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Non-synchronous changes in water, carbon and habitat functions of alpine swamp meadows on the Qinghai–Tibetan Plateau and future risk hotspots

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Abstract

Context Alpine swamp meadows on the Qinghai–Tibetan Plateau provide critical ecosystem functions—water yield, soil carbon storage, and waterbird habitat—yet the synchrony of their changes and the locations of future risks remain poorly quantified.

Objectives This study aimed to (1) reconstruct the spatiotemporal dynamics of water yield (WY), soil organic carbon (SOC), and habitat suitability (HS) for waterbirds from 1990 to 2020; (2) examine whether these functions changed synchronously and whether spatial co-occurrence of high values translated into temporal co-variation; and (3) project future changes under different emission scenarios and identify priority areas for adaptive management.

Methods The InVEST model, random forest regression, and MaxEnt were integrated to reconstruct the three functions across the Qinghai–Tibetan alpine swamp meadow distribution (73,153 km²) at 1-km resolution from 1990 to 2020. Future changes were projected to 2080 under SSP1-1.9, SSP2-4.5, and SSP5-8.5 scenarios. Spatial associations among functions were analyzed, and historical degradation and future risk hotspots were identified.

Results Regional mean WY and SOC increased by 3.6% and 31.3%, respectively, while the area of highly suitable waterbird habitat declined by 45.5% over 1990–2020. Although 52% of the study area showed co-occurrence of high values for at least two functions, 59% of the area exhibited divergent trends among the three functions, with near-zero correlation coefficients between trend slopes ($r = -0.079$ to 0.228). Future risks under SSP5-8.5 were projected to concentrate in the northeastern,

eastern, and southwestern margins, with approximately 24% of risk hotspots overlapping areas currently supporting high multifunctionality.

Conclusions The three ecosystem functions of alpine swamp meadows changed asynchronously over the past three decades. Spatial co-occurrence of high functional values did not imply temporal co-variation. Future climate change may drive multi-function degradation in specific regions, creating a “high-current-value–high-future-risk” conflict that requires spatially differentiated management strategies.

Keywords: Alpine swamp meadow, Ecosystem function, Spatiotemporal dynamics, Asynchronous change, Landscape sustainability, Qinghai–Tibetan Plateau

1 Introduction

The Qinghai–Tibetan Plateau, known as the Asian Water Tower, is the world’s highest and most extensive high-altitude plateau and one of the most ecologically sensitive regions globally (Yao et al. 2022). Despite their limited extent, alpine marshes and swamp meadows provide irreplaceable ecosystem services in water regulation, carbon sequestration, and habitat provision for rare waterbirds (Wei et al. 2022). The functional status of these ecosystems directly affects water security for hundreds of millions of people downstream and the carbon balance of the plateau (Yao et al. 2022; Yang et al. 2023). Over the past three decades, however, under accelerating climate warming and intensifying human activities, how these critical functions have evolved, whether improvements and degradations across functions have been synchronous, and what ecological risks climate change will bring remain unresolved questions.

The concept of ecosystem multifunctionality has provided a theoretical foundation for integrated assessments. Recent work by Gao et al. (2025) demonstrated that grassland degradation substantially weakened most ecosystem functions, with a mean decline of 20.3%, and shifted the relationship between biodiversity and multifunctionality from plant-dominated to microbe-dominated. These findings reveal the complexity and type-dependence of functional responses in alpine ecosystems, but they primarily focus on changes in overall multifunctionality rather than systematically addressing the relationships among the three core functional dimensions of water, carbon, and biodiversity. Importantly, these studies have not examined whether different functional dimensions exhibit distinct response patterns—which functions are improving, which are degrading, and what these divergences imply for ecosystem management.

Substantial progress has been made on individual functions. For carbon sequestration, soil organic carbon in alpine marshes is highly temperature-sensitive: warming may increase carbon inputs by extending the growing season and enhancing net primary productivity, but it also accelerates microbial activity and permafrost carbon release (Wei et al. 2022). Some studies show accumulation of SOC over the past three decades (Jiang et al. 2024), while grazing disturbance can cause carbon losses (Huang et al. 2025); under future scenarios, SOC in alpine wetlands is projected to increase overall, though its stability is threatened by continued warming (Jiang et al. 2025). For water yield, the capacity of swamp meadows is regulated by precipitation, evapotranspiration, and permafrost meltwater, showing a spatial pattern of higher in the east, lower in the west (Wang et al. 2022), though long-term trends remain uncertain. For biodiversity maintenance, road disturbance and land-use change have been identified as dominant anthropogenic factors affecting waterbird habitat suitability (An and Guo 2025; Ye et al. 2025). Notably, although alpine wetland area has increased overall—wetland area on the Qinghai–Tibetan Plateau expanded by 31.2% over the past 30 years (Li et al. 2023)—localized degradation persists in areas of permafrost thaw or intensive human activity (Zhu et al. 2023). This paradoxical pattern of overall expansion coexisting with local

degradation suggests that area-based metrics alone are insufficient for accurately assessing functional status.

These studies have advanced understanding of individual functional mechanisms, yet three critical knowledge gaps remain. First, no study has simultaneously integrated the three functional dimensions of water, carbon, and biodiversity to examine their long-term dynamics and interrelationships in swamp meadows. Second, against the backdrop of net area expansion, are improvements and degradations across different functions synchronous? Does asynchrony imply that “area expansion” may mask the loss of key ecological functions? Third, how will climate change affect the trajectories of different functions in the future, and which areas will face the risk of simultaneous multi-function degradation? Answering these questions is essential for establishing spatial priorities in adaptive management of alpine wetlands.

To address these gaps, this study focused on alpine swamp meadows on the Qinghai–Tibetan Plateau and selected three key indicators—water yield (WY), soil organic carbon content (SOC), and waterbird habitat suitability (HS)—to represent hydrological function, carbon storage and habitat maintenance functions, respectively. The InVEST model, random forest regression, and MaxEnt were used to reconstruct the spatiotemporal distributions of the three functions from 1990 to 2020 and to quantify their historical trends and interrelationships. These were then coupled with CMIP6 multi-scenario climate data (SSP1-1.9, SSP2-4.5, SSP5-8.5) to project functional trajectories to 2080 under different emission pathways and to identify high-risk areas for future functional degradation.

Three specific questions were addressed: (1) What were the spatiotemporal patterns of change in water yield, carbon storage, and habitat maintenance functions of Qinghai–Tibetan alpine swamp meadows over the past three decades? (2) Did the three functions change synchronously, and did spatial co-occurrence of high values coincide with consistent directional changes? (3) How will each function respond to different emission scenarios in the future, and which areas should be prioritized for conservation and adaptive management? A long-term integrated assessment framework spanning water–carbon–habitat dimensions was established, linking historical reconstruction with future projection. This framework provides empirical evidence for understanding functional maintenance mechanisms in alpine wetland ecosystems, methodological reference for integrated assessments in similar regions, and spatially explicit information for zoning management and adaptive conservation strategies.

2 Materials and methods

2.1 Study area

The study area encompasses the distribution of alpine swamp meadows on the Qinghai–Tibetan Plateau, located between 26°N–39°N and 73°E–104°E, with a total area of approximately 73,153 km². These meadows are primarily distributed in river source areas, lake shore lowlands, and permafrost degradation zones. The region has a mean elevation exceeding 4,000 m (Cuo et al. 2014), with a cold and dry climate (Qiu, 2008), mean annual temperature ranging from −2 to 4°C, and annual precipitation from 250 to 600 mm. Alpine swamp meadows are among the most widespread and ecologically active wetland types on the plateau, characterized by high soil moisture content and abundant soil organic matter, and play critical roles in water storage, carbon cycling, and biodiversity maintenance (Pimm et al. 2014; Li et al. 2012; Zhao et al. 2015) (Fig. 1).

