

Article

Contrasting Effects of Plant Functional Traits, Functional Diversity and Abiotic Factors on Ecosystem Service Multifunctionality Across Inner Mongolian Steppe Types

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Abstract

Plant functional traits, as indicators of community responses to disturbances, are key drivers of ecosystem service multifunctionality (ESMF). However, the relative contribution of these traits to ESMF across different steppe types remains unclear. Using data from 101 sampling sites across Inner Mongolia's meadow steppe (MS), typical steppe (TS), and desert steppe (DS), we examine the contributions and driving mechanisms of abiotic (climate and soil) and biotic factors (23 community-weighted mean functional traits and diversity indices) to ESMF across different steppe types. Our results show significant differences in ESMF across steppe types, with a decreasing trend from MS to TS to DS. Crucially, the driving factors of ESMF shift fundamentally across steppe types. In MS, ESMF is primarily driven by biotic factors (e.g., stem N:P ratio), whereas as aridity increases, abiotic factors (e.g., aridity and soil clay content) become more influential, ultimately dominating ESMF in DS. This shift from niche differentiation to environmental filtering as the dominant mechanism provides a crucial framework for predicting ecosystem service responses to global change. It highlights the importance of context-dependent grassland conservation strategies, advocating for location-specific management based on environmental gradients.

Keywords: ecosystem service multifunctionality; plant functional traits; functional diversity; steppe types; biotic factors; abiotic factors



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1. Introduction

Grasslands are among the most extensive terrestrial ecosystems globally [1], providing vital services such as forage production, nutrient cycling, water conservation, wind erosion control, and biodiversity maintenance [2,3]. Plant functional traits and their diversity are key links between environmental changes, community structure, and ecosys-

tem function [4,5], providing essential insights into ecosystem service multifunctionality. Given that habitat differences shape both plant community structure and its abiotic context [6], and that grassland types vary significantly in their physiological responses to drought [7,8], the impact of plant traits and diversity on ecosystem multifunctionality is likely grassland-type dependent. Elucidating the mechanisms that sustain multifunctionality in specific grassland types is essential for predicting functional changes and optimizing conservation strategies.

Plant functional traits are morphological, physiological, and chemical characteristics shaped by long-term adaptation and evolution, reflecting strategies for survival and resource utilization [9]. At the community level, studying functional traits offers key insights into community dynamics and changes in ecosystem functions [10]. Researchers often combine community structure with community-weighted mean (CWM) [11] and functional diversity indices (FD) [12] to characterize functional traits and clarify the relationship between biodiversity and ecosystem function. The functional trait driver theory posits that biotic, abiotic, and neutral processes together shape community trait distributions, thereby influencing ecosystem processes and functions [13]. Combining CWM and FD offers a more comprehensive representation of community functional traits, enhancing understanding of trait variation along environmental gradients and its impact on ecosystem function.

Plant functional traits represent community resource utilization strategies and drive multifunctionality through fundamental ecological processes [14,15]. Plant traits predict ecosystem function primarily through the mass-ratio and niche complementarity hypotheses. The mass-ratio hypothesis suggests that the functional traits of dominant species drive ecosystem processes [16], while the niche complementarity hypothesis highlights that functional diversity reflects species' resource acquisition and adaptation strategies, thereby enhancing and linking multiple ecosystem functions [17,18]. Studies have shown that in alpine meadows [19] and desert steppe [20], ecosystem multifunctionality is positively correlated with resource acquisition traits, such as specific leaf area. Research in temperate forests also identifies specific leaf area as a key determinant of multifunctionality [21]. Meanwhile, environmental stress may impair ecosystem function by promoting trait convergence and reducing functional diversity [22]. However, the influence of plant functional diversity on multifunctionality is not universally consistent. In arid grasslands, functional diversity is positively correlated with ecosystem multifunctionality [20,23], but in controlled experiments on the Tibetan Plateau and desert steppe, its explanatory power for soil multifunctionality is limited or insignificant [24,25].

Environmental factors, such as climate and soil, regulate multiple ecosystem services directly or indirectly by shaping plant community composition and structure [26,27]. Studies have shown that aridity significantly reduces grassland ecosystem multifunctionality, while soil clay content enhances multifunctionality [28]. Soil moisture promotes ecosystem multifunctionality by enhancing processes such as productivity and enzyme activity [29,30]. In degraded alpine meadows [31] and alpine swamp meadows [24], soil pH significantly inhibits ecosystem multifunctionality. Additionally, soil pH can also indirectly affect soil carbon storage through its regulation of belowground biomass [32]. These results highlight the pivotal role of abiotic factors, including climate and soil, in shaping ecosystem multifunctionality.

The Inner Mongolian grassland, a key representative of Eurasian grasslands, spans a significant moisture gradient, ranging from meadow steppe in the east to desert steppe in the west [33]. Existing studies demonstrate that variations in water and thermal conditions lead to significant differences in plant community traits, soil properties, and ecosystem

multifunctionality across grassland types [34–36]. In particular, aridity has been shown to affect ecosystem multifunctionality by regulating biodiversity [27]. Identifying the mechanisms underlying biotic and abiotic factors is crucial for predicting ecosystem function [37]. However, how plant functional traits, functional diversity, and ecosystem service multifunctionality vary among steppe types and respond to biotic and abiotic factors remains insufficiently understood. In this study, we conducted a field survey across 101 sites covering meadow, typical, and desert steppes in Inner Mongolia. Specifically, this study aimed to (1) compare plant functional traits, functional diversity, and ecosystem service multifunctionality among the three steppe types and (2) disentangle the relative roles of biotic factors (community-weighted mean traits and functional diversity) and abiotic factors (climate and soil properties) in shaping ecosystem service multifunctionality across steppe types. We hypothesized that (1) plant functional traits, functional diversity, and ecosystem service multifunctionality would differ significantly among steppe types because of contrasting habitat conditions associated with aridity; and (2) the drivers of ecosystem service multifunctionality would vary among steppe types, with biotic factors playing a greater role in meadow steppe and abiotic factors becoming more important in desert steppe.

2. Materials and Methods

2.1. Study Area

This study was conducted in the grassland ecosystems of Inner Mongolia Autonomous Region, encompassing 101 sampling sites (Figure 1 and Table S1). A transect-based sampling design was used across a 1500 km east–west aridity gradient to capture natural variation among the three steppe types. The study area (39.3–49.6° N, 107.2–120.3° E) lies within a temperate continental climate zone, exhibiting a significant climatic gradient from east to west, with annual precipitation ranging from 158 to 389 mm and temperatures ranging from −1.1 to 8.4 °C. Along the aridity gradient, the three steppe types differed markedly in climate, vegetation structure, and soil conditions (Tables S2 and S3). Meadow steppe in the relatively humid eastern region (24 sites) was characterized by higher plant cover and productivity and was dominated by *Stipa baicalensis*, *Spiraea salicifolia*, and *Sanguisorba officinalis*. Typical steppe in the central region (45 sites) represents the zonal temperate grassland of Inner Mongolia and occupied an intermediate position between meadow and desert steppes in terms of water availability, vegetation cover, and community structure; its vegetation was mainly composed of *Stipa grandis*, *Stipa capillata*, *Leymus chinensis*, and *Cleistogenes squarrosa*. Desert steppe in the drier western region (32 sites) was characterized by strong water limitation, sparse vegetation cover, and a higher abundance of drought-tolerant species, including *Stipa breviflora*, *Stipa tianschanica*, *Cleistogenes songorica*, and shrubs such as *Caragana* spp.

