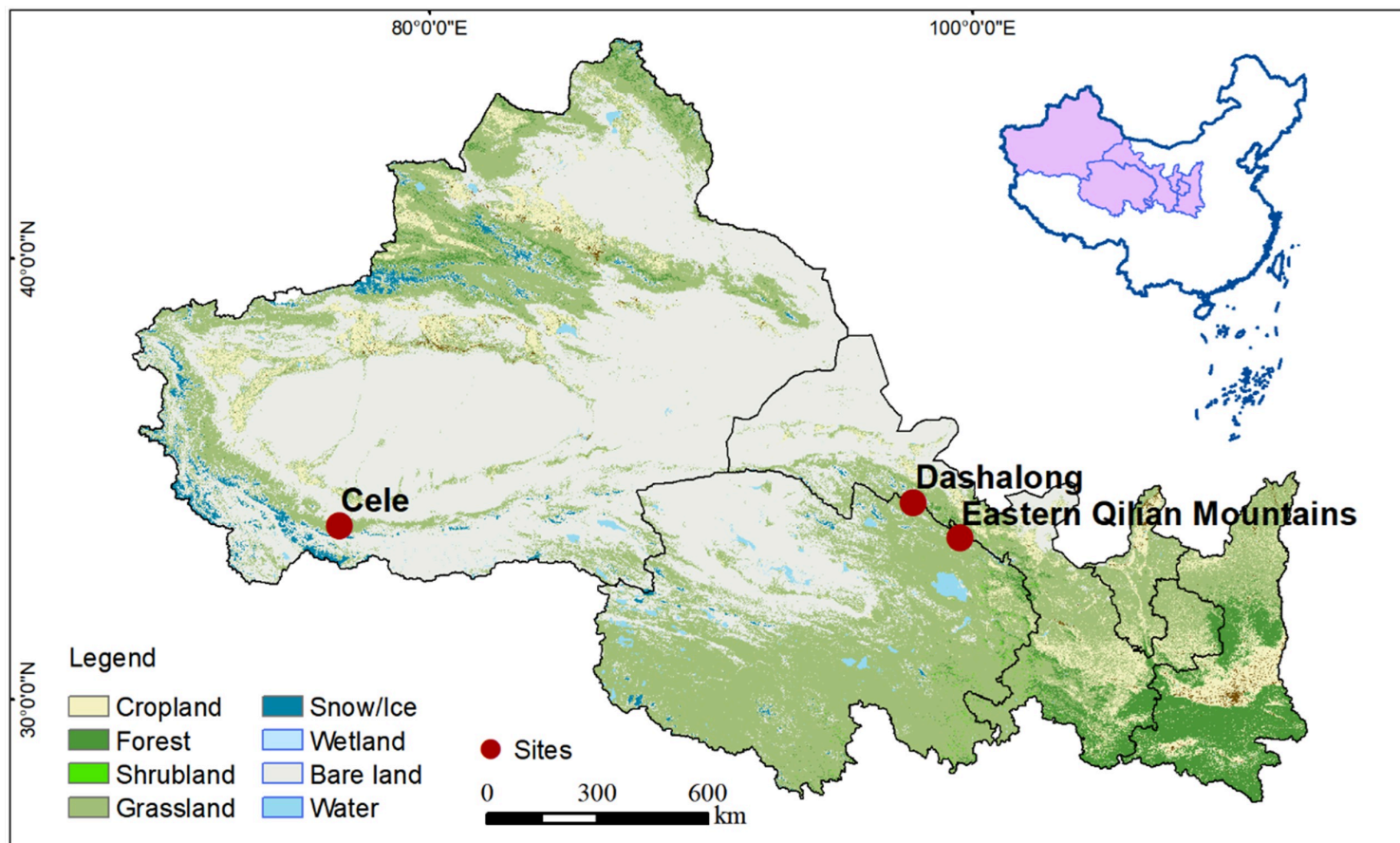


Figure 1

Location of the montane grasslands in this study and land cover and land use of the study area. EQM, Eastern Qilian Mountains; DS, Dashalong; CL, Cele.

