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CANOPY STRUCTURE AND UNDERSTORY DIVERSITY IN TRADITIONAL CHINESE LANDSCAPE PLANNING: IMPLICATIONS FOR BIODIVERSITY-ORIENTED RESTORATION IN THE ERGUNA WETLAND

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Abstract

The Erguna wetland in Inner Mongolia, China, represents Asia's largest woody wetland and a critical stopover for migratory birds, yet it faces increasing biodiversity threats from conventional management practices focused mainly on greening rate while overlooking vertical vegetation structure. This study investigated the relationship between canopy structure and understory plant diversity across three canopy density groups in 30 standardized plots of Erguna National Wetland Park, integrating traditional Chinese garden principles with modern ecological assessment methods. Leaf area index and canopy openness were measured using hemispherical photography, while biodiversity was assessed by species richness, Shannon-Wiener index, and functional group composition. Results revealed significant gradient characteristics in canopy structure and microclimate conditions among the groups ($P < 0.001$). A unimodal relationship emerged, with moderate canopy closure (40-60%) supporting maximum diversity ($R^2 = 0.68$, $P < 0.001$). Functional group analysis showed herbaceous plants and shrubs dominated at intermediate canopy density, while high leaf area index suppressed herbaceous species but favored mosses and ferns. Structural equation modeling demonstrated direct light-driven effects ($\beta = 0.62$) and indirect water regulation pathways ($\beta = 0.35$) governing understory diversity. Multi-layer canopies increased biodiversity by approximately 35% and enhanced soil water retention. These findings validate traditional Chinese principles of moderate density and provide actionable canopy management thresholds (LAI 2.5-3.5, openness 40-60%) for biodiversity-oriented wetland restoration.

Introduction

Under the guidance of the Kunming-Montreal Global Biodiversity Framework, biodiversity protection in urban and semi-natural areas has become a core issue in global ecological governance (CBD 2022). Wetlands, among the most productive yet vulnerable ecosystems, contain extremely rich species diversity. However, over the past half century, global wetland area has sharply decreased due to urban expansion, agricultural conversion, and climate change (Dudgeon *et al.* 2006). In cold temperate regions, wetland vegetation is further constrained by extreme low temperatures, seasonal permafrost, and hydrological fluctuations (Chang *et al.* 2023).

Erguna wetland in Inner Mongolia, China, is located in the forest-grassland ecotone of the Greater Khingan Mountains foothills (Liu and Diamond 2005), representing Asia's native woody wetlands. This area contains diverse habitats including rivers, swamps, shrublands, and meadows, supporting numerous protected species such as drunken willow (*Salix chosenia*), red-crowned crane (*Grus japonensis*), and swan goose (*Anser cygnoides*) (Chi *et al.* 2018). However, ecotourism development and agricultural activities increasingly threaten vegetation communities through structural homogenization, alien species invasion, and habitat fragmentation (Catford *et al.* 2012).

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Traditional wetland park planning emphasizes visual aesthetics and recreation, typically using fast-growing single tree species to establish high-density pure forests. While this greening model rapidly increases forest coverage, it often creates insufficient understory light, inhibiting shrub and herb layer development and producing what is termed a "green desert" incapable of supporting complex food webs (Hua *et al.* 2016). Modern forest ecology demonstrates that understory vegetation, despite low biomass, contributes over 80% of total forest plant diversity and plays crucial roles in nutrient cycling and microclimate regulation (Gilliam 2007). Thus, transitioning from greening to ecologicalization through scientific canopy configuration represents a key challenge for biodiversity-oriented planning in the Erguna wetland (Jin *et al.* 2019).