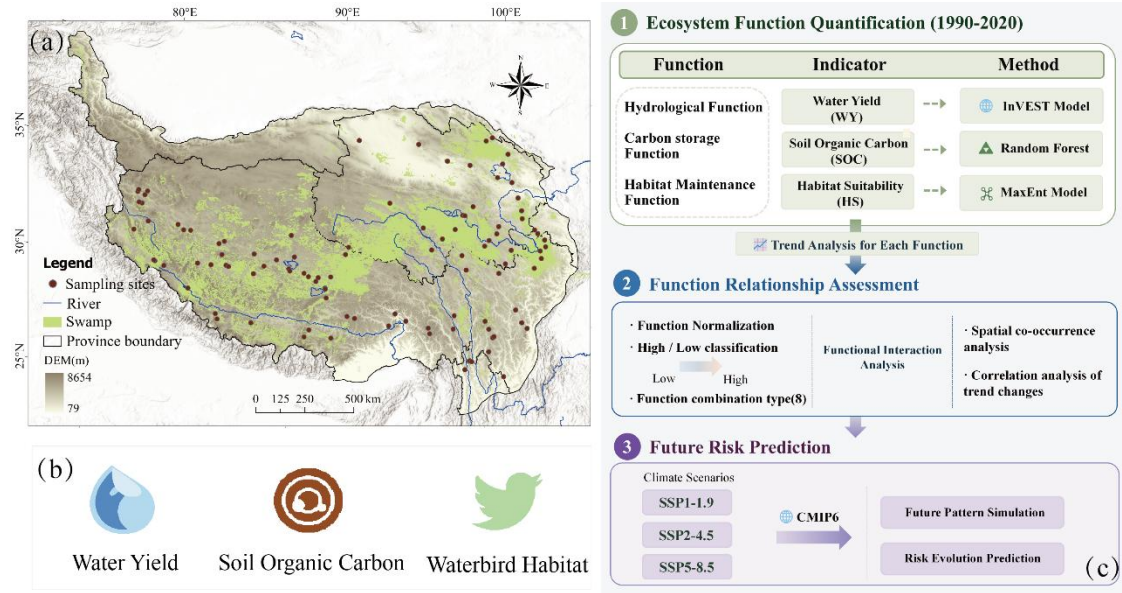


Fig. 1 Location of the study area and the multi-function assessment framework.

2.2 Data sources and processing

Data used in this study included: (1) Landsat series satellite imagery (USGS EarthExplorer, 30 m resolution) for annual extraction of swamp meadow distribution; (2) SRTM DEM data (90 m resolution) for elevation and slope calculation; (3) meteorological data (National Tibetan Plateau Data Center, 0.1° resolution) including precipitation, temperature, and potential evapotranspiration; (4) soil property data (SoilGrids, HWSD, and National Tibetan Plateau Data Center) for soil texture, bulk density, and layer depth; (5) 104 field sampling points with measured SOC data; (6) 278 validated waterbird occurrence records; and (7) CMIP6 future climate data (1 km resolution) including SSP1-1.9, SSP2-4.5, and SSP5-8.5 scenarios. Key intermediate variables—vegetation cover, soil moisture, and ground temperature—were reconstructed using three ensemble learning methods (Random Forest, XGBoost, and LightGBM) with model validation R^2 ranging from 0.85 to 0.95. All raster data were reprojected to a unified coordinate system and resampled to 1 km × 1 km resolution. Background points for MaxEnt modeling were randomly selected from the study area at a ratio of 10:1 to presence points (2,780 points) and spatially filtered before model calibration. Primary data sources are summarized in Table 1.

2.3 Assessment of the three ecosystem functions

Water yield (WY) was simulated using the water yield module of the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) model, based on the water balance principle at the grid-cell scale (Hu et al. 2020; Chen et al. 2024; Mei et al. 2024). For grid cell x , water yield $Y(x)$ is determined by the difference between precipitation $P(x)$ and actual evapotranspiration $AET(x)$:

$$Y(x) = \left(1 - \frac{AET(x)}{P(x)}\right) \cdot P(x) \quad (1)$$

Actual evapotranspiration was estimated following the Budyko curve:

$$\frac{AET(x)}{P(x)} = 1 + \frac{PET(x)}{P(x)} - \left[1 + \left(\frac{PET(x)}{P(x)}\right)^\omega\right]^{1/\omega} \quad (2)$$

$$PET(x) = K_c(l_x) \cdot ET_0(x) \quad (3)$$

$$\omega(x) = Z \cdot \frac{AWC(x)}{P(x)} + 1.25 \quad (4)$$

$$AWC(x) = \text{Min}(\text{MaxSoilDepth}_x, \text{RootDepth}_x) \cdot PAWC(x) \quad (5)$$

$$PAWC(x) = 54.509 - 0.132\text{Sand} - 0.003(\text{Sand})^2 - 0.055\text{Silt} - 0.006(\text{Silt})^2 - 0.738\text{Clay} + 0.007(\text{Clay})^2 - 2.688(\text{OM}) + 0.501(\text{OM})^2 \quad (6)$$

The parameter ω_x is a non-physical parameter characterizing local climate–soil conditions. K_c is the crop evapotranspiration coefficient, $ET_0(x)$ is the reference evapotranspiration (mm) for grid cell x . Max SoilDepth_x represents the maximum soil depth (mm), and RootDepth_x denotes plant rooting depth (mm). Z is the Zhang coefficient (a seasonal constant), which is positively correlated with precipitation duration, precipitation magnitude, and the number of precipitation events per year (N), typically ranging from 1 to 30. Following literature reference (Xiang et al. 2024) and parameter comparison, Z was set to 4 for this study. $PAWC(x)$ is the plant available water content, and Sand, Silt, Clay, and OM represent the percentages of sand, silt, clay, and organic matter in the soil, respectively.

Given that the study focuses on alpine swamp meadows on the Qinghai–Tibetan Plateau, the biophysical coefficients in the InVEST water yield module—including land use/land cover types, maximum root depth, and vegetation evapotranspiration coefficient (K_c)—were locally calibrated with reference to FAO-56 grass crop coefficients and previous InVEST applications in similar regions (Pereira et al. 2026; Hamel and Guswa, 2015). The K_c values were further assigned to five classes based on vegetation cover levels in the study area.

Soil organic carbon content (SOC) was spatially estimated using random forest regression (Breiman, 2001). The model was trained on 104 field sampling points with measured SOC values as the response variable, and used mean annual temperature, annual precipitation, vegetation cover, elevation, slope, soil moisture, soil temperature, and soil bulk density as predictors. Interaction terms—temperature–precipitation, elevation–soil moisture, vegetation cover–precipitation, topography–moisture, and soil moisture–temperature—were constructed based on ecological process assumptions. Hyperparameters were optimized through repeated 5-fold spatial block cross-validation. The model achieved R^2 of 0.520 on the training set and 0.367 on the independent test set. Annual SOC distributions were generated by model inversion, expressed as percentage concentration in the surface soil layer (0–30 cm).

Waterbird habitat suitability (HS) was assessed using the MaxEnt model (Phillips and Dudik, 2008 ; Phillips et al. 2006; Yan et al. 2023 ; Hu et al. 2020). The model was calibrated with 278 validated waterbird occurrence records as the response variable, and used annual evapotranspiration, annual precipitation, mean annual temperature, elevation, slope, vegetation cover, and road density as environmental predictors. The model output is a continuous suitability index ranging from 0 to 1, with values closer to 1 indicating higher environmental suitability for the target waterbird species. Model performance was evaluated using the area under the receiver operating characteristic curve ($AUC = 0.907$). Annual HS was predicted by applying the model to corresponding annual environmental layers. Following previous studies (Luo et al. 2025 ; Raj et al. 2025 ; Wu et al. 2025), HS was classified into four categories—unsuitable, low suitability, moderate suitability, and high suitability—using thresholds of 0.1, 0.3, and 0.6.

2.4 Trend analysis and functional interrelationships

Trend analysis combined Sen's slope estimator with the Mann–Kendall test (Chai et al. 2025 ; Liang et al. 2024). For a time series $\{x_1, x_2, \dots, x_n\}$, Sen's slope β is defined as:

$$\beta = \text{Median} \left(\frac{x_j - x_i}{j - i} \right), i < j \quad (7)$$

where $\beta > 0$ indicates an increasing trend and $\beta < 0$ indicates a decreasing trend.

At the significance level $\alpha = 0.05$, $|Z| > 1.96$ indicates a statistically significant trend.