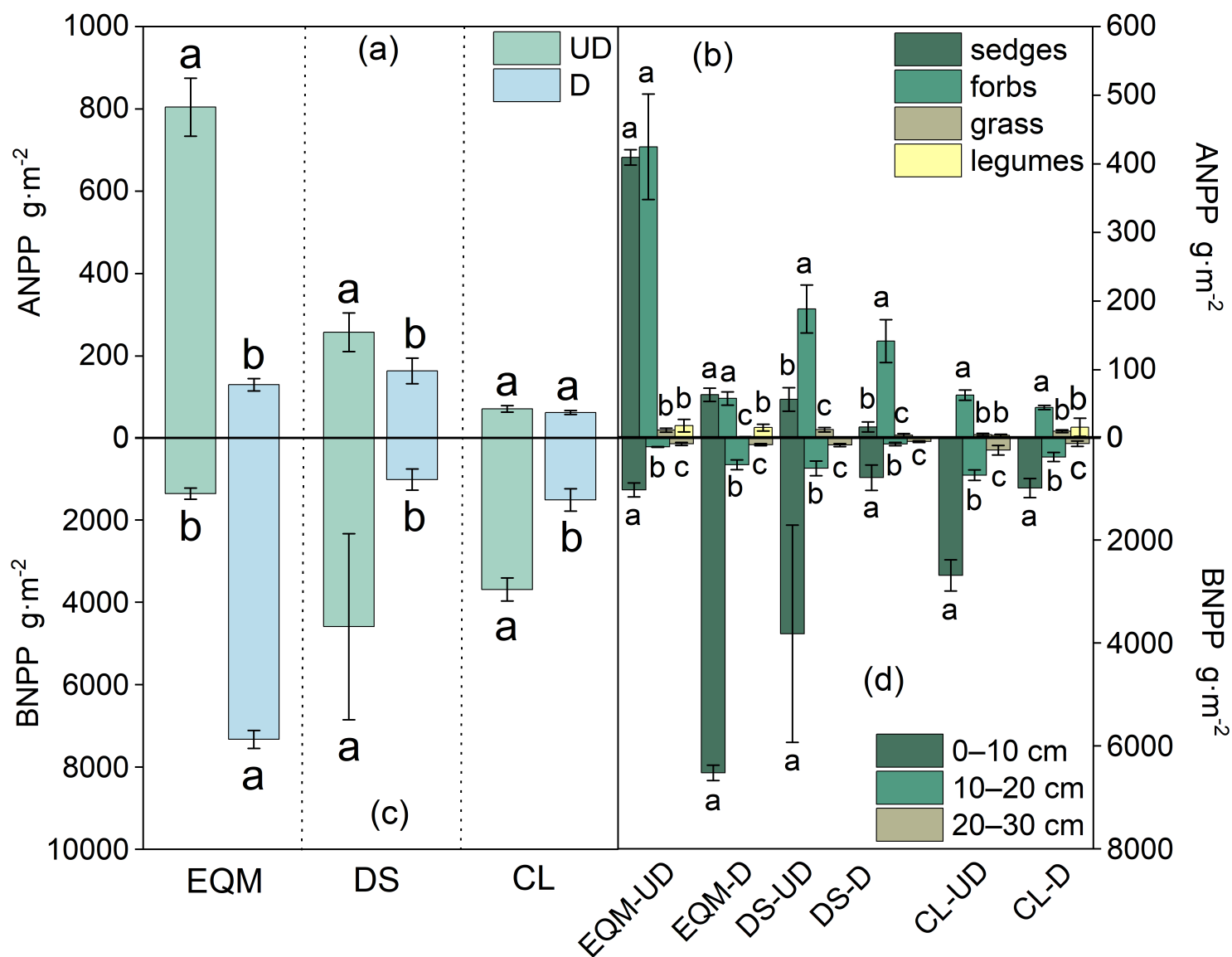


Figure 2

Contrasting biomass allocation in response to grassland degradation at three sites. ANPP and BNPP: Net primary productivity above ground and belowground net primary productivity; UD: undegraded grassland; D: degraded grassland. Values are means $\pm$ SE.