According to the USDA Soil Taxonomy, soils in the study area broadly corresponded to Mollisols in the meadow and typical steppes and to Aridisols in the desert steppe. Soil physicochemical properties varied systematically among steppe types, with soil pH and bulk density increasing, clay content decreasing, and electrical conductivity peaking in the desert steppe (Table S2). Together, these marked climatic, vegetation, and soil contrasts provide an ideal framework for studying grassland ecosystem dynamics.

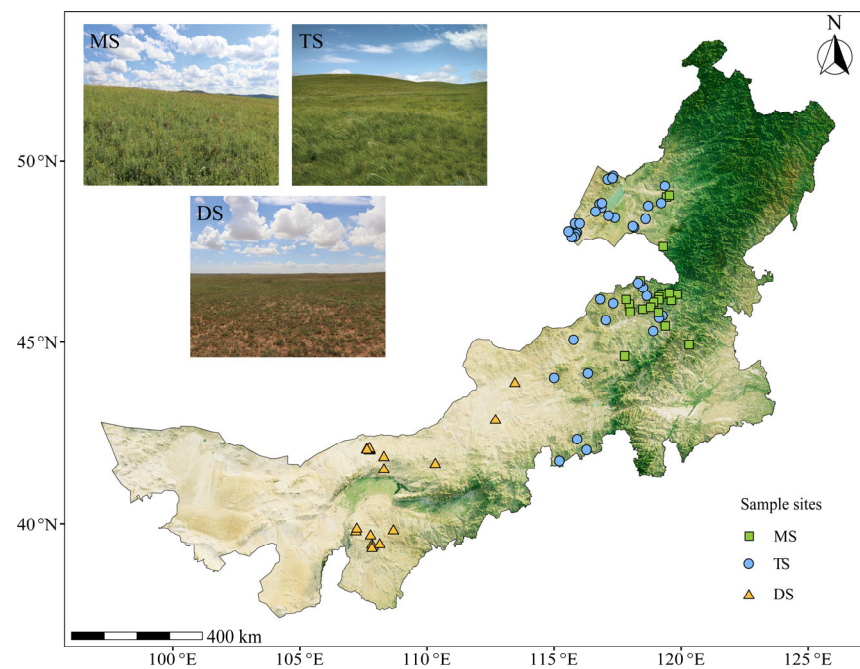


Figure 1. Study area and sampling design of Inner Mongolia's grassland ecosystems. Steppe types are classified as meadow steppe (MS), typical steppe (TS), and desert steppe (DS). Landscape photographs of each steppe type were taken during our field surveys.

2.2. Field Sampling

Field surveys for this study were conducted during the peak growing season, in July and August of both 2021 and 2022. At each sampling site, nine herbaceous quadrats, each measuring 1 m × 1 m, were established, and all aboveground vegetation within each quadrat was harvested for species diversity assessment and biomass measurement. Of these, three representative plots were selected for soil sampling. In each plot, surface soil from the 0–10 cm layer was collected using a five-point sampling method with a soil auger of 5.5 cm in diameter, and the five cores were pooled to form one composite sample. The soil samples were sieved through a 2 mm mesh, thoroughly mixed, and divided into two portions: one air-dried for soil physicochemical analysis and the other stored at 4 °C for fresh soil indicator analysis. A total of 101 sampling sites were surveyed, yielding 303 soil samples.

2.3. Soil Properties and Climate Data

Soil bulk density and moisture content were measured using the ring knife and drying methods, respectively. Particle composition was analyzed with a laser particle size analyzer (Analysette 22, FRITSCH, Idar-Oberstein, Germany) [38]. Soil pH and electrical conductivity were determined using a glass electrode method in soil-water extracts with ratios of 1:2.5 and 1:5, respectively. Organic matter was quantified using the potassium dichromate volumetric method [39], and total nitrogen was measured with an elemental analyzer (Vario MACRO cube, Elementar, Langenselbold, Germany). Total phosphorus, total potassium, available phosphorus, and available potassium were analyzed using ICP-OES (Optima ICP-OES8000, Perkin Elmer, Waltham, MA, USA) [38], while available nitrogen was determined with a flow analyzer (AA3, SEAL Analytical, Norderstedt, Germany). Soil β -glucosidase, urease, and alkaline phosphatase activities were assessed using commercial reagent kits (Solabio, Beijing, China) for colorimetric reactions, with absorbance readings taken using a multifunctional microplate reader (Epoch 2, BioTek, Winooski, VT, USA).

This study quantified key indicators of water availability and soil properties. Climate aridity was assessed using the aridity index ($AI = P/PET$), with $1 - AI$ serving as the “aridity” indicator, where higher values denote drier conditions. Precipitation (P) and potential evapotranspiration (PET) data were obtained from the China 1 km monthly hydrometeorological dataset (1901–2024) [40].

2.4. Functional Trait Analysis

2.4.1. Trait Measurements

To accurately characterize community properties and provide a robust basis for scaling trait information from the species to the community level [41], we measured functional traits for the dominant species within each community, which together accounted for more than 80% of total community biomass. To ensure comparability among communities, all plant traits were measured using unified and consistent procedures across all sites and samples [11]. Because intraspecific trait variation is generally much lower than interspecific variation [42], we preferentially sampled vigorous, healthy individuals growing under favourable habitat conditions, fully exposed to light and free from obvious shading [34,41]. Accordingly, variation in community-weighted trait values primarily reflected turnover among species with contrasting trait values. In total, 70 species were selected for trait measurements, and their taxonomic identity, family affiliation, and life form are listed in Supplementary Table S4. Species with low abundance or minor contribution to community biomass were not included in the trait measurements.

This study evaluated 23 plant functional traits, which include: (1) vegetative height (VH); (2) dry matter content of root, stem, and leaf (RDMC, SDMC, LDMC); (3) concentrations of elements and their ratios in root, stem, and leaf: carbon (RCC, SCC, LCC), nitrogen (RNC, SNC, LNC), phosphorus (RPC, SPC, LPC), carbon-to-nitrogen ratio (RCNR, SCNR, LCNR), and nitrogen-to-phosphorus ratio (RNPR, SNPR, LNPR); (4) key leaf traits: leaf carbon isotope ratio ($\delta^{13}C$), specific leaf area (SLA), leaf length (LL), and leaf thickness (LT). For each dominant species, 10 healthy individuals of similar size were selected for trait measurements. Plant height was measured in the field using a tape measure. For leaf trait measurements, fully expanded, undamaged mature leaves at a consistent position on the same individual, typically the third or fourth leaf from the apex, were selected, and leaf length and thickness were measured with a vernier caliper. During sampling, intact soil blocks containing the root system were carefully excavated to preserve root integrity and its connection with aboveground tissues. After gently removing adhering soil and debris from the root surface, samples were stored at low temperature and returned to the laboratory for further processing within 24 h.

During laboratory analysis, 5–10 leaves per sample were randomly selected, scanned, and analysed with ImageJ v1.53k to determine leaf area and calculate specific leaf area (SLA). Leaf, stem, and root samples were rehydrated at low temperature to full saturation, blotted dry, weighed for saturated fresh mass, and then oven-dried at 65 °C to constant mass with a precision of 0.001 g. Root, stem, and leaf dry matter content were calculated as the ratio of dry mass to saturated fresh mass, expressed as RDMC, SDMC, and LDMC, respectively. Carbon and nitrogen contents were measured using an elemental analyser (Vario MACRO cube, Elementar, Germany), and phosphorus content was determined by ICP-OES (Optima ICP-OES 8000, PerkinElmer, Waltham, MA, USA). Leaf $\delta^{13}C$ was measured via a coupled system consisting of an elemental analyser (Vario Micro Cube, Elementar, Langenselbold, Germany) and an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Bremen, Germany), following the method described in [34].