Functional interrelationships were examined at two levels. First, based on long-term means, each pixel was classified as high (H) or low (L) relative to the study-area median for each function, and the three binary classifications were overlaid to generate eight spatial combination types. Second, based on the sign of Sen's slope for each function, trend direction combinations were generated (e.g., “+++” indicates all three functions increasing; “++-” indicates WY and SOC increasing while HS decreasing). Additionally, pairwise Pearson correlation coefficients were calculated between the trend slope rasters of SOC–WY, SOC–HS, and WY–HS:

$$r = \frac{\sum_{i=1}^N (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^N (x_i - \bar{x})^2 \sum_{i=1}^N (y_i - \bar{y})^2}} \quad (8)$$

where $r > 0$ indicates a positive spatial association in rates of change, and $r < 0$ indicates a negative association.

2.5 Historical degradation and future risk identification

Historical degradation risk index (HRI): For each pixel from 1990 to 2020, a function was assigned a value of 1 if Sen's slope was negative and the Mann–Kendall test was significant ($p < 0.05$), and 0 otherwise. The three functions were summed:

$$HRI_i = \sum_{k=1}^3 I(\beta_{i,k} < 0, p_{i,k} < 0.05) \quad (9)$$

HRI ranges from 0 to 3, with higher values indicating more functions showing significant declines.

Future functional change: Based on the established assessment models and CMIP6 climate scenario data, functional values were projected for 2040, 2060, and 2080, and changes relative to the baseline period (1990–2020 mean) were calculated:

$$\Delta F_{i,k,s} = F_{\text{future } i,k,s} - F_{\text{baseline } i,k} \quad (10)$$

where $\Delta F_{i,k,s}$ denotes the future change in function k for pixel i under scenario s , $F_{\text{future},i,k,s}$ is the projected functional value for the target year, and $F_{\text{baseline},i,k}$ is the multi-year mean of the function during the baseline period. All three functions are positive ecological indicators, so negative changes indicate functional decline, while positive changes indicate functional improvement.

To highlight future ecological degradation risks, the change in each function was converted into a unidirectional degradation risk (Eq. 11).

$$R_{i,k,s} = \max(0, -\Delta F_{i,k,s}) \quad (11)$$

When the future functional value is lower than the baseline, the risk value increases with greater decline; when the future value is higher than or equal to the baseline, the risk is set to 0. Because SOC, WY, and HS have different units and value ranges, min-max normalization was applied to transform each function's degradation risk to a 0–1 scale.

$$R' = \frac{R - R_{\min}}{R_{\max} - R_{\min}} \quad (12)$$

Future comprehensive degradation index (FRI): The future comprehensive degradation index was constructed using an equal-weight aggregation method (Eq. 13).

$$FRI_{i,s} = \frac{1}{3} \sum_{k=1}^3 R'_{i,k,s} \quad (13)$$

Here, $FRI_{i,s}$ is the future comprehensive degradation index for pixel i under scenario s , ranging from 0 to 1. A higher index indicates more pronounced declines in one or more ecosystem functions relative to the baseline, and thus higher comprehensive degradation risk. Because this index primarily reflects the magnitude of functional decline and does not fully incorporate social exposure, vulnerability, or adaptive capacity, it is defined here as a relative biophysical degradation risk, rather than a complete climate risk assessment.

To identify priority areas for future ecological management, the top 10% of pixels with the highest FRI values were identified as future relative degradation hotspots, following the quantile-based ecological hotspot identification method (Schröter and Remme, 2016). This threshold represents areas with relatively high degradation within the study region. Hotspot pixels were assigned a value of 1, and all other valid pixels were assigned 0, to map the spatial distribution of priority management areas for future degradation.

3 Results

3.1 Historical trends of the three functions

From 1990 to 2020, WY, SOC, and HS of Qinghai–Tibetan alpine swamp meadows exhibited pronounced spatial heterogeneity and divergent temporal trends (Fig. 2). High-value areas of all three functions were concentrated in the eastern, southeastern, and several riverine wetland areas, while most areas in the west and northwest had relatively low functional values.

Regional mean WY showed a fluctuating upward trend over the study period, increasing from 163.34 mm·yr⁻¹ in 1990 to 169.32 mm·yr⁻¹ in 2020, an absolute increase of 5.98 mm·yr⁻¹ (3.6% relative increase; Table 2). The linear trend slope was 0.199 mm·yr⁻², reaching statistical significance ($p < 0.05$). Spatially, high WY areas were concentrated in the eastern, southeastern, and parts of the central-eastern region, generally corresponding to areas with relatively abundant precipitation and greater topographic relief (Lv et al. 2023; Wen et al. 2023), while western and northwestern areas had consistently lower values. Areas with significant WY increases and decreases accounted for only 0.084% and 0.369% of the study area, respectively, indicating relatively small overall change intensity.

SOC showed an overall increasing trend from 1990 to 2020. Regional mean SOC increased from 4.98% in 1990 to 6.54% in 2020, an absolute increase of 1.56 percentage points (31.3% relative increase; Table 2). The annual rate of increase was 0.052%·yr⁻¹, with a highly significant trend ($p < 0.001$). Spatially, high SOC areas were concentrated in the eastern and southeastern parts of the study area, with local values exceeding 9%; low-value areas were mainly in the drier or sparsely vegetated western and northern regions. SOC increased significantly across 22.167% of the study area, while significant decreases occurred in only 0.598%, indicating overall enhancement of soil carbon storage function over the past three decades.

In contrast to WY and SOC, HS showed a declining trend over the study period. The area of highly suitable waterbird habitat decreased from 2,470.50 km² in 1990 to 1,346.21 km² in 2020, a reduction of 1,124.29 km² (45.5% decline; Table 2). The linear trend slope was -37.48 km²·yr⁻¹, but this decline did not reach statistical significance ($p = 0.174$). Spatially, areas of higher suitability were distributed as fragmented patches in the eastern, southeastern, northern, and parts of the southwestern wetland areas, while the western and central regions were predominantly low-suitability areas. Areas with significant HS increases and decreases

accounted for 1.138% and 1.419%, respectively, indicating limited overall extent of significant change.

Overall, regional mean WY and SOC both showed significant increasing trends, while the area of highly suitable waterbird habitat declined, indicating that the three functions did not change synchronously.