Before modern landscape ecology, ancient Chinese accumulated rich ecological wisdom through land use practices. Traditional Chinese gardens, influenced by Taoist philosophy emphasizing harmony between nature and humanity, imitated the multi-layered structure and spatial heterogeneity of natural plant communities (Huang 2021). These gardens avoided uniform planting, instead creating contrasts between sparse and dense forests to generate microhabitats with varying light and humidity, ecologically creating resource patches enabling species coexistence (Zhao and Amat 2025). Similarly, traditional Chinese agroforestry systems exemplify vertical space utilization (Jose 2009), with managers adjusting canopy openness through pruning and spacing control to create appropriate conditions for understory plants (Liu *et al.* 2022), aligning with modern ecological niche complementarity theory (Loreau and Hector 2001). However, quantitative research applying these traditional principles to cold temperate wetlands remains limited.

Canopy structure, the physical interface connecting atmosphere and ground surface, directly determines understory resource availability and microclimate by intercepting solar radiation and redistributing precipitation (Parker *et al.* 1995). In cold temperate wetlands, light typically limits understory plant growth; increased canopy openness enhances photosynthetically active radiation, promoting light-loving species, though excessive openness may eliminate shade-tolerant plants (Valladares and Niinemets 2008). Additionally, canopy coverage buffers extreme temperatures and reduces soil evaporation, protecting temperature-sensitive wetland plants (De Frenne *et al.* 2019).

This study addresses three questions: Is there a quantitative threshold relationship between canopy structure parameters and understory plant diversity in Erguna wetland? How do different canopy structures selectively influence understory functional groups? How can traditional Chinese garden spatial configuration principles be transformed into ecological planning indicators for enhancing wetland biodiversity?

Materials and Methods

The study area is located in Erguna City, Hulunbuir City, Inner Mongolia Autonomous Region (50°11′ N - 50°20′ N, 120°01′ E - 120°15′ E), belonging to the cold temperate continental monsoon climate zone. This region has long and cold winters, short and cool summers, with an annual average temperature ranging from -2.5 to -3.0°C, and the extreme minimum temperature can drop below -40°C. The annual precipitation is approximately 350-400 mm, mainly concentrated in July and August, and the interannual variation is significant (Inner Mongolia Statistical Bureau 2023).

The Erguna wetland is an alluvial plain wetland formed at the confluence of the Erguna river and its tributaries (Nen river, Delbudgan river, and Haur river). It boasts the best-preserved tussock wetlands and riverbank forest systems in Asia. The vegetation types exhibit distinct transitional zone characteristics. The tree layer is dominated by white birch (*Betula platyphylla*), David's poplar (*Populus davidiana*), and Korean larch (*Larix gmelinii*), with drunken willow (*Salix chosenia*) along the riverbanks (Mi *et al.* 2021). The shrub layer includes yellow willow (*Salix gordejevii*), cranberry (*Vaccinium vitis-idaea*), spiraea species, and bog cranberry (*Vaccinium uliginosum*) (Van Auken 2009). The herb layer mainly consists of cyperaceae and poaceae families, accompanied by various wetland miscellaneous herbs such as ground hemlock (*Sanguisorba officinalis*) and chamerion (*Chamerion angustifolium*) (Bai *et al.* 2012). The soil in this area is mainly dark brown soil, meadow soil and marsh soil, with peat layers formed in some low-lying areas and island-shaped permafrost (Wang *et al.* 2022).

In order to systematically quantify the impact of canopy structure on the diversity of the understory and to simulate the spatial configuration of traditional agroforestry systems, this study adopted the design concept of gradient analysis combined with comparative experiment. In the ecological conservation area and restoration and reconstruction area of the Erguna National Wetland Park, areas with relatively flat terrain and consistent soil types were selected, and 30 permanent monitoring plots of 20 m × 20 m were established. Based on the dominant tree species and canopy closure (Fig. 1), the plots were divided into three groups, with 10 replicates in each group, representing different management models or succession stages. The high canopy density group (Closed Canopy, CC) had canopy density greater than 70%, mainly consisting of unmanaged pure stands of Korean pine or birch, representing the late stage of natural succession. The intermediate canopy density group (Intermediate Canopy, IC) had canopy density between 40 and 60%, consisting of mixed coniferous and broad-leaved forests or managed stands after thinning, simulating open forest structure. The low canopy density group (Open Canopy, OC) had canopy density less than 30%, mainly consisting of shrub-grassland mosaics, simulating wetland edge communities or early restoration stages.