2.4.2. Community-Weighted Mean Traits

The community-weighted mean (CWM) traits, derived from species functional traits, represent the overall functional characteristics of a community. The calculation formula [34] is as follows:

$$CWM = \sum_{i=1}^S P_i \times trait_i \quad (1)$$

where S denotes the total number of species in the plot, P_i is the proportion of the above-ground biomass of the i -th species, and $trait_i$ represents the functional trait value of the i -th species.

2.4.3. Functional Diversity

We quantified five complementary dimensions of functional diversity: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (RaoQ). These indices were calculated from the species-by-trait matrix and plot-by-species abundance matrix using the dbFD function in the FD package (v1.0–12.1) in R (v4.0–4.1.2), with Lingoes correction for negative eigenvalues. The trait matrix was constructed using the 23 plant functional traits described in Section 2.4.1, and the abundance matrix was derived from species composition in each plot.

2.5. Quantifying Ecosystem Services Multifunctionality

Ten ecosystem service indicators (Table S5) were measured to represent the multi-dimensional functions and service provisioning of the ecosystem. To account for unit differences, all indicators were normalized to a 0–1 scale. The ecosystem service multifunctionality index for each sampling site was then calculated as the mean of these normalized values [43].

2.6. Statistical Analyses

Differences in ecosystem services, plant functional traits, and functional diversity among the three steppe types were assessed using one-way analysis of variance (ANOVA). When the overall ANOVA was significant, least significant difference (LSD) tests were used for post hoc pairwise comparisons among meadow steppe (MS), typical steppe (TS), and desert steppe (DS). Statistical significance was set at $p < 0.05$. Relationships between ecosystem service multifunctionality, plant functional traits, and functional diversity were examined using ordinary least squares (OLS) regression, with the significance of regression coefficients evaluated by t -tests. Spearman rank correlation analyses were conducted separately for MS, TS, and DS, as well as for all samples combined (ALL), to examine the relationships between plant community characteristics, environmental factors, and ecosystem service multifunctionality (ESMF). The correlation coefficients and their significance were visualized using a circular heatmap. For the ESMF prediction model, multiple linear regression was applied, coupled with multimodel inference for model selection. Before modeling, we iteratively removed explanatory variables with high collinearity, calculated the variance inflation factor (VIF), and ensured that all retained variables had VIF values < 5 .

To analyze the direct and indirect effects of abiotic and biotic factors on ESMF across the three steppe types, we constructed a structural equation model (SEM) with six categories of predictor variables: (1) climate variable (aridity); (2) soil properties, including soil pH, clay content, bulk density, and electrical conductivity; (3) community-weighted mean traits (23 plant functional traits); (4) functional richness (FRic); (5) functional diversity divergence indices (FDiv, FDis, and RaoQ); and (6) functional evenness (FEve). To avoid overfitting, principal component analysis (PCA) was performed on factor groups containing

≥ 3 variables, retaining only the first principal component (PC1) for inclusion in the model. Standardized path coefficients were used to quantify direct and indirect effects, and model fit was assessed using Fisher's C and its p -value. All analyses were conducted in R 4.4.0.

3. Result

Across all sampling sites, 265 plant species belonging to 135 genera and 42 families were recorded in the Inner Mongolian steppe. Taxonomic richness showed a clear decline from meadow steppe (195 species, 104 genera, and 35 families) to typical steppe (129 species, 84 genera, and 31 families) and desert steppe (64 species, 45 genera, and 19 families). An overview of the dominant species composition across steppe types is provided in Table S3. The 70 species selected for trait measurements, along with their corresponding families and life forms, are presented in Table S4.

3.1. Ecosystem Services

Grassland productivity, biodiversity, carbon cycling, nitrogen cycling, phosphorus cycling, water retention, soil erosion prevention, soil carbon stocks, and ecosystem service multifunctionality (ESMF) all exhibited significant differences across the three steppe types, following the pattern meadow steppe (MS) > typical steppe (TS) > desert steppe (DS) ($p < 0.05$, Figure 2 and Table 1). Potassium cycling was significantly higher in TS compared to MS and DS, with no significant difference between the latter two (Table 1). DS exhibited significantly higher sand fixation service than MS and TS, with no significant difference between the latter two (Table 1).

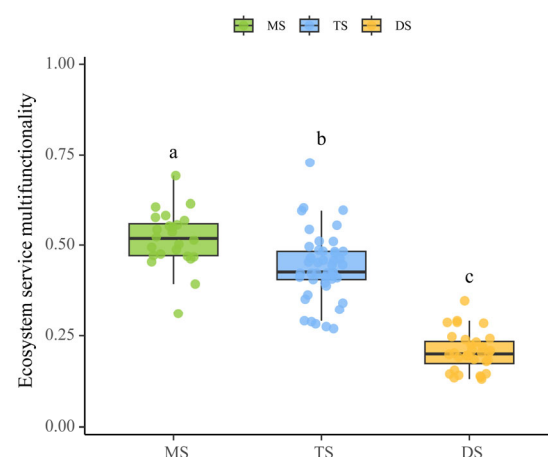


Figure 2. Variations in ecosystem service multifunctionality across steppe types. MS, meadow steppe; TS, typical steppe; DS, desert steppe. Different lowercase letters indicate significant pairwise differences among steppe types based on Fisher's LSD test following one-way ANOVA ($p < 0.05$).

Table 1. Variations in ten ecosystem services across steppe types.

Ecosystem Services	Meadow Steppe	Typical Steppe	Desert Steppe	Inner Mongolian Steppe
Grassland productivity ($\text{g} \cdot \text{m}^{-2}$)	199.95 ± 15.92 a	129.72 ± 7.04 b	32.14 ± 3.81 c	115.49 ± 8.05
Biodiversity	2.15 ± 0.09 a	1.50 ± 0.06 b	0.96 ± 0.08 c	1.48 ± 0.06
Carbon cycling	0.61 ± 0.03 a	0.52 ± 0.03 b	0.11 ± 0.01 c	0.41 ± 0.02
Nitrogen cycling	0.55 ± 0.02 a	0.44 ± 0.02 b	0.12 ± 0.01 c	0.36 ± 0.02
Phosphorus cycling	0.47 ± 0.02 a	0.46 ± 0.02 a	0.18 ± 0.02 b	0.37 ± 0.02
Potassium cycling	0.38 ± 0.03 b	0.50 ± 0.03 a	0.39 ± 0.03 b	0.44 ± 0.02
Water retention (%)	21.87 ± 2.21 a	8.74 ± 0.74 b	2.71 ± 0.35 c	9.95 ± 0.95
Soil erosion prevention (%)	89.83 ± 1.58 a	75.33 ± 1.79 b	40.64 ± 1.62 c	67.79 ± 2.18

Table 1. Cont.

Ecosystem Services	Meadow Steppe	Typical Steppe	Desert Steppe	Inner Mongolian Steppe
Soil carbon stocks ($\text{kg} \cdot \text{m}^{-2}$)	3.37 ± 0.21 a	3.10 ± 0.13 a	1.17 ± 0.08 b	2.55 ± 0.12
Sand fixation ($\text{t} \cdot \text{hm}^{-2}$)	3.85 ± 0.50 b	4.00 ± 0.37 b	24.93 ± 2.28 a	10.59 ± 1.23

Different lowercase letters indicate significant pairwise differences among steppe types based on Fisher's LSD test following one-way ANOVA ($p < 0.05$).