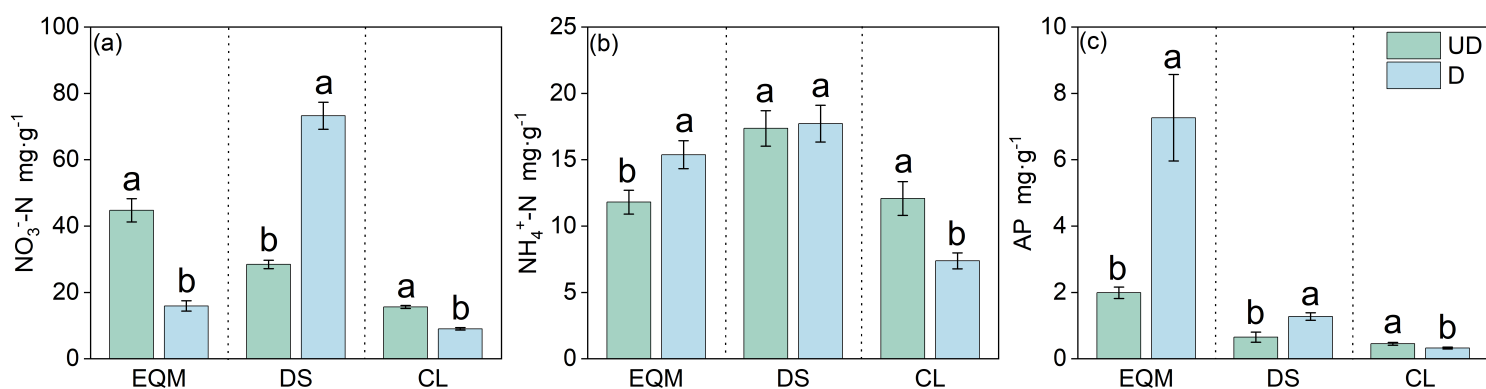


Figure 3

Differential effects of grassland degradation on soil nutrients across an aridity gradient. (a) Nitrate N (NO_3^- -N), (b) ammonium N (NH_4^+ -N), and (c) available P between undegraded (UD) and degraded (D) states at the three study sites (EQM, DS, CL). Values are means $\pm$ SE.