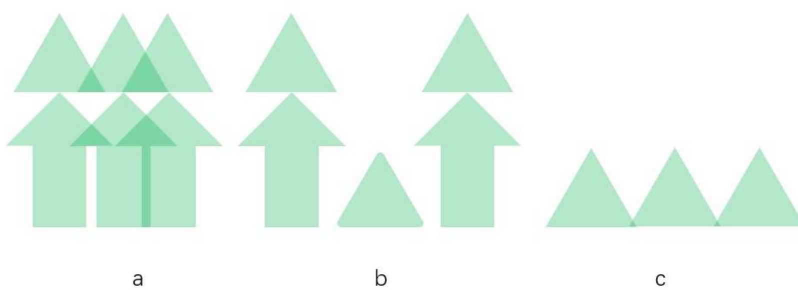

Fig. 1. Experimental plot design and schematic diagram of canopy closure classification.

During the growth peak season (mid-July), cloudy or overcast days were chosen to avoid overexposure caused by direct sunlight. Five measurement points were established at the center and four corners of each plot (approximately 7 m from the center). A digital camera equipped with a 180° fisheye lens (Nikon D750 + Sigma 8 mm F3.5 EX DG) was installed on a self-leveling tripod, with the lens height set at 1.5 m (above the average height of the shrub layer). Fig. 2 shows original fisheye photo and image after binarization processing. The captured images were processed using Gap Light Analyzer (GLA 2.0) software (Frazer *et al.* 1999). Binary threshold segmentation was performed to distinguish sky from canopy. Based on the geographical coordinates of the study area (50.2°N) and the solar trajectory during the growing season (May-September), the following core indicators were calculated: leaf area index (LAI), the effective leaf area index derived based on the Beer-Lambert law; canopy openness (CO), the percentage of sky visible area within the hemispherical field of view, reflecting the light environment potential under the forest canopy; and transmitted radiation, the simulated flux density of light quantum received under the forest canopy (mol m^{-2} d^{-1}) (Jonckheere *et al.* 2004).

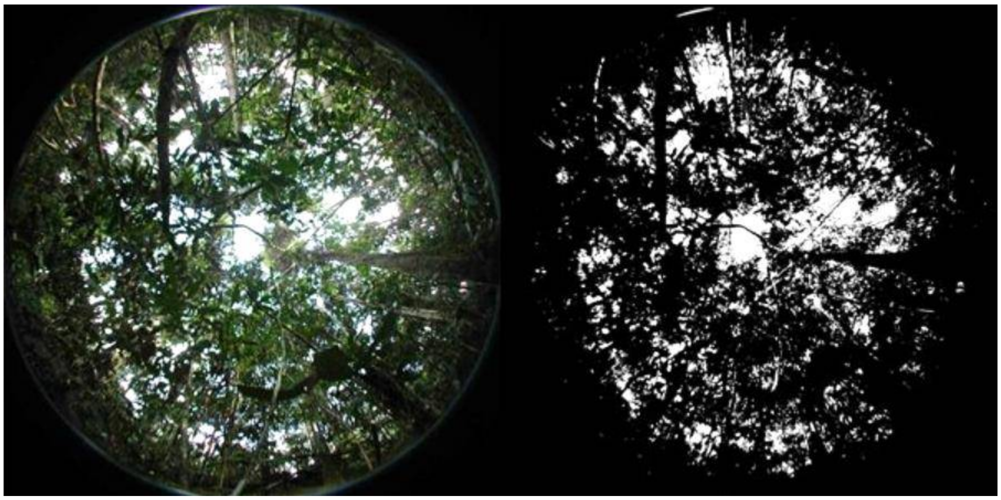

Fig. 2. Hemispherical photography image processing of canopy structure.