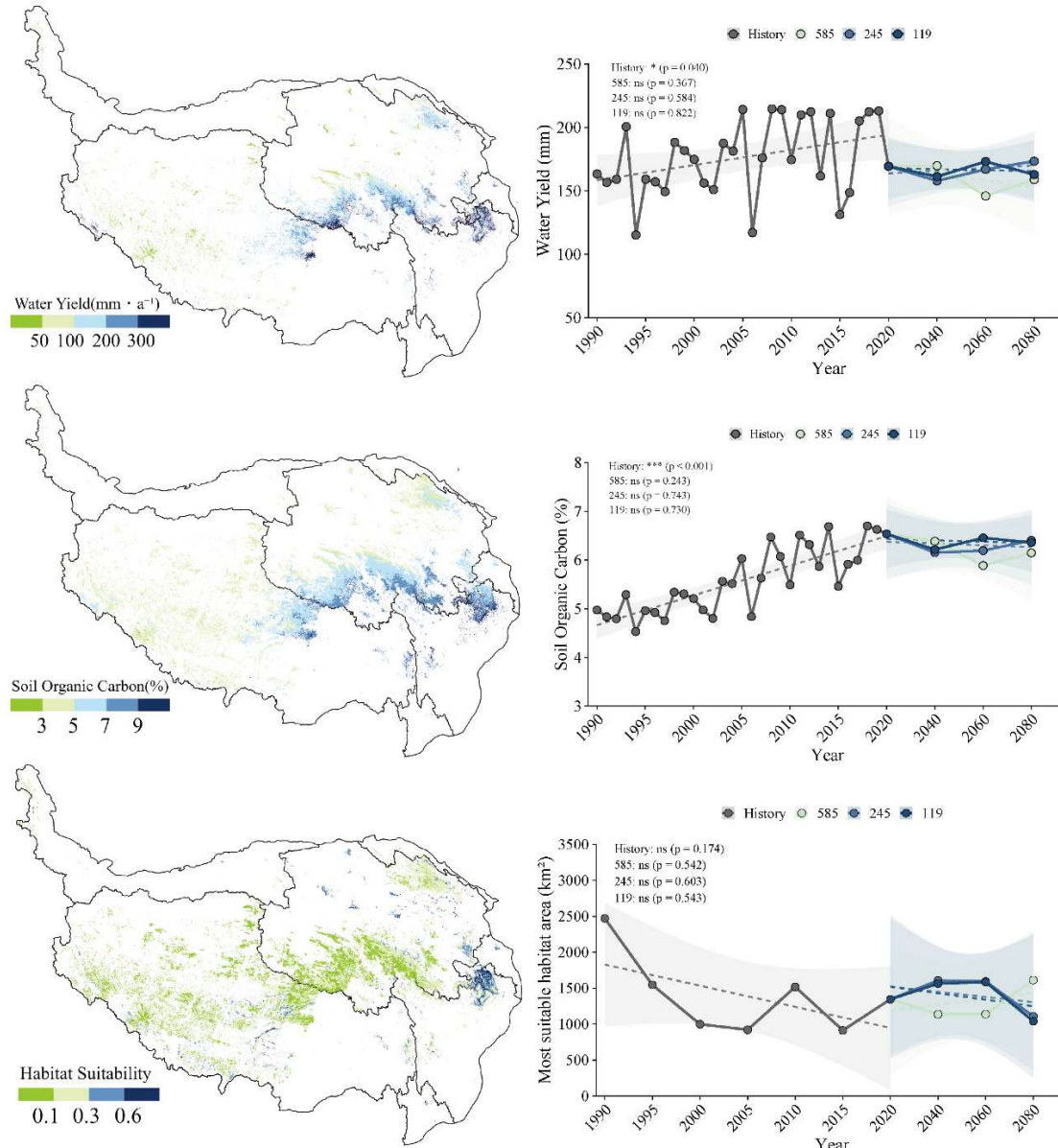


Fig. 2 Spatiotemporal patterns and dynamics of the three ecosystem functions during the historical period (1990–2020).

Table 2 Statistical trends in three ecosystem functions of alpine swamp meadows on the Qinghai-Tibet Plateau from 1990 to 2020

Indicator	Mean (1990)	Mean (2020)	Absolute change	Relative change (%)	Average annual change	p-value	Area with a significant increase (%)	Area with a significant decrease (%)
Water Yield (mm/yr)	163.34	169.32	+5.98	+3.6	+0.199	0.04	0.084	0.369

SOC(%)	4.98	6.54	+1.56	+31.3	+0.052	<0.001	22.167	0.598
highly suitable habitat area (km ²)	2470.50	1346.21	-1124.29	-45.5	-37.48	0.174	—	—

3.2 Spatial and directional associations among the three functions

Based on long-term means and median thresholds, the study area was classified into eight spatial combination types (Fig. 3a, b). The HHL type (WY and SOC high, HS low) occupied the largest area (22.61% of effectively classified area), followed by LLL (all three functions low; 20.79%) and LLH (HS alone high; 20.55%). The HHH type (all three functions high) accounted for 18.73%, while HLH, LHH, HLL, and LHL accounted for 6.89%, 3.83%, 1.78%, and 4.83%, respectively. Areas with at least two functions in high-value co-occurrence (HHH, HHL, HLH, LHH) together accounted for 52.06% of the effectively classified area, indicating that over half the area exhibited co-occurrence of high values for two or three functions. Spatially, HHH and HHL types were concentrated in the eastern, southeastern, and parts of the central transition zone, forming relatively continuous high-value patches and clusters; LLL and LLH types were more widely distributed in the western, northwestern, and some interior areas.

Pairwise high-value co-occurrence showed that WY and SOC co-occurred as high in 41.34% of the area, higher than WY–HS (25.62%) and SOC–HS (22.56%). Thus, under long-term average conditions, WY and SOC showed higher spatial overlap, while HS high-value areas had more limited overlap with the other two functions.

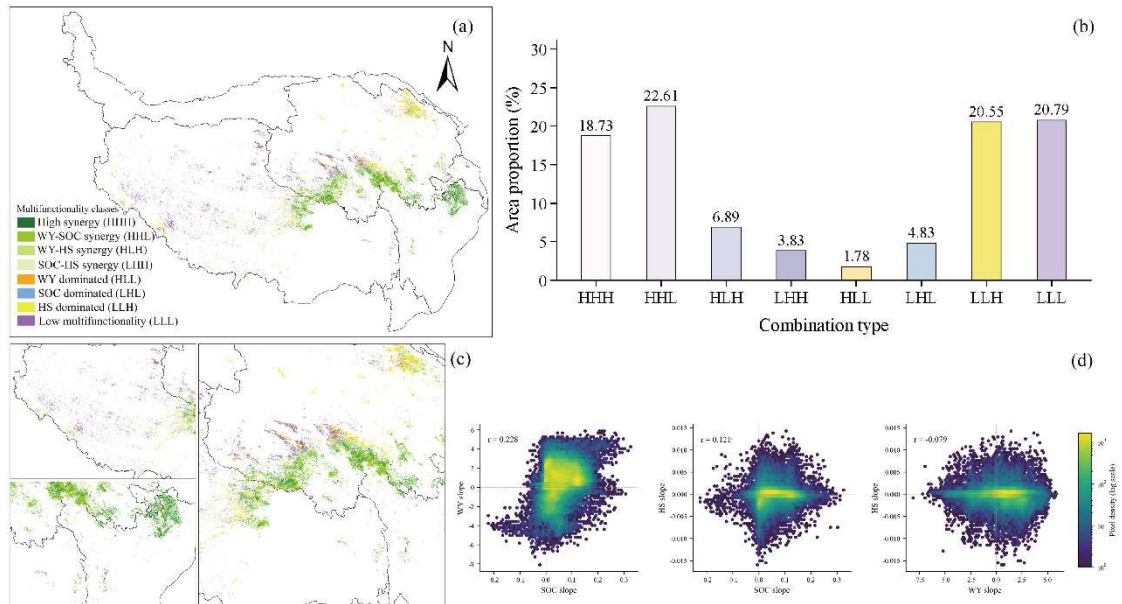


Fig. 3 Relationships between the spatial patterns and long-term trends of the three ecosystem functions.

Trend direction combinations (Table 3) showed that the “+++” type (all three functions increasing) accounted for 38.98% of the area, the largest trend combination; the “++-” type (WY and SOC increasing, HS decreasing) accounted for 32.45%. The “-++” type (SOC and HS increasing, WY decreasing) accounted for 12.14%, and the “+-+” type (only SOC increasing) accounted for 9.37%. The remaining four trend combinations each accounted for less than 3%. Areas with inconsistent trend directions among the three functions accounted

for 59.23% of the total, substantially higher than the 1.79% of areas with synchronous declines, indicating that at the pixel scale, the dominant pattern was divergence in change directions rather than synchronous change.

Pairwise correlations of trend slopes (Fig. 3d) showed a weak positive correlation between SOC and WY ($r = 0.228$), a weak positive correlation between SOC and HS ($r = 0.121$), and a near-zero weak negative correlation between WY and HS ($r = -0.079$). The spatial associations in rates of change were consistently weak across all three pairs, with HS showing the lowest synchrony with the other two functions.

In summary, WY and SOC showed higher spatial overlap and greater consistency in change direction than HS with either function, reflecting a substantial spatial mismatch and temporal asynchrony between habitat suitability and water supply and soil carbon functions.

Table 3 Area statistics of trend combinations between two ecosystem functions

Type ID	WY	SOC	HS	Area (km ²)	Proportion of total area (%)
1	+	+	+	28515	38.98
2	+	+	-	23740	32.45
3	+	-	+	538	0.74
4	-	+	+	8883	12.14
5	+	-	-	2031	2.78
6	-	+	-	6852	9.37
7	-	-	+	1286	1.76
8	-	-	-	1307	1.79

3.3 Future functional changes and risks

3.3.1 Functional changes under different emission scenarios

Projections under SSP1-1.9, SSP2-4.5, and SSP5-8.5 scenarios showed that all three functions exhibited pronounced spatial heterogeneity, with positive and negative changes intermingled, and the temporal trajectories of different functions were not consistently aligned.

By 2080, WY changes showed substantial spatial variation, with ranges of -209 to 209 mm under SSP1-1.9, -233 to 845 mm under SSP2-4.5, and -232 to 476 mm under SSP5-8.5 (Fig. 4). The northeastern and central areas showed widespread WY declines across multiple scenarios, while the southeastern areas showed predominantly positive changes. In terms of regional totals (Table 4), SSP1-1.9 showed a fluctuating trajectory of initial decline, then increase, then decline; SSP2-4.5 shifted from persistent decline in the early and middle periods to increase in the longer term; SSP5-8.5 remained below the baseline throughout, with the largest decline occurring in 2060.