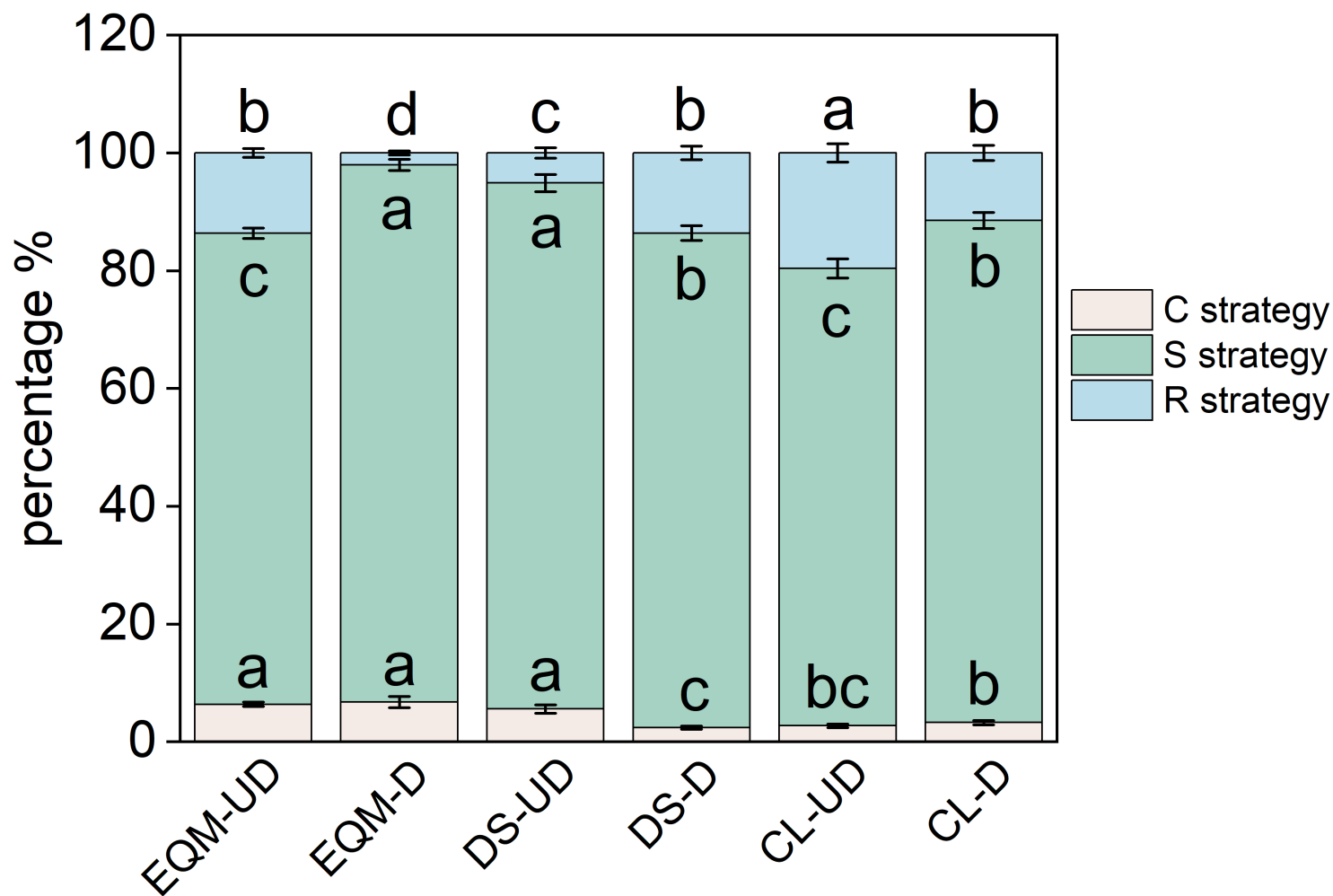


Figure 4
Changes in CSR plant strategies across sites with different aridity and grassland degradation states.

