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# Spatiotemporal Evolution of Ecosystem Service Supply–Demand Shaped by Nonlinear Thresholds in Socio-ecological Drivers

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Improving the zonal management of the ecosystem service (ES) supply–demand balance requires a thorough understanding of its spatiotemporal variability and the nonlinear characteristics of the driving mechanisms. Coordinated social–ecological development at the regional level depends on this understanding. Consequently, we delineated bundles of the ES supply–demand relationship within the Harbin–Changchun urban agglomeration, examined interactions between ES supply and demand across these bundles, and investigated the mechanisms by which social–ecological drivers shape the spatial pattern of this relationship over an extended time series. The findings show that deficit areas for the 5 ESs are concentrated in construction zones and have expanded annually; synergies outweigh trade-offs among the 5 bundles, and the trade-off relationship intensifies markedly over time. Social drivers dominate bundles 1 (key synergetic bundle), 2 (carbon fixation–water yield–crop production synergetic bundle), and 5 (carbon fixation–crop production–habitat quality synergetic bundle), whereas ecological drivers prevail in bundles 3 (water yield bundle) and 4 (ecological transition bundle). The ES supply–demand relationship is increasingly strained by social disturbances over time. A normalized value near 0.5 emerges as a recurrent threshold at which the effects of several metrics such as digital elevation model, average precipitation, and normalized difference vegetation index shift over a 20-year period. Implementing precise optimization and rational planning for bundle-level ecological management benefits sustainable development and human well-being.

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## Introduction

Ecosystem services (ESs) are the benefits that ecosystems provide to humans, serving as a vital link between natural ecosystems and human well-being [1]. The functioning of ESs is shaped by the interaction between ecological supply and socio-economic demand. ES supply reflects the capacity and potential of a region to provide services, whereas ES demand indicates the preferences and needs of local communities. However, rapid population growth and unregulated urban expansion have degraded ecosystems and weakened ES supply capacity [2]. Meanwhile, urbanization and industrialization have further widened the ES supply–demand gap [3]. Consequently, coordinating regional ecological spatial arrangements, fostering synergistic development between ES supply and demand, and addressing the imbalance and misalignment in these relationships have become urgent priorities.

Complex interactions between ES supply and demand relationships, which include trade-offs, synergies, and bundles, exist [4]. Trade-offs occur when enhancing one service reduces another, while synergies occur when multiple services improve together. ES bundles represent ES supply and demand relationships that exhibit repeated interactions in space or time [5]. Numerous studies have been carried out so far to examine the mechanisms of action between different services and the relationships between a region's supply and demand for ESs [6], including intrinsic linkages [7], dynamic spatial evolutions [8], and future trend analyses [9], and to achieve coordinated regional development by balancing their interactions [10]. Previous research shows substantial regional variation in ES supply–demand dynamics and their trade-offs. Ecologically intact zones such as ecological barrier areas commonly exhibit synergy, with concurrent gains in services (e.g., carbon fixation [CF], water yield [WY], and soil conservation [SC]) under favorable ecological conditions, and they are usually characterized by high ES supply and comparatively low demand. Human-disturbed areas such as urban cores are marked by widespread trade-offs and progressively widening supply–demand gaps, which amplify spatial mismatches and elevate risks, particularly at urban expansion fringes [11]. The spatiotemporal heterogeneity of ES supply–demand trade-offs and synergies reveals intricate interlinkages among services, underscoring the need for region-specific and longitudinal investigation of ESs [12]. These factors are frequently taken into account independently, despite the fact that some research has concentrated on trade-off synergies or bundles of ES supply and demand. In other words, few studies have examined the variations in trade-off synergies within ES supply and demand bundles [13]. Although service-bundle-based zoning identifies spatial units, it rarely probes the fine-grained trade-offs and synergies among constituent ES supply and demand components within those units, leaving the underlying interaction mechanisms within ES bundles largely overlooked. Clarifying these connections is crucial for ecological management and restoration initiatives in sizable urban agglomeration areas. Such clarification enables a deeper understanding of ES supply–demand matching across diverse ecosystems. In this context, ecological management zoning and monitoring in urban areas require a thorough and precise understanding of the trade-offs and synergies between the various ES supply and demand bundles, the nonlinear interactions of the drivers, and the key thresholds within each ES supply and demand bundle. However, there are also intricate intrinsic linkages between interactions, where bundles contain both synergies and trade-offs. For ecological management and restoration efforts in large-scale regions, it is essential to clarify these linkages in order to gain a more nuanced understanding of the matching of supply and demand for various ESs across different regions, a perspective that remains largely underexplored.