By 2080, SOC showed mosaic patterns of increasing and decreasing patches across all three scenarios, with change ranges of -2.82 to 6.54 percentage points under SSP1-1.9, -3.76 to 7.71 under SSP2-4.5, and -3.57 to 5.81 under SSP5-8.5 (Fig. 4). SOC declines were more likely in the western, southwestern, northeastern, and eastern margins, while the south-central and southeastern wetlands showed predominantly increases. Regional mean SOC remained above the baseline across all scenarios and time periods (Table 4), but trajectories differed: SSP1-1.9 showed peak increase in 2060 followed by slight decline; SSP2-4.5 showed continued expansion of increases; SSP5-8.5 showed initial decline followed by recovery. Overall regional increases coexisted with local decreases, reflecting strong spatial heterogeneity in SOC responses.

By 2080, HS also showed mosaic patterns of positive and negative changes, with ranges of -0.55 to 0.58 under SSP1-1.9, -0.51 to 0.62 under SSP2-4.5, and -0.45 to 0.59 under SSP5-8.5 (Fig. 4). Suitability increases were concentrated in the south-central, central-eastern, and southeastern wetlands, while declines were more common in the southwestern, northern, and eastern margins. The area of highly suitable habitat (Table 4) showed early-to-middle

expansion followed by later decline under SSP1-1.9 and SSP2-4.5, while SSP5-8.5 showed early-to-middle decline followed by later recovery.

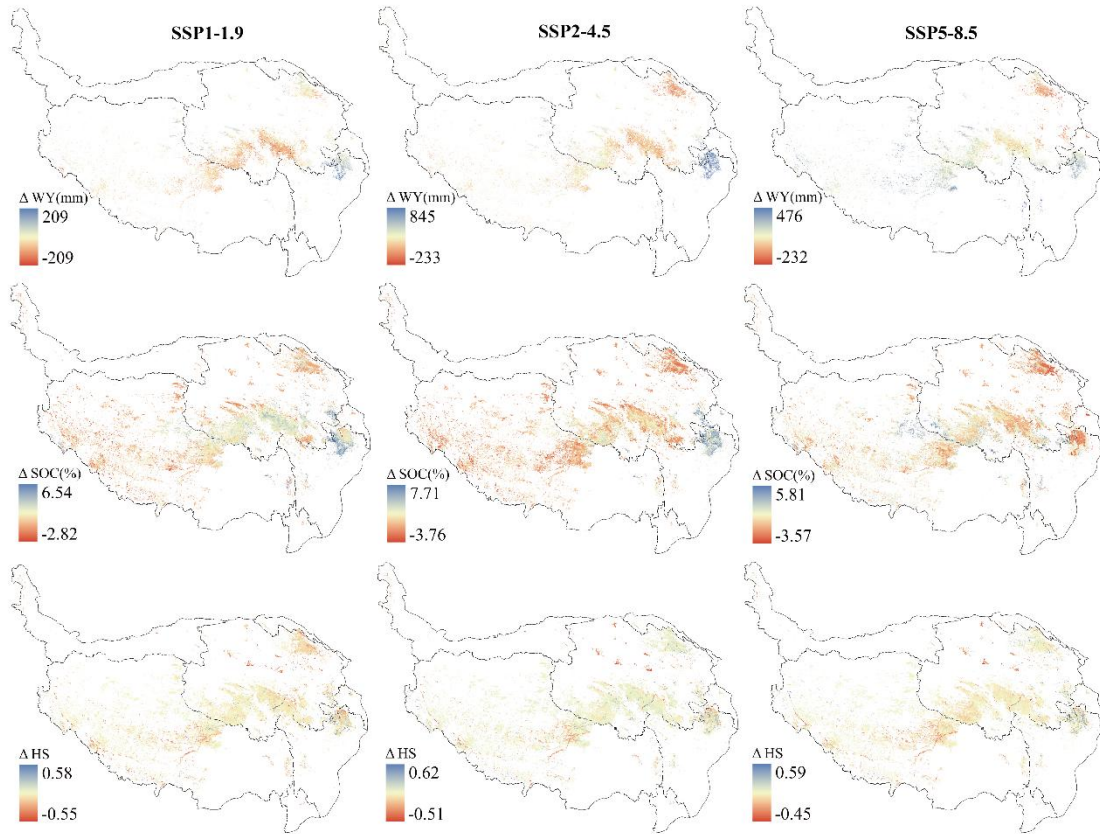


Fig. 4 Spatial distributions of projected changes in the three ecosystem functions under different SSP scenarios in 2080.

Overall, the three functions exhibited substantial spatial mismatch and temporal asynchrony. The northeastern, eastern margins, and parts of the southwestern areas were focal regions for multi-function synchronous decline across multiple scenarios, while the south-central and southeastern areas showed multi-function synchronous improvement. Regional mean SOC remained above baseline across all scenarios; WY showed scenario-dependent fluctuations; and HS showed opposing phase-dependent trajectories under different emission pathways.

Table 4 Projected changes in the three functions under different SSP scenarios for 2040, 2060, and 2080

Function	Scenario	$\Delta 2040$	$\Delta 2060$	$\Delta 2080$	Risk trajectory
WY(10^8 $m^3 yr^{-1}$)	SSP1-1.9	-11.645	+3.35	-8.29	Fluctuating trajectory; values remain below the baseline in both the short and long term, indicating a moderate risk of long-term decline
	SSP2-4.5	-15.817	-4.9	+4.69	A continued decline in the short and medium term
	SSP5-8.5	-1.148	-30.44	-14.72	Remains below the baseline throughout the projection period, with the strongest decline in the medium term and the highest long-term risk
SOC(%)	SSP1-1.9	+0.635	+0.878	+0.781	A sustained increase across all periods, with relatively stable changes and low long-term risk

	SSP2-4.5	+0.574	+0.616	+0.825	An overall increasing trajectory, with a larger increase in the long term
	SSP5-8.5	+0.809	+0.309	+0.569	An overall increasing trajectory, but with a markedly reduced increase in the medium term
Highly suitable waterbird habitat area (km ²)	SSP1-1.9	176.858	198.116	-347.188	Optimal habitat expands in the short term but declines substantially in the long term, indicating a relatively high risk of long-term habitat degradation
	SSP2-4.5	219.492	206.276	-278.418	Marked improvement in the short and medium term, followed by a decline in the long term, indicating a potential risk of long-term habitat degradation.
	SSP5-8.5	-249.512	-249.587	225.013	Continued degradation in the short and medium term, followed by some recovery in the long term, but with substantial uncertainty and relatively high risk under the high-emissions scenario.

389

390 3.3.2 Historical degradation and future comprehensive risk

391 The historical degradation risk index reflects the number of functions showing significant
392 declines at the pixel scale from 1990 to 2020. Most of the study area had HRI = 0, with only
393 small areas showing one-function (Level 1) or two-function (Level 2) significant declines,
394 scattered in the southeastern, eastern, and parts of the central and northeastern areas (Fig.
395 5a). Over 1990–2020, most alpine swamp meadows did not experience simultaneous
396 significant declines in multiple functions; historical multi-function degradation was localized
397 and dispersed.

398 The future comprehensive risk index (Fig. 5b) showed substantially stronger spatial
399 clustering than historical degradation. High-risk areas were concentrated in the northeastern
400 Qinghai Lake region, the eastern margins, and parts of the southwestern areas, while the
401 central and western regions were predominantly low-risk. Compared with historical patterns,
402 both the extent and spatial continuity of future risk were enhanced, suggesting that future
403 climate change may become a major external driver of multi-function degradation in swamp
404 meadows.

405 Risk hotspots—defined as the top 10% of pixels by FRI—were concentrated in the
406 northeastern and eastern parts of the study area, with scattered patches in the southwestern
407 and central areas (Fig. 5c). Spatial overlay analysis revealed that approximately 24.3% of
408 future risk hotspots overlapped with current HHH areas (areas where all three functions are
409 currently at high values), indicating that some areas with currently high ecological function
410 are facing elevated future degradation pressure. These areas should be prioritized for wetland
411 conservation, ecological restoration, and climate-adaptive management.