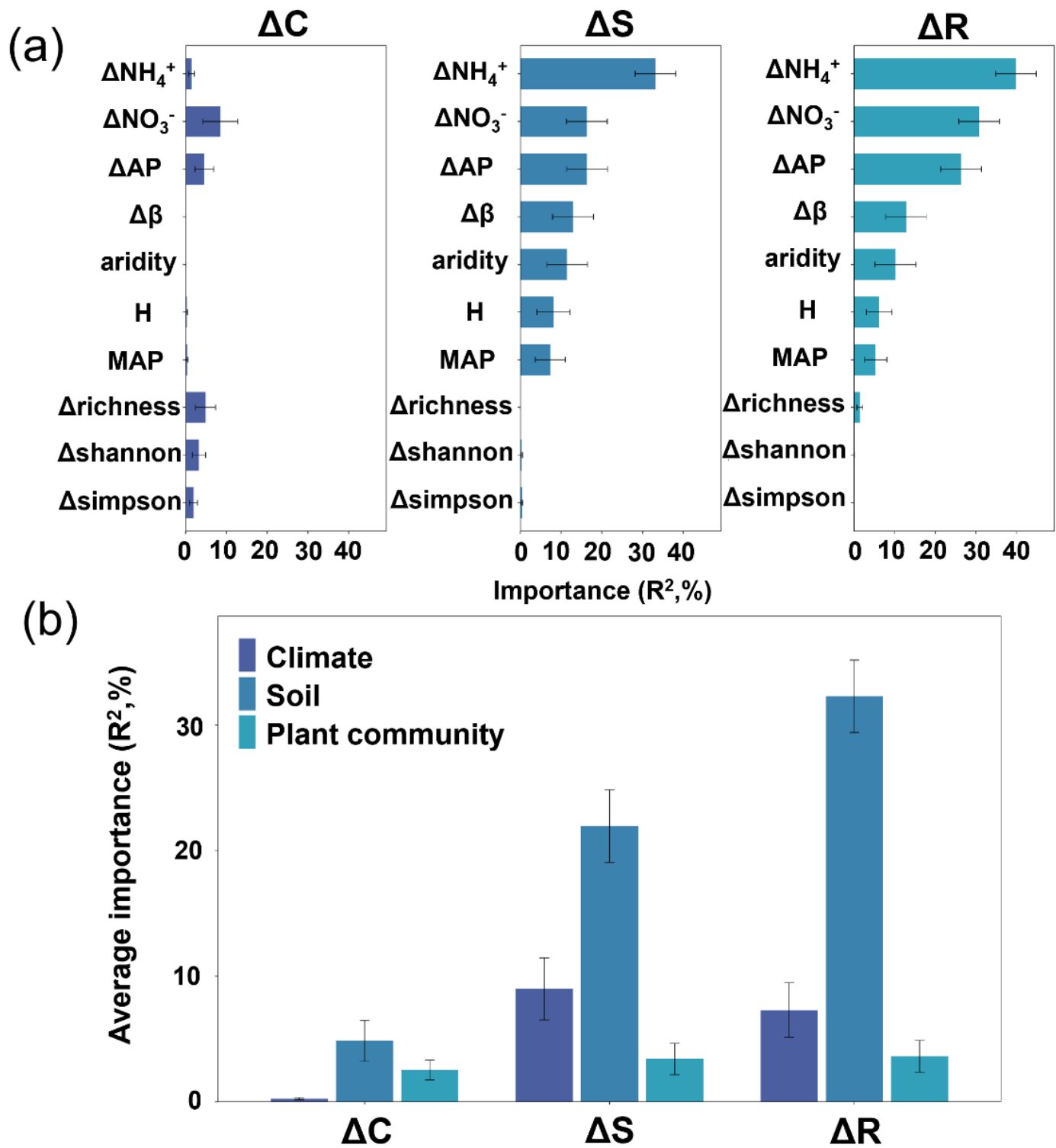


Figure 5

Relative importance of environmental drivers for degradation-induced changes in CWM CSR strategies. (a) Importance of individual variables within each group. (b) Importance of factor groups (climate, plant community, soil).