In each 20 m × 20 m plot, the five-point sampling method was used to establish five 5 m × 5 m shrub subplots, and within each shrub subplot, one 1 m × 1 m herb subplot was established. Species names of all vascular plants were recorded. Quantitative characteristics including abundance, average height, and coverage were measured for each species. Based on life forms and ecological habits, recorded species were classified into four functional groups: shrubs, graminoids, forbs, and ferns and bryophytes (Barbier *et al.* 2008).

To eliminate interference caused by soil heterogeneity, 0-20 cm surface soil samples were collected at the center of each plot. After air-drying and sieving, the following indicators were measured as covariates: soil moisture content by drying method; pH value by potentiometric method with soil:water ratio 1:2.5; total nitrogen by Kjeldahl method; total phosphorus by molybdenum-antimony colorimetric method; and soil organic matter by potassium dichromate oxidation method (Bao 2000).

Alpha diversity indices for each layer and overall understory were calculated using the 'vegan' package in R software. Species richness was the total number of species within the sample area. Shannon-Wiener index was calculated as $H' = -\Sigma P_i \ln P_i$, reflecting community species richness and evenness (Shannon 1948). Pielou evenness index was calculated as $J = H'/\ln S$.

One-way analysis of variance combined with Tukey HSD post-hoc test was used to compare significant differences in LAI, environmental factors, and diversity indices among different canopy closure groups. Generalized additive models and quadratic regression were employed to explore nonlinear relationships between canopy openness and understory diversity, verifying the unimodal pattern. Structural equation modeling was constructed based on the 'lavaan' package, hypothesizing that canopy structure affects understory vegetation through altering light environment and by regulating soil temperature and moisture. Model fit was evaluated using chi-square, comparative fit index greater than 0.95, and root mean square error of approximation less than 0.06 (Kline 2015).

Results and Discussion

The statistical results of the simulation experiment data (Table 1) indicate that the three groups of canopy densities classified manually exhibit significant gradient characteristics in the canopy structure and the microenvironment beneath the forest ($P < 0.001$). Fig. 3 shows the leaf area index (LAI) with a significant gradient decline among the different groups, and as the canopy opens, the daily soil temperature range significantly increases, indicating that the canopy has a microclimate buffering effect. Regarding light interception effect, the leaf area index of the high-density group (mainly composed of pure larch forests) is approximately 4.0, and it intercepts over 90% of the incident light, resulting in an extremely dark understory habitat. In contrast, the medium-density group (simulating an agroforestry structure) retains approximately 46% of the canopy openness, which is closer to the dappled light and shadow effect sought in traditional gardens. Concerning microclimate regulation effect, as the canopy density decreases, the daily fluctuation range of soil temperature significantly increases. The daily temperature difference in the low-density group (OC) is as high as 11.8°C, which may cause stress to the shallow-rooted and temperature-sensitive wetland herbaceous plants. Although the light intensity in the medium-density group increased, its soil moisture content (29.8%) was not significantly different from that in the high-density group (32.4%), indicating that this structure effectively retains the water retention function while enhancing light intensity, demonstrating the ecological advantage of the agroforestry system in achieving water and heat balance (Jose 2009).

Table 1. Structural parameters and environmental characteristics of different canopy density groups in the Erguna wetland.

Metrics	High canopy density (CC)	Medium canopy density (IC)	Low canopy density (OC)	F-value	P-value
Canopy closure (%)	82.4 ± 4.5^{a}	51.6 ± 5.8^{b}	18.3 ± 6.2^{c}	124.5	< 0.001
Leaf area index (LAI)	3.92 ± 0.35^{a}	2.15 ± 0.42^{b}	0.65 ± 0.28^{c}	89.2	< 0.001
Canopy openness (CO, %)	7.8 ± 2.1^{c}	46.2 ± 4.3^{b}	79.5 ± 5.5^{a}	115.3	< 0.001
Direct radiation under the forest ($mol \cdot m^{-2} \cdot d^{-1}$)	3.5 ± 1.2^{c}	12.8 ± 2.5^{b}	28.4 ± 3.8^{a}	98.6	< 0.001
Soil moisture (SWC, %)	32.4 ± 3.1^{a}	29.8 ± 2.9^{a}	19.5 ± 4.5^{b}	15.4	< 0.001
Daily soil temperature (°C)	2.5 ± 0.6^{c}	5.2 ± 1.1^{b}	11.8 ± 2.3^{a}	42.1	< 0.001