412 Figure 5d compares the standardized values of the three functions in 1990 and 2020. SOC
413 showed substantial improvement, WY increased slightly, and HS declined over this period,
414 confirming the asynchrony of functional changes—hydrological and carbon storage
415 functions improved while habitat function did not.

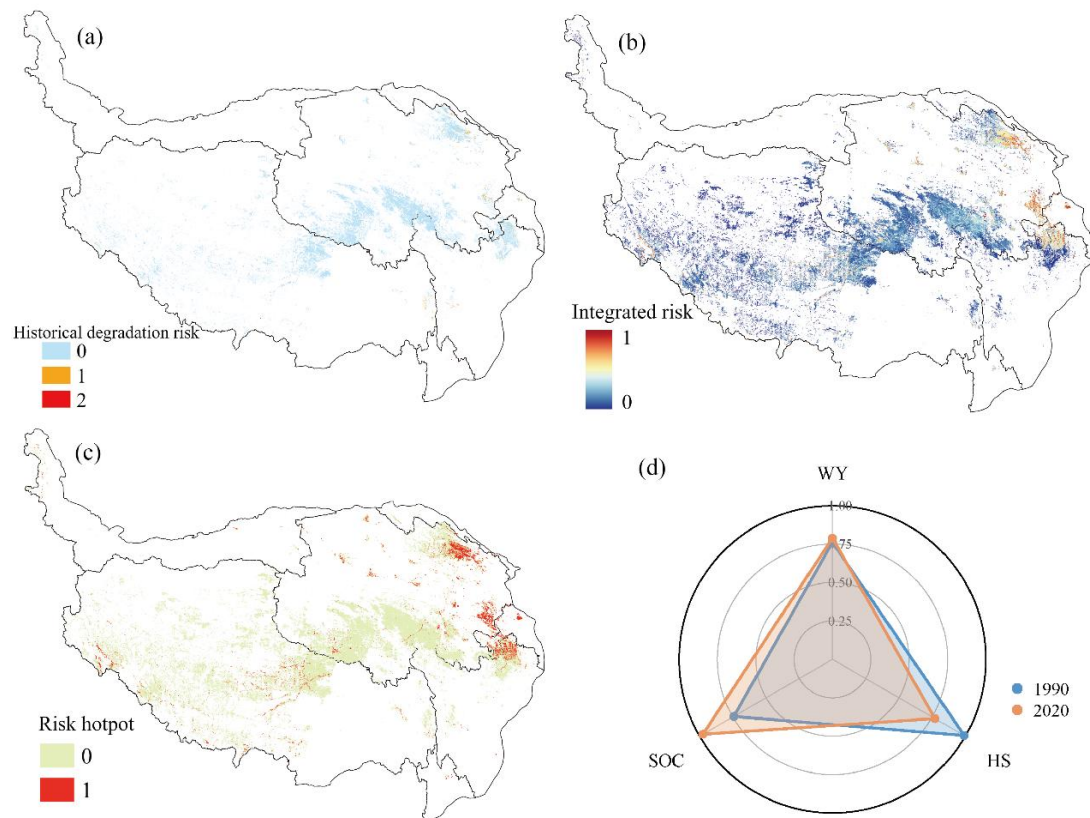


Fig. 5 Spatial patterns of historical degradation risk and future integrated risk of alpine swamp meadow on the Qinghai-Tibetan Plateau

Historical multi-function synchronous degradation was limited in extent, but under SSP5-8.5, future comprehensive risk by 2080 showed spatial concentration in the northeastern, eastern margins, and parts of the southwestern areas. Future risk hotspots may face multi-function synchronous degradation pressure and require differentiated management strategies based on the dominant degradation drivers in each area.

4 Discussion

4.1 Historical changes in the three functions were asynchronous

The results revealed that from 1990 to 2020, regional mean WY and SOC of Qinghai-Tibetan alpine swamp meadows both increased significantly, while the area of highly suitable waterbird habitat declined by 45.5%. This pattern reveals an important phenomenon: against the backdrop of net swamp meadow “expansion,” different ecological functions did not all change in the same direction. Improvements in hydrological regulation and carbon sequestration were not accompanied by synchronous improvements in habitat maintenance function.

The increase in WY was primarily driven by increased precipitation and glacier meltwater contributions. Previous work on Qinghai-Tibetan Plateau hydrology showed that historical runoff increases were mainly related to changes in precipitation and temperature (Wang et al. 2023). This interpretation is supported by the correspondence between high WY areas and regions with relatively abundant precipitation observed in the present study. Based on model estimates, SOC increased from 4.98% to 6.54%, suggesting that the net balance between plant carbon inputs and organic matter decomposition shifted toward accumulation.

Precipitation has been identified as the primary control on SOC density spatial heterogeneity, with most alpine wetland areas showing SOC accumulation from 2000 to 2018 (Jiang et al. 2024); precipitation, aboveground and belowground biomass jointly regulate SOC storage (Nie et al. 2023). Warming and wetting likely promoted carbon inputs through enhanced vegetation productivity, which may be the main driver of SOC increase. However, given the uncertainty in SOC spatial estimation (test set $R^2 = 0.367$), this conclusion requires further validation with additional field sampling data.

The declining trend in HS, however, points to different processes at work. Waterbirds are more sensitive to local habitat structure and anthropogenic disturbance—black-necked crane migratory stopover sites preferred areas away from roads and villages (An and Guo 2025). Even with regional increases in WY and SOC, reductions in shallow-water habitat, patch fragmentation, or road disturbance may still drive declines in suitable habitat. Notably, the declining trend in HS did not reach statistical significance ($p = 0.173$), indicating substantial uncertainty in its long-term trajectory and suggesting that biodiversity maintenance functions may respond to climate change in more complex and nonlinear ways than hydrological and carbon functions. This finding echoes the observation that degradation alters biodiversity—multifunctionality relationships, and that different functional dimensions have fundamentally different response thresholds and lag times to the same drivers (Gao et al. 2025).

4.2 Spatial co-occurrence of high values did not imply temporal co-variation

A second major finding reveals a seemingly paradoxical but highly instructive pattern: under long-term average conditions, areas with at least two functions in high-value co-occurrence accounted for 52.06% of the study area, with WY–SOC spatial overlap (41.34%) substantially higher than HS with either function; yet in terms of change trajectories, areas with inconsistent trend directions among the three functions accounted for 59.23%, and trend slope correlations were uniformly low (SOC–WY $r = 0.228$; SOC–HS $r = 0.121$; WY–HS $r = -0.079$). This indicates that spatial co-occurrence of high functional values does not translate into temporal co-variation.

How can this “spatial overlap but trend divergence” phenomenon be explained? Spatial co-occurrence of high values primarily reflects the long-term adaptive responses of different functions to common environmental gradients—moist, well-vegetated areas typically have higher water yield capacity, carbon accumulation potential, and habitat suitability simultaneously. However, the trajectories of individual functions are also influenced by function-specific processes, local disturbances, and ecological response lags, so spatial co-occurrence based on average conditions cannot substitute for examination of temporal dynamics. The near-zero correlation coefficients are themselves an important finding: they indicate that in Qinghai–Tibetan alpine swamp meadows, water yield, carbon sequestration, and habitat maintenance functions are largely independent of one another in their temporal dynamics. This conclusion is consistent with the finding that ecosystem service relationships have strong spatial and temporal scale dependence—spatial patterns and temporal dynamics cannot substitute for one another (Zheng et al. 2020).

From a management perspective, this finding has clear policy implications: conservation priority setting should not be based solely on overlay of long-term mean high values, but should integrate three types of information—current status, change trends, and future risks. Areas with all three functions currently high (HHH) should receive preventive protection; areas with all three functions low (LLL) should undergo comprehensive restoration; and functionally mismatched areas such as HHL (WY and SOC high, HS low) should prioritize improvement of habitat connectivity and reduction of road disturbance rather than continued pursuit of further increases in water yield or carbon storage.

4.3 Future responses showed temporal phasing and spatial concentration

Future projections revealed that the three functions exhibited distinct temporal phasing and spatial differentiation in their responses to climate pathways.