3.2. Functional Traits and Diversity

Community-weighted mean (CWM) traits show distinct variation across different steppe types (Figure 3). CWM of vegetative height (VH_{CWM}), stem C:N ratio (SCNR_{CWM}), and root C:N ratio (RCNR_{CWM}) followed a clear gradient: MS (Meadow Steppe) > TS (Typical Steppe) > DS (Desert Steppe) ($p < 0.05$, Figure 3a,p,v). CWM of stem nitrogen content (SNC_{CWM}), stem phosphorus content (SPC_{CWM}), root nitrogen content (RNC_{CWM}), and root N:P ratio (RNPR_{CWM}) exhibited an opposite trend, with DS > TS > MS (Figure 3n,o,t,w). CWM of leaf length (LL_{CWM}), leaf carbon isotope ratio ($\delta^{13}\text{C}_{\text{CWM}}$), leaf phosphorus content (LPC_{CWM}), leaf C:N ratio (LCNR_{CWM}), and stem dry matter content (SDMC_{CWM}) were significantly higher in DS compared to MS and TS (Figure 3b,e,i,j), with no significant difference between the latter two. In contrast, CWM of specific leaf area (SLA_{CWM}), leaf N:P ratio (LNPR_{CWM}), and stem carbon content (SCC_{CWM}) were significantly higher in MS and TS than in DS (Figure 3d,k,m). CWM of leaf thickness (LT_{CWM}) was significantly higher in TS and DS than in MS (Figure 3c). CWM of leaf dry matter content (LDMC_{CWM}), leaf nitrogen content (LNC_{CWM}), and stem N:P ratio (SNPR_{CWM}) differed only between specific steppe types (Figure 3f,h,q). CWM of leaf carbon content (LCC_{CWM}), root dry matter content (RDMC_{CWM}), root carbon content (RCC_{CWM}), and root phosphorus content (RPC_{CWM}) showed no significant differences across the three steppe types ($p > 0.05$, Figure 3g,r,s,u).

Functional richness (FRic) differed significantly across steppe types, with MS exhibiting the highest value ($p < 0.05$, Figure 4a). Functional divergence (FDiv) was significantly higher in DS than in TS (Figure 4c). Functional dispersion (FDis) and Rao's quadratic entropy (RaoQ) were significantly higher in the desert steppe compared to the MS and TS, with no significant differences between the latter two (Figure 4d,e). Functional evenness (FEve) showed no significant differences among the three steppe types ($p > 0.05$, Figure 4b).

3.3. Relationships Between Ecosystem Service Multifunctionality and Various Abiotic and Biotic Factors

In MS, ESMF exhibited a significant positive correlation with VH_{CWM} , LL_{CWM} , LNC_{CWM} , and soil clay content (Clay) ($p < 0.05$), and a significant negative correlation with aridity and SNPR_{CWM} (Figure 5). In TS, ESMF exhibited a significant positive correlation with Clay and LDMC_{CWM} , and a significant negative correlation with SLA_{CWM} , SDMC_{CWM} , FDiv, and RaoQ. In DS, ESMF exhibited a significant positive correlation with soil electrical conductivity (EC), Clay, LNC_{CWM} , and LPC_{CWM} , and a negative correlation with aridity and soil bulk density (BD). At the regional scale, ESMF decreased with increases in aridity, soil pH (pH), and BD, while it increased with rising Clay. ESMF showed significant positive correlations with FRic, as well as VH_{CWM} , SLA_{CWM} , LNPR_{CWM} , SCC_{CWM} , SCNR_{CWM} , RCC_{CWM} , and RCNR_{CWM} . In contrast, it exhibited significant negative correlations with FDiv, FDis, RaoQ, and traits such as LL_{CWM} , LT_{CWM} , $\delta^{13}\text{C}_{\text{CWM}}$, LNC_{CWM} , LPC_{CWM} , SDMC_{CWM} , SNC_{CWM} , SPC_{CWM} , SNPR_{CWM} , RNC_{CWM} , and RNPR_{CWM} (Figure 5), suggesting that ESMF at the regional scale is jointly regulated by both abiotic and biotic factors.