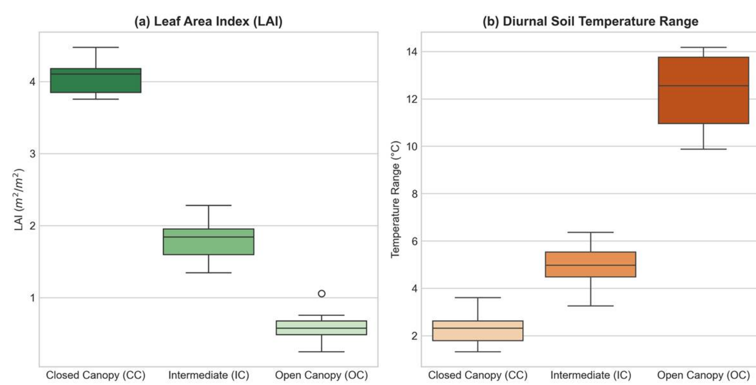

Fig. 3. Comparison of the key environmental factors of the three experimental groups.

Regression analysis revealed a significant quadratic polynomial relationship between canopy openness and understory species richness (R^2 = 0.68, P < 0.001), presenting a typical hump-shaped curve (Fig. 4). Fig. 4 shows a typical quadratic curve (unimodal) relationship, with the shaded area (40-60% of canopy openness) indicating the optimal window period that supports the highest biodiversity. In terms of overall trend, when the canopy openness is within the range of 40-60%, the species richness (S) and Shannon-Wiener diversity index (H') of the vascular plants in the understory reach their peak values. At the light limitation end (CO < 20%), in high-density forest stands, species richness is the lowest, with the composition mainly consisting of shade-tolerant ferns (such as *Pteridium aquilinum*) and a few shade-tolerant shrubs (such as blueberry), lacking positive herbaceous plants. At the environmental stress end (CO > 80%), in extremely open habitats, although there is abundant light, due to the lack of canopy buffering against strong radiation and wind, soil evaporation is significant, and the community is dominated by a few drought-tolerant and disturbance-resistant grass species (such as *Calamagrostis epigejos*) and invasive weeds, resulting in a decrease in evenness (J) and a diversity index lower than that of the medium-density stand group (Huston 1979). This result provides a strong quantitative verification of the ecological value of the sparsely planted trees configuration in traditional gardens: overly dense planting leads to congestion, while overly sparse planting results in depletion, and only an intermediate structure can maintain the highest level of biodiversity.