Temporally, under SSP5-8.5, WY remained below baseline across all periods, with the largest decline occurring in 2060 ($-30.44 \times 10^8 \text{ m}^3 \cdot \text{yr}^{-1}$), suggesting that water supply risk may manifest first around mid-century. Regional mean SOC remained above baseline across all scenarios, but the increase was substantially attenuated in the middle period under SSP5-8.5 (from 0.809 to 0.309 percentage points), indicating that soil carbon accumulation stability is threatened under high-emission pathways—consistent with experimental evidence that warming reduces microbial carbon use efficiency and weakens mineral-associated organic carbon protection (Qin et al. 2024). The area of highly suitable waterbird habitat showed opposing phase-dependent trajectories under different scenarios: early-to-middle expansion followed by later decline under low- and medium-emission scenarios, versus early-to-middle decline followed by later recovery under the high-emission scenario. This non-monotonic response pattern suggests that projections from a single time point cannot represent long-term trends, and adaptive management needs to adjust strategies dynamically based on phased change characteristics.

Spatially, future comprehensive risk showed clear concentration—high-risk areas were mainly in the northeastern region (around Qinghai Lake), the eastern margins, and parts of the southwest, contrasting sharply with the dispersed pattern of historical degradation. This spatial differentiation suggests that future climate change may become the dominant driver of multi-function degradation in swamp meadows. Pronounced spatial differentiation and medium-to-long-term decline risks in terrestrial water storage on the Qinghai–Tibetan Plateau have been projected (Li et al. 2022), which broadly aligns with the spatial pattern of WY changes in the present study, further validating the sensitivity of alpine wetland water security to climate change.

Notably, future risk hotspots overlapped partially with current high-function areas (approximately 24.3% overlap with HHH areas), meaning that some areas with currently good ecological function face the greatest future degradation pressure. This “high-current-value–high-future-risk” conflict pattern requires conservation strategies to shift from reactive response to proactive prevention—implementing proactive measures such as hydrological connectivity maintenance, soil disturbance control, and habitat restoration before risks manifest, rather than reacting after functions have already degraded.

4.4 Limitations and future directions

Several limitations should be acknowledged. Data-wise, SOC spatial estimation relied on 104 field sampling points, with a test set R^2 of only 0.367, limiting prediction accuracy and potentially affecting the robustness of SOC trend analyses. The extrapolation from point sampling to 1-km raster resolution also introduces spatial autocorrelation and scale mismatch issues; future work should increase sampling density and incorporate uncertainty analysis. Model assumption-wise, future projections assume that historical relationships remain unchanged—i.e., that the relationships established by random forest and MaxEnt models within the current climate range will hold in the future—but continued warming may break this assumption, particularly when temperatures exceed certain ecological thresholds. Function coverage-wise, this study focused on only three functional dimensions and did not address nutrient cycling, pollination, or cultural services; multi-trophic diversity has been shown to have significant positive effects on ecosystem multifunctionality (Su et al. 2024), so the present study may underestimate the overall functional vulnerability of swamp

meadows. Future research should strengthen long-term field validation and model ensemble projections, develop multi-model, multi-scenario ensemble forecasting frameworks, and conduct sensitivity analyses under different thresholds and weighting schemes to improve the reliability of risk assessments. Nevertheless, through long-term integrated assessment of multiple functions, this study quantitatively reveals the asynchrony of functional changes in swamp meadows, the divergence between spatial patterns and trend directions, and the spatiotemporal differentiation of future risks, providing empirically based scientific reference for alpine wetland ecosystem conservation and adaptive management.

5 Conclusions

The water yield, carbon sequestration, and habitat maintenance functions of Qinghai–Tibetan alpine swamp meadows exhibited significant asynchronous change patterns over the historical period—water regulation and soil carbon storage functions generally strengthened, while habitat maintenance function showed degradation. This asynchrony is further manifested as a contradiction between spatial patterns and change trends: spatial co-occurrence of high functional values does not equate to temporal co-variation, and the three functions are largely independent in their temporal dynamics. Under different future emission pathways, water supply risk under medium- and high-emission scenarios is most pronounced around mid-century; soil carbon storage, while generally increasing, faces stability threats under high-emission pathways; and habitat suitability shows non-monotonic trajectories.

Comprehensive risk is spatially concentrated in the northeastern, eastern margins, and parts of the southwestern areas, with some areas facing a “high-current-value–high-future-risk” conflict. These findings indicate that conservation management of Qinghai–Tibetan alpine swamp meadows should shift from single-function orientation to multi-function zonal governance, with differentiated adaptive strategies formulated for each area based on its functional combination status and future risk profile.

Statements & Declarations

Supplementary Information The online version contains supplementary material available at Table 1.

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Author contributions Ning Ning, Lu Zhang and Zhiyun, Ouyang contributed to the conception and design of the study. Ning Ning, Luo Guo, Xian Li, and Xiaoping Sun contributed to material preparation, data collection and analysis. Lu Zhang supervised the

research and contributed to the interpretation of the results and manuscript revision. All authors critically reviewed the manuscript and approved the final version.

Data Availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Conflict of Interest The authors declare no competing interests.

Table 1 Summary of data sources used in this study

Data category	Description	Processing and usage	Source
DEM	90 m resolution, digital elevation model	Cropped and used as input for Random Forest and MaxEnt models	Geospatial Data Cloud (https://www.gscloud.cn)
Land surface temperature	1 km resolution	Cropped and used as input for Random Forest model	Earth Resource Data Cloud Platform (www.gis5g.com)
Precipitation (mm)	1 km resolution, 1990–2020	Cropped; annual precipitation calculated and used as input for InVEST, Random Forest, and MaxEnt models	National Tibetan Plateau Data Center (https://data.tpdac.ac.cn/)
Future precipitation	1 km resolution, 2021–2100	Cropped; annual precipitation calculated and used as input for InVEST, Random Forest, and MaxEnt models	National Tibetan Plateau Data Center (http://data.tpdac.ac.cn)
Future temperature	1 km resolution, 2021–2100	Cropped; annual temperature calculated and used as input for InVEST, Random Forest, and MaxEnt models	National Tibetan Plateau Data Center (http://data.tpdac.ac.cn)
Future potential evapotranspiration	1 km resolution, 2021–2100	Cropped; annual potential evapotranspiration calculated and used as input for InVEST model	National Tibetan Plateau Data Center (http://data.tpdac.ac.cn)
Potential evapotranspiration (mm)	1 km resolution, 1990–2020	Cropped; annual potential evapotranspiration calculated and used as input for InVEST model	National Tibetan Plateau Data Center (https://data.tpdac.ac.cn/)
Root restricting layer depth	250 m resolution, 2020	Cropped and used as input for InVEST model	ISRIC (https://data.isric.org/)

(soil depth as proxy)			
Plant available water content (PAWC)	250 m resolution, 2020	Calculated from database; cropped and used as input for InVEST model	HWSD v1.21 (https://www.fao.org/)
Soil moisture (m ³ /m ³)	1 km resolution, 2001–2020	Cropped; annual mean soil moisture calculated and used as input for Random Forest model	National Tibetan Plateau Data Center (https://data.tpdac.ac.cn/)
Soil bulk density (g/cm ³)	1 km resolution, 2022	Resampled; cropped and used as input for Random Forest model	National Tibetan Plateau Data Center (https://data.tpdac.ac.cn/)
Mean annual temperature (°C)	1 km resolution, 1990–2020	Cropped; annual mean temperature calculated and used as input for Random Forest and MaxEnt models	National Tibetan Plateau Data Center (https://data.tpdac.ac.cn/)
Slope	1 km resolution, 2022	Derived from DEM; resampled, cropped, and used as input for Random Forest and MaxEnt models	Derived from DEM
Fractional vegetation cover (FVC)	1 km resolution	Cropped and used as input for Random Forest and MaxEnt models	National Tibetan Plateau Data Center
Road density	1 km resolution, 1990–2020	Using annual road polyline datasets with consistent road classifications, road density was calculated in GIS and used as a predictor in the MaxEnt model	National Geomatics Center of China (https://www.ngcc.cn/) and OpenStreetMap (https://www.openstreetmap.org/)

Note: All raster data were reprojected to a unified coordinate system and resampled to 1 km × 1 km resolution. Continuous variables were interpolated using bilinear interpolation; categorical variables were resampled using nearest-neighbor resampling.

Supplementary Model Evaluation and Explanatory Analyses

This appendix provides supplementary analyses related to model performance, model interpretation, environmental controls, and baseline temporal changes. These results provide additional support for the model evaluation and interpretation presented in the main text.