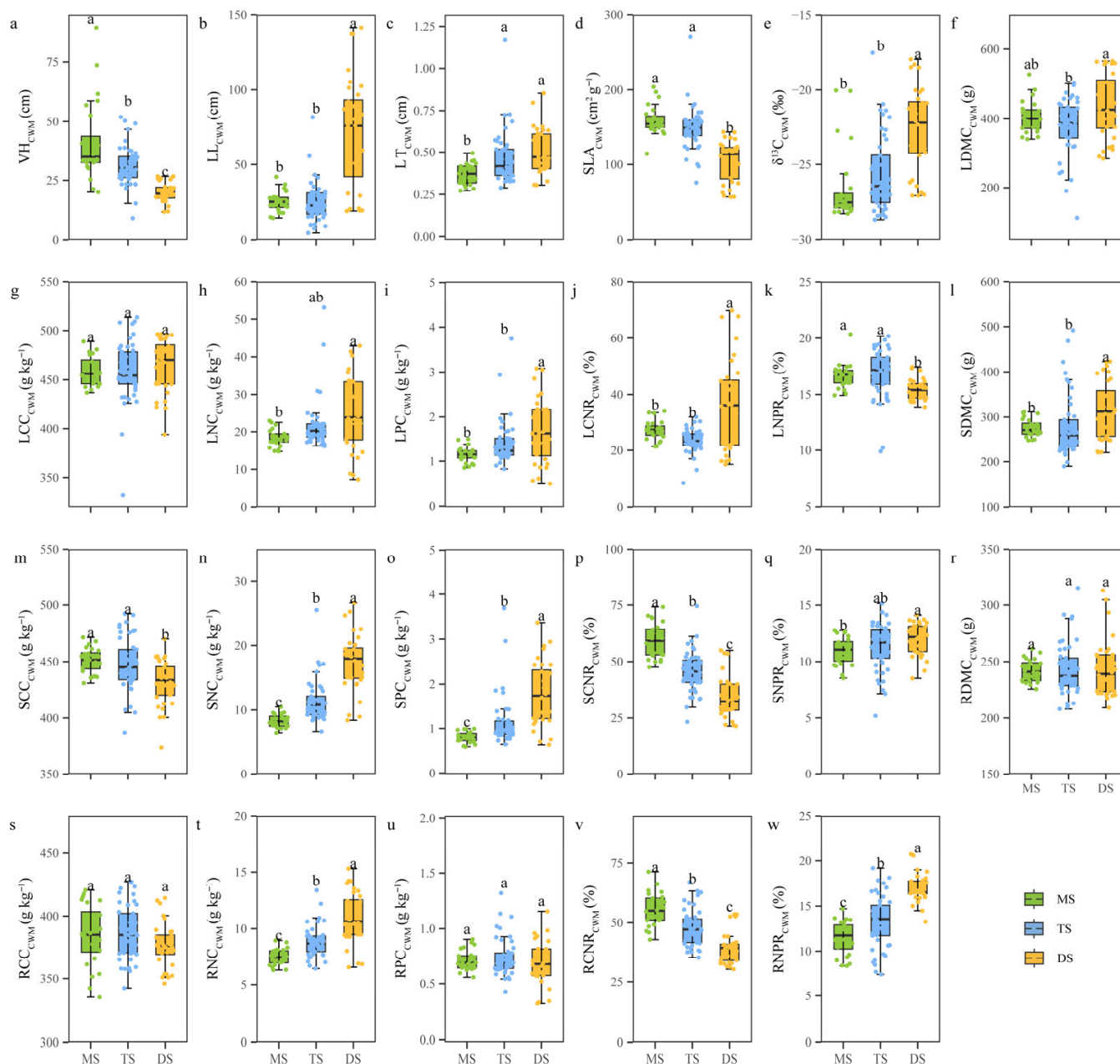


Figure 3. Variations in community-weighted means (CWMs) of plant functional traits across steppe types. Subfigures show CWM values for (a) VH_{CWM} , (b) LL_{CWM} , (c) LT_{CWM} , (d) SLA_{CWM} , (e) $\delta^{13}C_{CWM}$, (f) $LDMC_{CWM}$, (g) LCC_{CWM} , (h) LNC_{CWM} , (i) LPC_{CWM} , (j) $LCNR_{CWM}$, (k) $LNPR_{CWM}$, (l) $SDMC_{CWM}$, (m) SCC_{CWM} , (n) SNC_{CWM} , (o) SPC_{CWM} , (p) $SCNR_{CWM}$, (q) $SNPR_{CWM}$, (r) $RDMC_{CWM}$, (s) RCC_{CWM} , (t) RNC_{CWM} , (u) RPC_{CWM} , (v) $RCNR_{CWM}$, and (w) $RNPR_{CWM}$. For plant functional trait abbreviations, refer to Section 2.4.1. MS, meadow steppe; TS, typical steppe; DS, desert steppe. Different lowercase letters indicate significant pairwise differences among steppe types based on Fisher's LSD test following one-way ANOVA ($p < 0.05$).

The multiple regression model assessing the impact of various driving factors on ESMF showed that, across steppe types, aridity consistently acted as the dominant negative factor inhibiting ESMF, while clay emerged as the most critical positive contributor. Meanwhile, the explanatory power of biotic factors (plant functional traits and functional diversity) on ESMF exhibited a significant moisture gradient dependence: in the water-rich MS, their relative contribution was as high as 79%, but as aridity increased, this contribution steadily declined, reaching 15.22% in DS (Figure 6a,c).

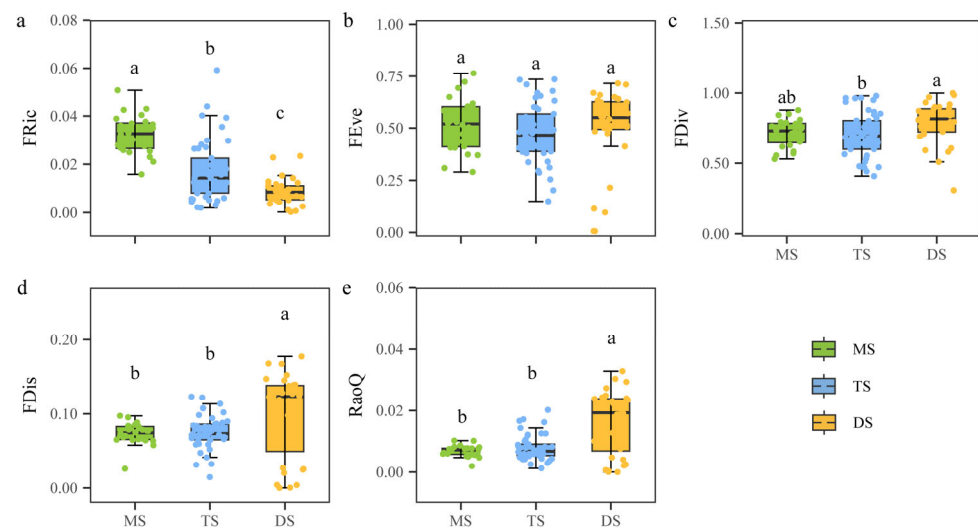


Figure 4. Variations in plant functional diversity across steppe types. (a) Functional richness (FRic), (b) Functional evenness (FEve), (c) Functional divergence (FDiv), (d) Functional dispersion (FDis), and (e) Rao's quadratic entropy (RaoQ). MS, meadow steppe; TS, typical steppe; DS, desert steppe. Different lowercase letters indicate significant pairwise differences among steppe types based on Fisher's LSD test following one-way ANOVA ($p < 0.05$).

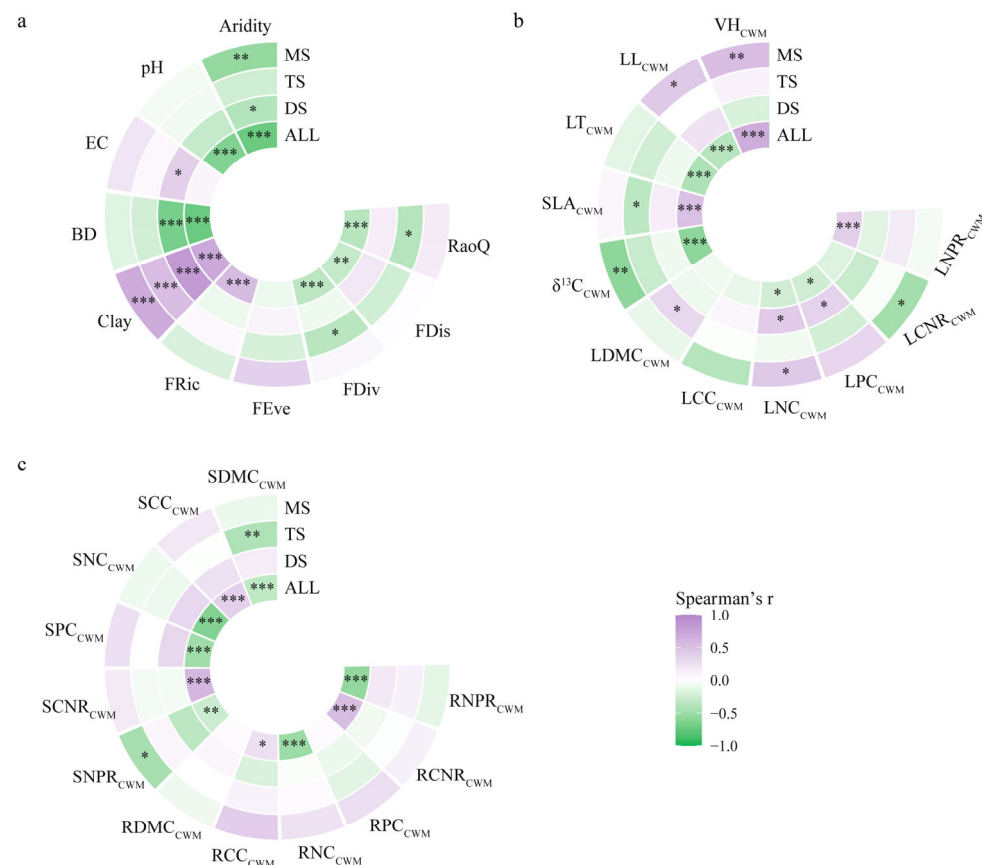


Figure 5. Relationships between ecosystem service multifunctionality (ESMF) and environmental factors at the regional scale. Spearman rank correlations between environmental drivers and ESMF

are shown for meadow steppe (MS), typical steppe (TS), desert steppe (DS), and the overall region (ALL). (a) Climate, soil, and plant functional diversity, (b) Vegetative height and leaf traits, (c) Stem traits and root traits. pH, soil pH; EC, soil electrical conductivity; BD, soil bulk density; Clay, soil clay content. The circular heatmap displays correlation coefficients between ESMF and both abiotic (climate, soil) and biotic (vegetation) factors. The color gradient indicates positive correlations (purple) and negative correlations (green). Asterisks denote significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