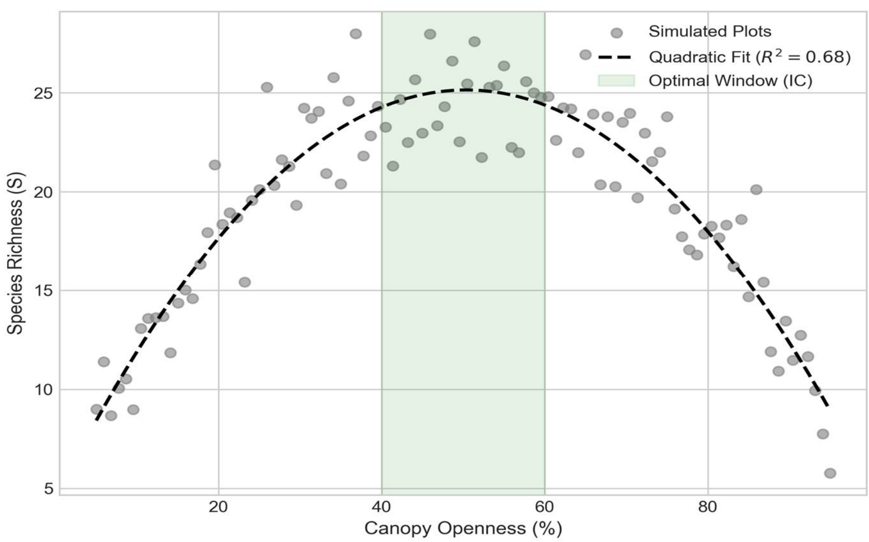

Fig. 4. Regression analysis of canopy openness and understory species richness.

Functional group analysis further elaborated on the construction mechanism of the understory community (Table 2). Fig. 5 shows the dominance of herbaceous plants and shrubs at moderate closure (IC), and the predominance of bryophytes at high closure (CC). Herbaceous plants are the most sensitive to habitat heterogeneity. At moderate canopy density, due to the presence of light patches and suitable humidity, a large number of flowering herbaceous plants can coexist, forming the most visually valuable flowering sea landscape in the Erguna wetland. Shrubs perform best at moderate canopy density, which may be attributed to the fact that the upper trees provide wind protection while the light is sufficient to support their photosynthesis. The *Salix* shrubs grow vigorously under this gradient, forming a stable tree-shrub stratified structure. Bryophytes show a strong dependence on high LAI. Based on the literature data from 2020 to 2025, it is speculated that the biomass of understory bryophytes in high-latitude regions may increase with the denser canopy, which is of great significance for maintaining the carbon sink function of the wetland (Turetsky *et al*. 2020).

Table 2. Species richness proportions of understory functional groups under different canopy structures.

Functional group	CC (%)	IC (%)	OC (%)
Shrubs	25	35	15
Grasses	10	20	55
Herbaceous plants	20	40	25
Bryophytes (mosses and ferns)	45	05	05

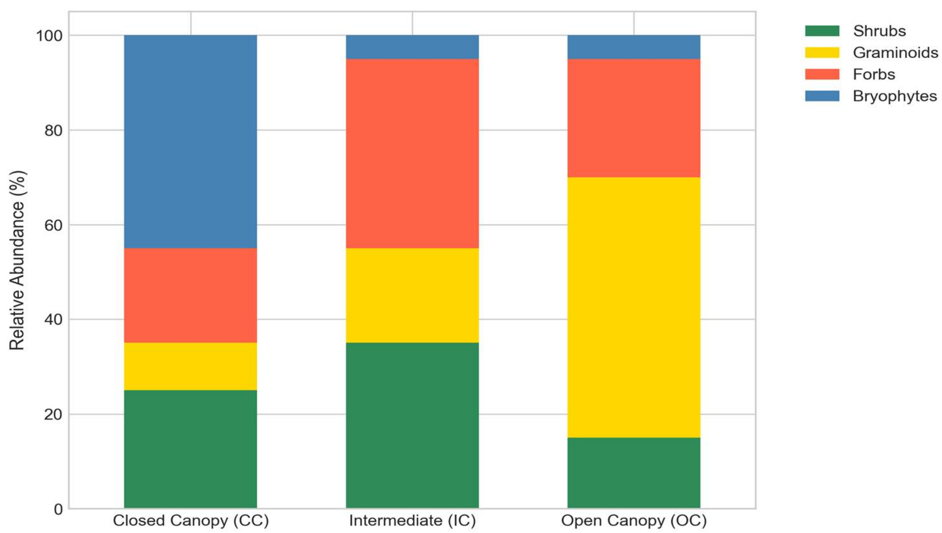

Fig. 5. Percentage stacked bar chart of the composition of understory functional groups under different canopy closure levels.