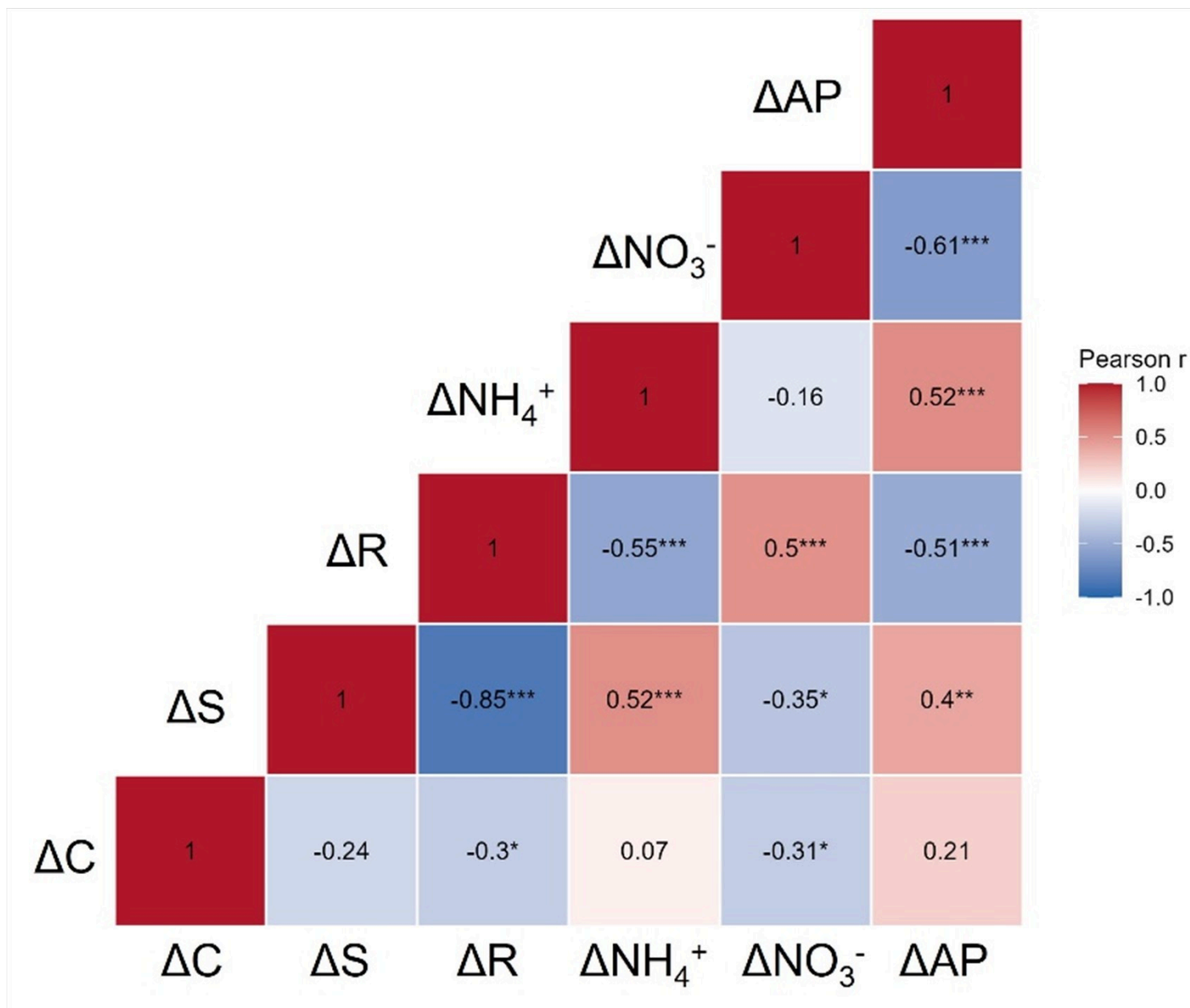


Figure 6

Correlation matrix among changes in CSR strategies and soil nutrient variables. Values represent Pearson correlation coefficients. The size of the circle is proportional to the absolute value of the correlation coefficient, with blue and red indicating positive and negative correlations, respectively. ΔC , ΔS , and ΔR represent changes in community weighted C, S, and R-scores; ΔNH_4^+ , ΔNO_3^- , and ΔP represent changes in soil ammonium nitrogen, nitrate nitrogen, and available phosphorus concentrations, respectively. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