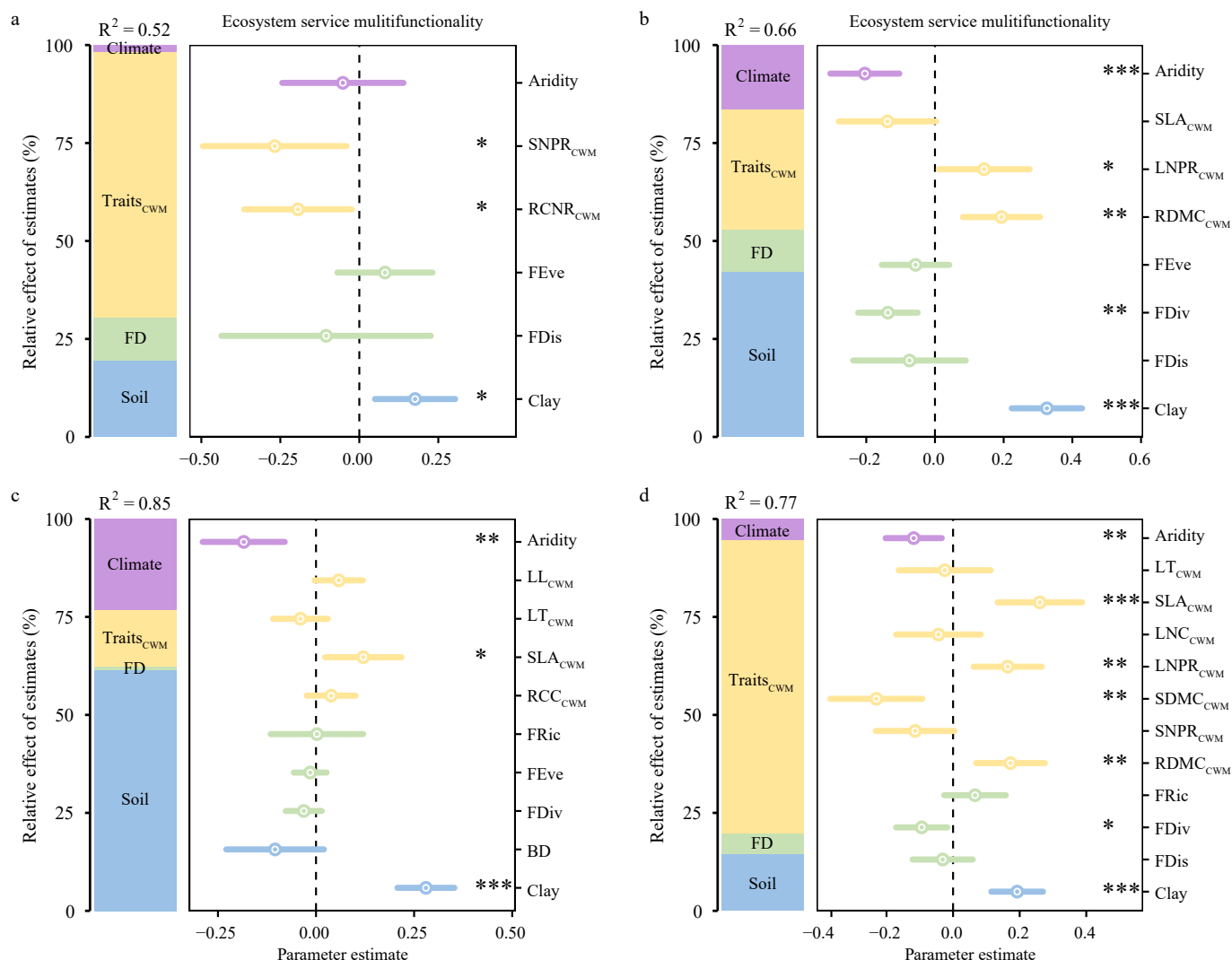


Figure 6. Drivers of ecosystem service multifunctionality across steppe types. Model results are shown for (a) meadow steppe, (b) typical steppe, (c) desert steppe, and (d) the overall region. Traits_{CWM}, community-weighted means of functional traits; FD, functional diversity. The bars represent standardized regression coefficients (model-averaged estimates) and their 95% confidence intervals. Stacked bars indicate the relative importance of each predictor category (percentage of explained variance). The best models were selected based on the corrected Akaike Information Criterion (AICc). Asterisks denote significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.4. Dominant Determinants of Ecosystem Service Multifunctionality

Structural equation modeling (SEM) was used to reveal the mechanisms through which plant functional traits, functional diversity, and climate and soil factors jointly regulate ESMF across different steppe types in Inner Mongolia through various pathways (Figure 7). Overall, aridity primarily exerts an indirect effect at both the TS and regional scales: in TS, it mainly influences functional diversity by altering soil factors, while at the regional scales, it further affects ESMF indirectly by regulating FRic and FDdiv. In

contrast, soil factors dominate ESMF variation through significant direct paths at TS, DS, and the regional scale. Notably, Traits_{CWM} significantly positively influences ESMF only in DS, indicating that under extreme resource limitation, ESMF is more dependent on the buffering capacity provided by trait differences and functional diversity. At the overall region, FRic promotes ESMF, while FDdiv inhibits it.