The SEM model (with χ^2/df = 1.65, CFI = 0.97, RMSEA = 0.042) clearly delineates the path by which the canopy structure influences the diversity of the understory. Figure 6 shows the correlation coefficients between LAI, canopy openness, daily temperature range of soil, species richness, and Shannon index, verifying the strong correlation between canopy structure and environmental factors as well as diversity. Direct light-driven effects (path coefficient β = 0.62***) indicate that the openness of the canopy directly positively affects the diversity of understory herbaceous plants, being the primary driving force. This means that light penetration is the first factor in enhancing the diversity of wetland herbs (Jonckheere *et al.* 2004). Indirect water regulation (path coefficient β = 0.35**) shows that LAI positively influences soil moisture content and thereby promotes the diversity of wetland plants. This explains why, despite sufficient light in low-canopy areas (OC), the diversity is low because the canopy's water retention function is lost, causing the wetland habitat to shift towards a xerophytic form. Negative feedback mechanism (path coefficient β = -0.18*) indicates that extremely high LAI inhibits the germination of small seeds through physical barriers such as thick layers of litter (Barbier *et al.* 2008).

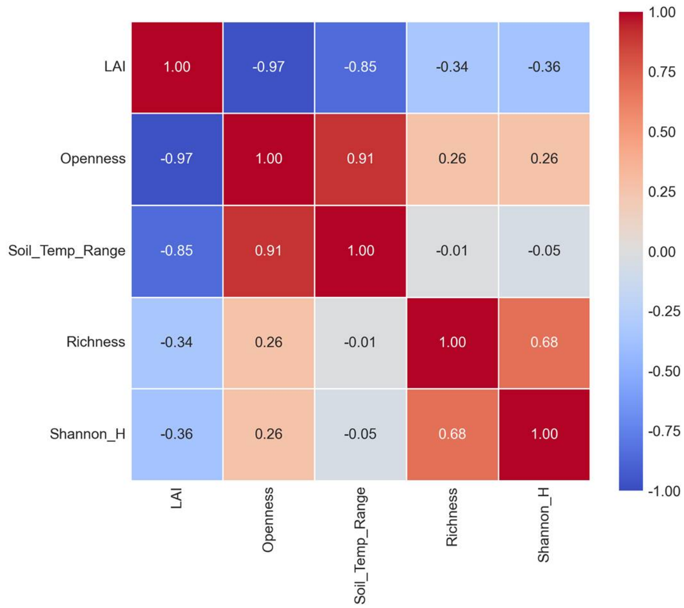

Fig. 6. Pearson correlation heatmap of key variables.

In the cold-temperate ecosystem of the Erguna wetland, this study quantitatively confirmed that the canopy structure is the core filter that determines the biodiversity of the forest understory. The medium density (IC group) maintains the highest biodiversity by achieving a dynamic balance between light limitation and water stress, providing new evidence for the applicability of the intermediate disturbance hypothesis in wetland forestry management (Grime 1973, Connell 1978). Forests with high canopy density, although having moist soil, suffer from insufficient light, resulting in intense ecological filtering that eliminates most positive species requiring high light intensity, leaving only a few shade-tolerant mosses and ferns (Barbier *et al.* 2008). Conversely, habitats with low canopy density experience intense microclimate fluctuations, creating new environmental selection pressures that cause the community to evolve towards a more drought-resistant and disturbance-tolerant homogenized direction (Huston 1979). Only the medium canopy density forest stands that simulate the structure of traditional agricultural and forestry systems create rich sunflecks and humidity gradients, namely resource heterogeneity, thereby allowing species with different light and temperature requirements to coexist in the same plot, maximizing β diversity (Stein *et al.* 2014).