The non-parametric Mann–Kendall (M–K) test was used to assess the statistical significance of temporal trends. The Mann–Kendall test statistic S was calculated as:

$$S = \sum_{i=1}^{n-1} \sum_{j=i+1}^n \text{sgn}(x_j - x_i) \quad (1)$$

where the sign function is defined as:

$$\text{sgn}(x_j - x_i) = \begin{cases} 1, & \text{if } x_j > x_i \\ 0, & \text{if } x_j = x_i \\ -1, & \text{if } x_j < x_i \end{cases} \quad (2)$$

For $n \geq 10$, S approximately follows a normal distribution. When tied observations were present, the variance of S was corrected as:

$$\text{Var}(S) = \frac{n(n-1)(2n+5) - \sum_{k=1}^m t_k(t_k-1)(2t_k+5)}{18} \quad (3)$$

where t_k is the number of observations in the k -th group of tied values and m is the number of tied groups. The standardized test statistic Z was calculated as:

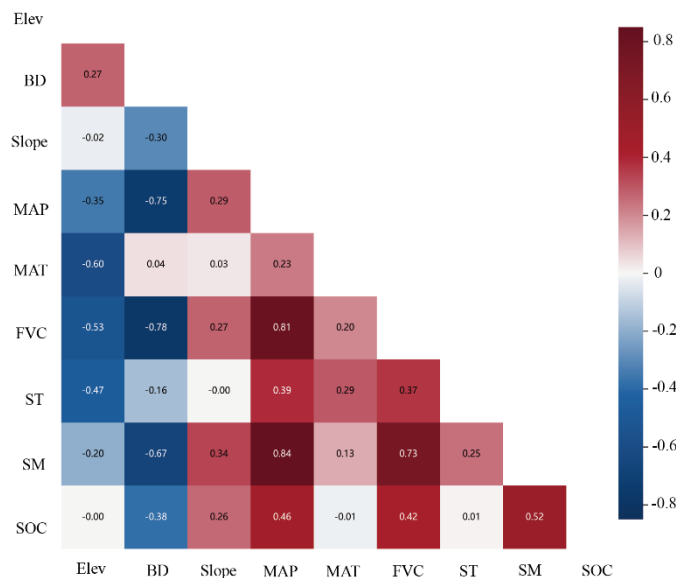
$$z = \begin{cases} \frac{S-1}{\sqrt{\text{Var}(S)}}, & S > 0 \\ 0, & S = 0 \\ \frac{S+1}{\sqrt{\text{Var}(S)}}, & S < 0 \end{cases} \quad (4)$$

A positive Z indicates an increasing trend, whereas a negative Z indicates a decreasing trend. At the 0.05 significance level, the null hypothesis of no monotonic trend was rejected when $|Z| > 1.96$. Sen's slope estimator was subsequently used to quantify the magnitude of the temporal trend, with positive and negative slope values indicating increasing and decreasing trends, respectively. This combination of the Mann-Kendall test and Sen's slope provides a robust non-parametric framework for detecting and quantifying temporal trends in ecological and environmental variables.

Table T1. Model validation results for the three ecosystem functions.

Model/Method	Validation metric	Validation result	Sample size
InVEST Water Yield model(WY)	Relative error (%)	Underestimation by 5.63%	—
Random forest model (SOC)	RMSE	4.462	104
MaxEnt model (waterbirds HS)	AUC	0.907	278

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614

Fig.S1 Heatmap of correlation coefficients between environmental factors and soil organic carbon (SOC)

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Note: The figure illustrates the relationships between key environmental predictors and SOC identified by the random forest model. The direction and magnitude of the responses indicate how variation in individual environmental factors is associated with model-predicted SOC.

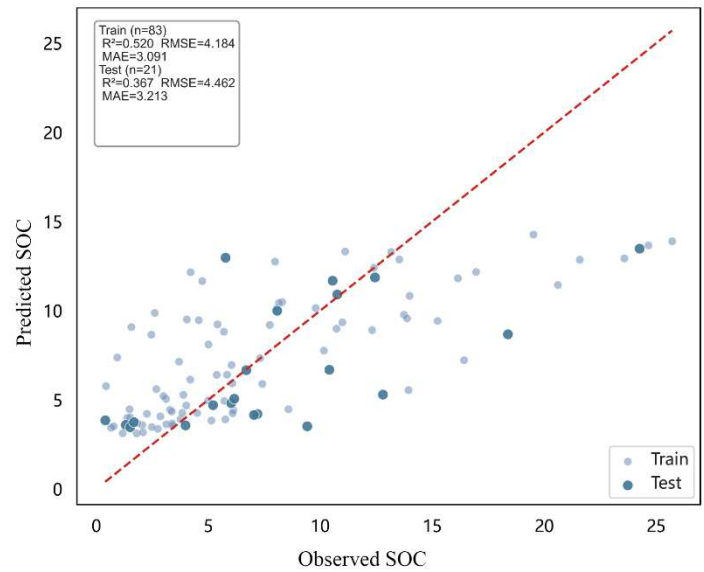


Fig.S2 Predictive performance of the random forest model for SOC.

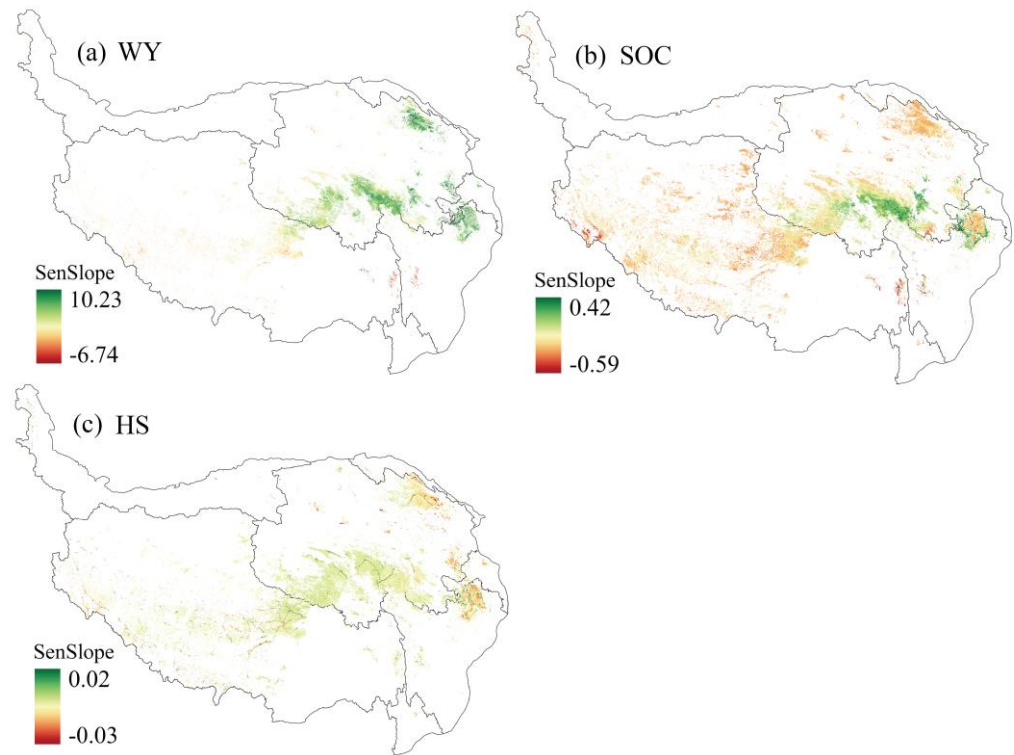


Fig.S3 Spatial patterns of trends for the three ecosystem functions during the baseline period

Table T2. Shared Socioeconomic Pathway (SSP) scenarios used in this study.

Scenario	Emissions pathway	Main characteristics
SSP1-1.9	Low	A low-emissions, sustainability-oriented pathway, with global warming projected to

		remain relatively limited by the end of the century.
SSP2-4.5	Intermediate	An intermediate-emissions pathway characterized by moderate socioeconomic development, greenhouse gas concentrations, and climate change.
SSP5-8.5	Very high	A very high-emissions pathway characterized by fossil-fuel-intensive development and substantially greater long-term warming and climate-related risks.

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