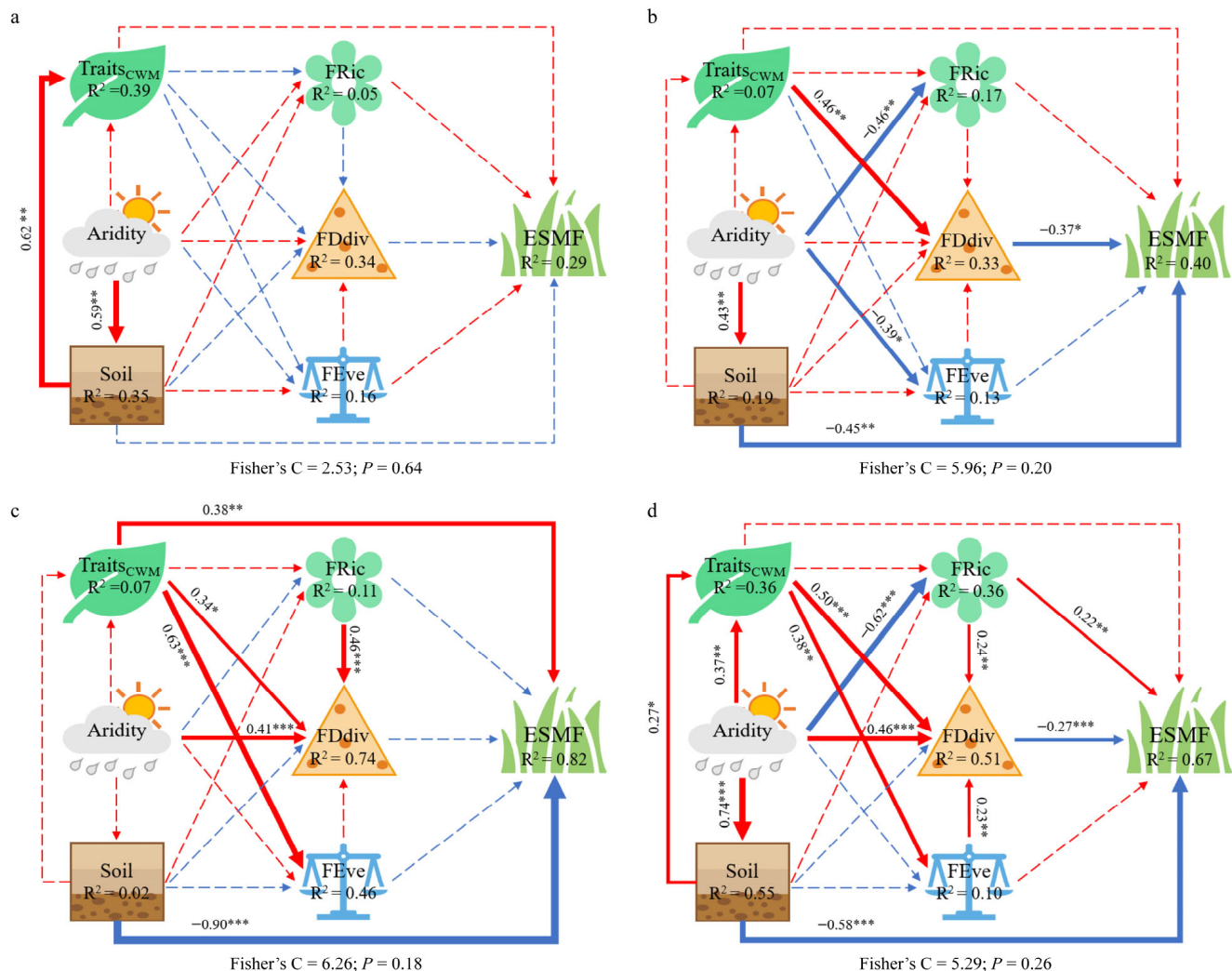


Figure 7. Path analysis of abiotic and biotic drivers of ecosystem service multifunctionality in grassland ecosystems. Structural equation modeling (SEM) results are displayed for (a) meadow steppe, (b) typical steppe, (c) desert steppe, and (d) the entire region. FDdiv, functional diversity divergence indices (FDdiv, FDis, and RaoQ). Solid red lines represent significant positive effects, while solid blue lines indicate significant negative effects. Line width corresponds to effect strength, and dashed lines indicate non-significant pathways. Asterisks denote significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Further analysis revealed that as aridity increases, the variation in ESMF is increasingly driven by abiotic factors such as aridity and soil properties (Figure 8b,d,f). In MS, ESMF is primarily driven by biotic factors, including plant functional traits and functional diversity, while in DS, ESMF is mainly regulated by abiotic factors such as aridity and soil properties (Figure 8a,e).

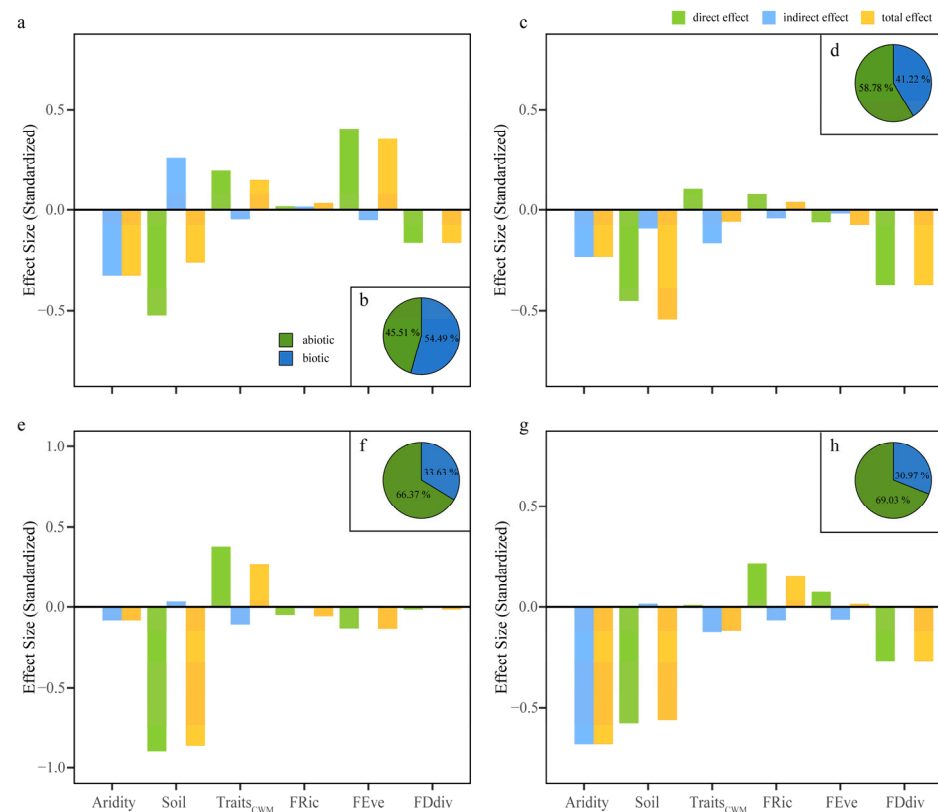


Figure 8. Standardized direct, indirect, and total effects of climate, soil, community-weighted means of functional traits, and functional diversity on ecosystem service multifunctionality (ESMF). Standardized effects for meadow steppe (a), typical steppe (c), desert steppe (e) and Inner Mongolia steppe (g) are shown. Panels (b,d,f,h) illustrate the relative contributions of abiotic factors (Aridity and Soil) versus biotic factors (Traits_{CWM}, FRic, FEve, and FDdiv) to the total effects on ESMF.

4. Discussion

4.1. Variation Across Steppe Types in Plant Functional Traits and Diversity

Aridity in the Inner Mongolian grasslands increases significantly from east to west, driving a gradual transition in vegetation from meadow steppe to typical steppe and desert steppe, accompanied by adaptive shifts in community functional traits. Consistent with our first hypothesis, the results show that MS and TS have higher VH_{CWM} , $SCNR_{CWM}$, and $RCNR_{CWM}$, with SLA_{CWM} significantly greater than that of DS (Figure 3a,d,p,v). This suggests that under water-rich conditions, communities primarily adopt a “resource-acquisition” strategy, sustaining high growth rates through large plant size and rapid tissue turnover [44,45]. In contrast, the desert steppe, constrained by both water and nutrient limitations, favors small, low-construction-cost species, driving the community toward a “resource-conservative” strategy [46,47]. Specifically, LL_{CWM} , LT_{CWM} , $LDMC_{CWM}$, and $SDMC_{CWM}$ are highest in DS among the three steppe types (Figure 3b,c,f,l), indicating that dominant species enhance mechanical support by developing thicker, denser defensive structures to mitigate water deficits caused by intense evapotranspiration and high radiation [48]. Furthermore, the $\delta^{13}C_{CWM}$ and tissue nutrient characteristics (such as LNC_{CWM} , SNC_{CWM}) are highest in DS (Figure 3e,h,i,n,o,q,t,w), suggesting that plants adapt to extreme arid conditions and potential phosphorus limitations by enhancing water use efficiency and concentrating nutrients in more durable tissues [34,49]. Overall, the transition from meadow steppe to desert steppe reflects a shift in plant communities from a “rapid turnover” strategy to a “robust stress-tolerant” strategy.

Consistent with our first hypothesis, this study found significant differences in functional diversity across steppe types. FRic exhibited notable differentiation, with the highest values in the meadow steppe ($p < 0.05$, Figure 4a). This may be attributed to the more favorable water, thermal, and nutrient conditions, as well as greater microhabitat heterogeneity in the meadow steppe, which promote species coexistence and expand functional space [50]. Previous studies have shown a significant positive correlation between FRic and soil nutrients [51]. As aridity increases, environmental filtering intensifies, compounded by more stringent ecological constraints, leading to a decline in species diversity and functional volume [52], consistent with the findings of this study. This study also found that FDiv, FDis, and RaoQ were highest in the desert steppe ($p < 0.05$, Figure 4c–e), indicating that under resource-limited conditions, species reduce competition and enhance resource use efficiency through trait separation [53,54]. This is consistent with findings from the Tibetan Plateau grasslands, where FDiv increases under resource constraints [55]. In contrast, in the water-rich meadow and typical steppe, dominant species traits converge, leading to lower functional divergence.