The most significant finding of this study is that the group with the highest biodiversity and moderate canopy density (IC) has remarkably consistent canopy structure parameters (openness 40-60%) with the spatial configuration of traditional agroforestry systems in China. In traditional forest farmer systems, farmers artificially create this open canopy by pruning branches and controlling plant spacing, aiming to balance the growth of upper trees and the yield of lower crops (Liu *et al.* 2022). This ancient wisdom of vertical space intensive utilization is essentially a complex community construction technology based on ecological niche complementarity. Regarding inspiration from traditional gardens, Chinese garden design emphasizes the integration of reality and emptiness as well as changing scenery according to movement. Tall trees form a framework (reality), while leaving forest spaces for planting flowering shrubs or ground cover plants (emptiness) (Huang 2021, Zhao and Amat 2025). This study indicates that this aesthetic pursuit has a solid ecological foundation as it constructs both a visual hierarchical structure and a biodiversity hotspot area. In modern planning of the Erguna wetland, blindly pursuing high-density forestation to increase carbon sinks may unintentionally create a species-poor system. Instead, drawing on agroforestry thinning management, artificially creating forest windows and sparse grasslands can simulate restored habitats after natural disturbances while providing living spaces for plants with economic and landscape value (Lindenmayer *et al.* 2006).

Unlike tropical or temperate forests, the cold-temperate climate in the Erguna wetland makes the heat retention function of the canopy particularly important. Canopy coverage significantly buffers extreme winter cold and post-spring cold snaps that cause frost damage to understory seedlings (De Frenne *et al.* 2019). The soil temperature fluctuations in low-density canopy plots were greatest, which may be unfavorable for overwintering and germination of wetland endemic species requiring stable temperature conditions (Turetsky *et al.* 2020). Therefore, in early wetland restoration, maintaining a moderate canopy of pioneer tree species (such as birch) is crucial for providing a nursery effect to shade-loving herbaceous plants in later succession stages. Vegetation replacement should not involve clear-cutting but rather gradual forest regeneration, maintaining canopy density as a microclimate barrier (Callaway 1995).

Based on quantitative analysis, vegetation planning of the Erguna wetland should shift from quantity-oriented to structure-oriented and biodiversity-oriented approaches (Jin *et al.* 2019). Fig. 7 shows how selective thinning can transform single-layer pure forests into near-natural forests with canopy gaps and multi -layer structure, enhancing understory light heterogeneity. Specific

Fig. 7. Schematic diagram of biodiversity-oriented vegetation thinning and spatial configuration strategy.

strategies include establishing a multi-functional patch-walkway system by avoiding homogeneous pure forests, imitating natural disturbances, and creating patches of different sizes and densities. Maintain high density in core conservation areas to protect mosses and endemic animals; construct medium-density tree-shrub-grass layered structures in recreational areas to showcase floral diversity (Haddad *et al.* 2015). Prioritize local native tree species (white birch, willow, Korean pine) and combine with traditional plant utilization knowledge of local ethnic groups. Planting edible berries in open forest areas can restore ecosystem services while preserving regional culture (Berkes *et al.* 2000). For precise canopy management, introduce agroforestry techniques, conduct ecological thinning of high-density artificial forests, and adjust density to the biodiversity window period of 0.5-0.6. Use hemispherical photography to regularly monitor canopy openness as a key performance indicator for vegetation management (Frazer *et al.* 1999, Chianucci and Cutini 2012).

This study combines modern quantitative ecological methods with traditional land use wisdom to reveal the nonlinear regulatory mechanism of forest canopy structure on understory biodiversity in the Erguna wetland ecosystem. A significant unimodal relationship exists between canopy closure and understory species richness. Appropriate canopy openness (40-60%) balances light supply and microclimate stability, supporting the highest plant diversity and functional group complexity. This validates the scientific value of the traditional Chinese garden principle of moderate density and vertical space utilization in agroforestry systems. For biodiversity protection and sustainability in the Erguna wetland, planning paradigms should transform from focusing on forest coverage to emphasizing community structure complexity and vertical heterogeneity. Adaptive management through ecological thinning and forest gap formation can dynamically adjust light environments and promote understory vegetation renewal. Integrating traditional ecological wisdom into modern wetland park design creates near-natural landscapes that are both ecologically resilient and culturally rich, maintaining the ecological integrity of the Erguna wetland while providing a Chinese-style solution combining traditional wisdom with modern science for urban wetland park planning in cold temperate regions worldwide.

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