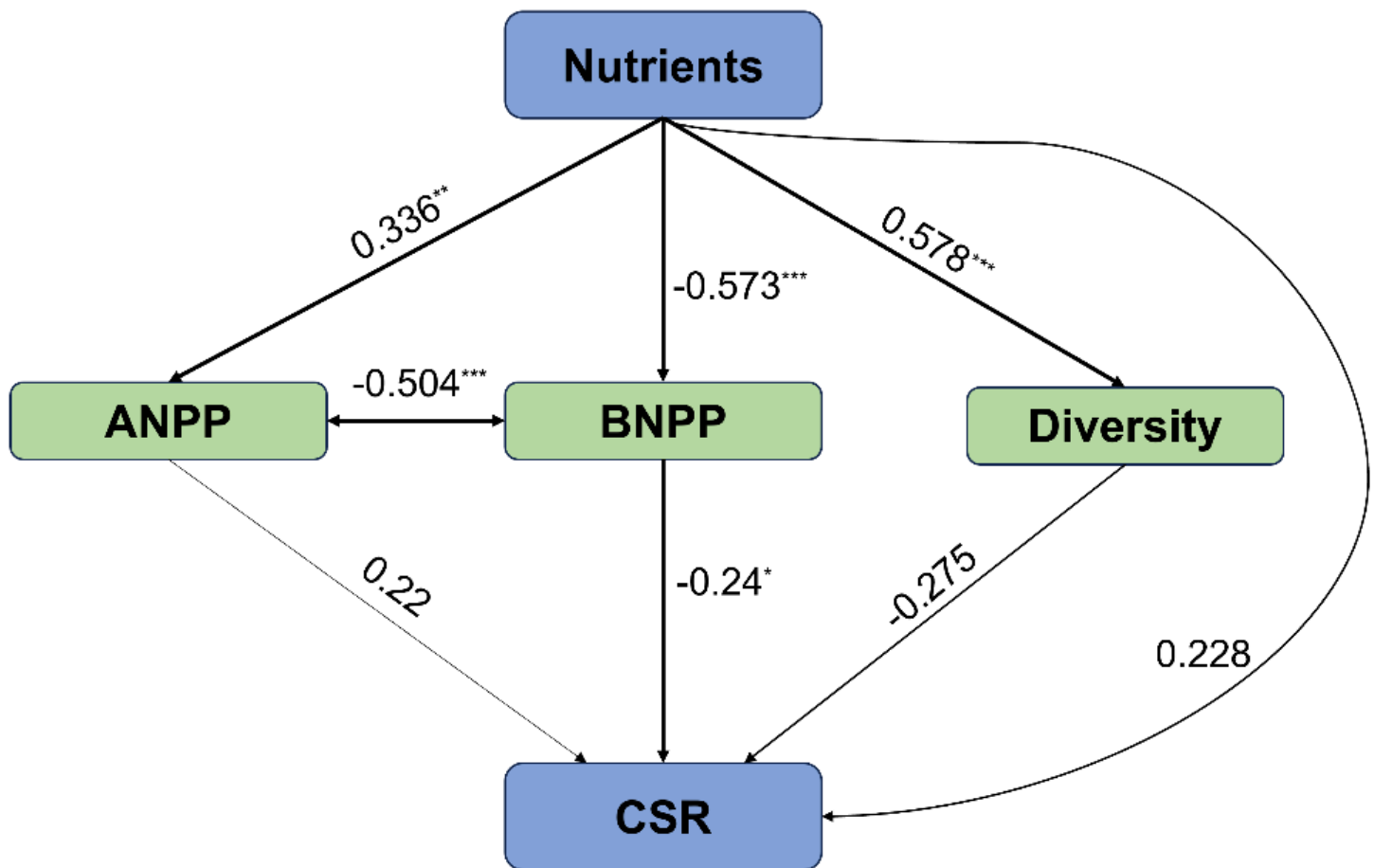


Figure 7

Model of the structural equation of differences (Δ , degraded minus nondegraded) between soil nutrients (mean of ΔNH_4^+ , ΔNO_3^- , ΔP), diversity (mean of $\Delta\text{Shannon}$, $\Delta\text{Simpson}$, $\Delta\text{Richness}$), ANPP and BNPP, and CSR strategy. The numbers are standardized path coefficients. Thick and thin arrows denote significant ($P < 0.05$) and non-significant paths, respectively (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns $P \geq 0.05$). Model fit: CFI = 0.906, SRMR = 0.075.