4.2. Effect of Plant Functional Traits and Diversity on Ecosystem Service Multifunctionality

At the steppe-type scale, we found that Traits_{CWM} within the three steppe types generally showed no significant relationship with ESMF (Figures 5 and S1). This may be due to the long-term environmental similarity within each steppe type, leading to trait convergence in dominant species [34], which weakens the explanatory power of traits for ESMF. In contrast to the steppe-type scale, at the regional scale of Inner Mongolia grasslands, ESMF showed an increasing trend in communities with taller plant height and stronger resource-acquisition traits (e.g., higher SLA_{CWM} and LNPR_{CWM}; Figures 5b and S1d,k). Plant functional traits are key links between plants and their environment, regulating ecosystem functions [15]. Existing studies have also shown that resource acquisition traits, such as plant height and specific leaf area, have stronger explanatory power for multifunctionality [25,56]. Under long-term drought stress, desert steppe plants can enhance drought resistance through trait adjustments, thereby buffering climate and soil fluctuations to some extent [34]. However, this adaptation is more focused on survival maintenance than functional enhancement: in conservative communities characterized by longer leaves (LL_{CWM}), thicker leaves (LT_{CWM}), and higher $\delta^{13}\text{C}_{\text{CWM}}$, ESMF actually decreased (Figures 5b,c and S1b,c,e). Conservative strategies may reduce productivity and nutrient turnover [57], thereby limiting multifunctionality. Resource-acquisition strategies foster synergistic enhancement of ecosystem services, while resource-conservative, stress-tolerant strategies may suppress multifunctionality due to the “function-survival” trade-off, despite improving environmental adaptability.

At the overall scale of Inner Mongolia grasslands, ESMF was positively correlated with FRic and negatively correlated with FDiv, FDis, and RaoQ (Figures 5b and S2a,c–e). This suggests that the influence of “trait space extent” and “trait distribution in space” on multifunctionality is not consistent. Higher FRic indicates a broader functional trait space, reflecting a richer strategy pool and stronger potential for functional complementarity [58,59]. In communities with higher functional diversity, species utilize resources more efficiently through niche complementarity, enhancing ecosystem functions [20]. This mechanism aligns with evidence from alpine grasslands, where “high FRic supports high multifunctionality” [24,60]. In contrast, the increase in FDiv, FDis, and RaoQ in this study suggests trait trade-offs and niche separation in stressful environments. Under resource-poor conditions, communities tend to diverge towards more extreme conservative traits for survival. While this configuration increases functional distance, it may reduce biomass accumulation and nutrient cycling efficiency [55], ultimately diminishing multifunctionality.

4.3. Abiotic and Biotic Drivers of Ecosystem Service Multifunctionality

Clarifying the key biotic and abiotic drivers is essential for unraveling the complex relationship between biodiversity and ecosystem service multifunctionality (ESMF) [24,37]. This study found that ESMF decreases significantly with increasing aridity at the typical steppe, desert steppe, and regional scales (Figures 5a and 6), consistent with the conclusion that aridification weakens the synergistic maintenance of multifunctionality [27,61]. In contrast, ESMF increases with higher clay content (Figures 5a and 6), suggesting that the water and nutrient retention capacity of clay-rich soils supports multifunctionality by promoting nutrient accumulation and turnover, particularly in water-limited arid and semi-arid regions [6,62]. Increased soil bulk density reduces porosity and weakens nutrient stocks, thereby suppressing ESMF [63,64]. This study similarly found a significant negative effect at both the desert steppe and overall scales (Figure 5a). In conclusion, changes in ESMF are primarily driven by aridity and soil texture/structure consistency, regardless of grassland type or regional scale, indicating a stable abiotic control mechanism underlying multifunctionality changes.

However, the mechanisms through which biotic factors, such as plant functional traits and diversity, influence ESMF vary significantly across steppe types. In the more favorable water and thermal conditions of the meadow steppe, ESMF is primarily driven by biotic factors (Figures 6a and 8b), promoting resource complementarity and sustaining multiple ecological functions through dominant trait configurations and increased functional richness [65]. As aridity increases, the primary driver of ESMF shifts from biotic factors to environmental constraints imposed by abiotic factors. In the desert steppe, ESMF variation is primarily driven by abiotic factors such as aridity and soil properties (Figures 6c and 8f), yet Traits_{CWM} still shows a significant positive effect on ESMF (Figure 7c). This supports our second hypothesis, indicating that under extreme aridity and resource-poor conditions, multifunctionality relies more on the buffering and compensatory effects of stress-tolerant traits in dominant species [66,67]. Our results show that the mechanisms maintaining grassland ecosystem multifunctionality are highly environment-dependent, and management should adopt steppe-type-specific strategies. In relatively humid and resource-rich grasslands such as meadow steppe, management should focus on maintaining plant diversity and functional composition, for example, through moderate grazing and avoiding excessive disturbance, so as to enhance resource complementarity and sustain multiple ecosystem functions. In contrast, in more arid and resource-limited grasslands, especially desert steppe, multifunctionality is mainly constrained by abiotic filtering. Therefore, protection and management should prioritize conserving habitat and soil heterogeneity, preventing deterioration of soil physical properties (e.g., declining clay content and increasing bulk density), and reducing pressures that may further destabilize vegetation and soil functioning. These results highlight that grassland management should be adapted to local aridity conditions rather than applied uniformly across all steppe types.

5. Conclusions

This study systematically evaluated plant functional traits, functional diversity, and ecosystem service multifunctionality (ESMF) across three Inner Mongolian steppe types spanning contrasting aridity levels. Plant functional traits, functional diversity, and ESMF all differed significantly among meadow, typical, and desert steppes, revealing strong ecological differentiation across steppe types. ESMF was highest in the meadow steppe and lowest in the desert steppe. The drivers of ESMF also varied among steppe types and across spatial scales. Across both steppe-type and regional scales, aridity and soil clay content emerged as relatively consistent abiotic drivers of ESMF. By contrast, the effects of biotic factors, including plant functional traits and functional diversity, were

strongly context dependent. In the relatively humid meadow steppe, biotic factors (e.g., stem nitrogen-to-phosphorus ratio) contributed more strongly to ESMF, whereas under increasingly arid conditions, abiotic constraints became more important. Our study provides a scientific foundation for developing context-specific grassland conservation and management policies. In humid grasslands, the focus should be on nutrient regulation to promote resource complementarity and niche differentiation, thereby maintaining biodiversity. In arid grasslands, efforts should prioritize preserving habitat and soil heterogeneity, mitigating soil degradation, and ensuring the continued provision of key ecosystem services. The conceptual framework developed in this study provides a key reference for predicting the dynamic evolution of grassland ecosystem multifunctionality in the context of global climate change.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/agronomy16070685/s1>. Figure S1: Relationships between ecosystem service multifunctionality and community-weighted means (CWMs) of plant functional traits across steppe types; Figure S2: Relationships between ecosystem service multifunctionality and plant functional diversity across steppe types; Table S1: List of sampling sites across the Inner Mongolian steppes; Table S2: Variations in aridity and soil physicochemical properties across steppe types; Table S3: Dominant species and taxonomic richness of plant communities across steppe types in Inner Mongolia; Table S4: Lists of sampled species, corresponding families, and life forms; Table S5: Definitions and quantification methods for ten ecosystem services. References [68–70] are cited in Supplementary Materials.

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