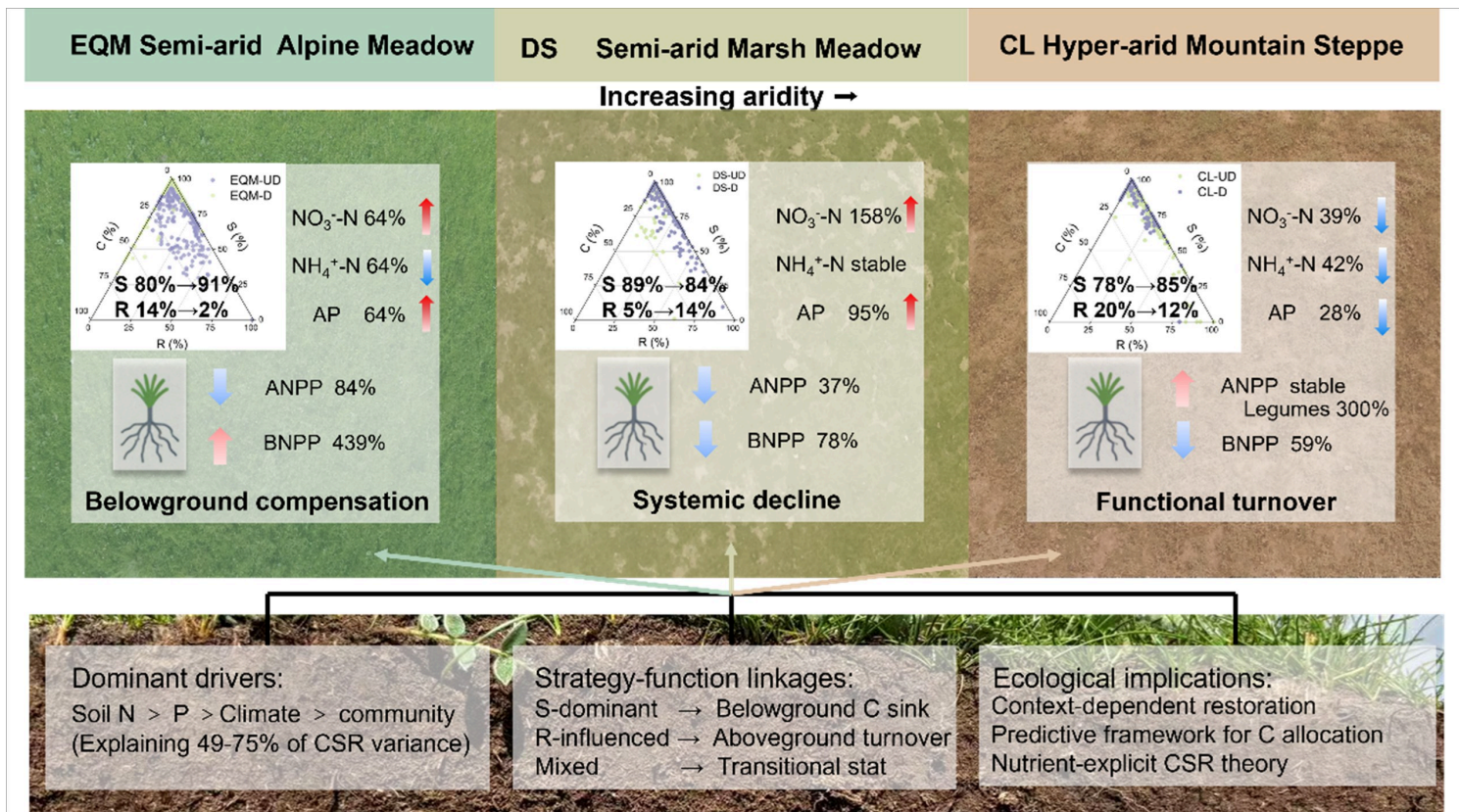


Figure 8

Conceptual framework illustrating divergent pathways of plant CSR strategy shifts and ecosystem functional responses to grassland degradation across an aridity gradient.

Supplementary Files

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