Simultaneously, the implementation of an appropriate management scheme can maximize its effectiveness by leveraging the similarity of the ES supply and demand structure within the ecological units defined based on the bundles. Compared with restoration zoning based on spatiotemporal changes, hierarchical conservation zoning [14], or spatial autocorrelation analysis, the bundling-based ecological restoration zoning approach emphasizes the intrinsic linkages and interactions between ES supply and demand. This approach supports management strategies better aligned with complex dynamic processes and provides greater foresight and resilience in rapidly changing ecological environments [15].

The temporal and spatial heterogeneity of ES supply–demand synergies and trade-offs is influenced by regional environmental changes and the intensity of anthropogenic use, resulting in variation in their direction and intensity [16]. Simultaneously, the social–ecological factors driving these disruptions can have substantial effects on the supply and demand of ESs across different periods and geographical areas. These drivers are distinguished by nonlinear dynamics and potential threshold effects. Therefore, a clear understanding of trade-offs and synergies among diverse ES supply–demand bundles, along with the nonlinear interactions and key thresholds of their drivers, is essential for effective ecological management and monitoring in urban areas. A major challenge in addressing ES shortages and mismatches lies in identifying how social–ecological drivers influence individual ecosystem service supply–demand ratios (ESDRs) over time and in mitigating supply–demand deficits by monitoring the main drivers that shape the comprehensive ecosystem service supply–demand ratio (CESDR) and their underlying mechanisms [17]. Among them, redundancy analysis (RDA) is widely applied to identify potential thresholds and explore multidimensional relationships between drivers and ESs [18]. Meanwhile, the response curves derived from generalized additive models (GAMs) reveal nonlinear mechanisms between drivers and ES supply and demand, facilitating targeted intervention and management. Building on previous studies [19], we conduct long time-series RDA and GAM modeling for bundles, which captures ES supply–demand relationships with greater horizontal analytical depth and extends them into a vertical time-series perspective.

In summary, the literature has largely focused on unilateral assessments of ES supply and demand, trade-offs, or bundles, with limited attention to the nonlinear properties of synergy and trade-off mechanisms and their drivers. The lack of long-term, spatially explicit inquiry hinders the formulation of region-specific ecological management for urban agglomerations. Accordingly, we pose 2 core questions concerning the spatiotemporal evolution and drivers of ES supply and demand: (a) How do bundle structures and their synergy and trade-off patterns change through time under complex social–ecological interactions? (b) Under nonlinear coupling, which drivers dominate within each bundle, and where are the optimal thresholds that inform management?

With the advancement of China's Northeast Revitalization Plan, the demand for economic development in the Harbin–Changchun urban agglomeration (HCUA) has grown substantially, exacerbating the disparity between ES supply and demand and creating a heterogeneous structure within the urban agglomeration [20]. The HCUA will continue to shoulder the important responsibility of guaranteeing food security as the "breadbasket of China", safeguard its key strategic position as the ecological barrier of northeastern China, and maintain its central position as an important economic growth pole in northeastern Asia. Therefore, a comprehensive diagnosis of synergies within the internal structure of ES supply and demand is essential for regionally differentiated management and the promotion of ecological well-being and sustainable development in urban agglomerations. The specific objectives of this study are to (a) analyze the spatial and temporal heterogeneity of ES supply–demand relationships and identify ES supply–demand bundles in the HCUA in the years 2000, 2010, and 2020; (b) reveal the dynamic evolution patterns of synergistic trade-offs between ES supply–demand bundles; and (c) explore the direction and intensity of the influence of socio-ecological drivers within different bundles and examine the multipeak threshold effect of socio-ecological drivers. By studying the mutual influence of the main ES supply and demand relationships within different bundles and the nonlinear driving mechanism of socio-ecological drivers, this method enables the differentiation and precise formulation of ES management strategies and programs in different regions and is capable of efficiently coordinating the link between ecological changes and human interference to alleviate the issues that ES faces and to encourage the peaceful coexistence of humans and nature (Fig. 1).

## Materials and Methods

### Study area

The HCUA, located in the south-central part of Heilongjiang Province and the central part of Jilin Province, is a key region for the revitalization of northeastern China and serves as a gateway for international trade. It encompasses 10 prefectural-level municipalities and one autonomous prefecture, covering a total area of 323,210 $km^2$ (Fig. 2). The region experiences a temperate monsoon climate with pronounced annual temperature variation. Its dominant vegetation consists of temperate broad-leaved deciduous forests. There are notable elevational differences between the eastern mountains and the western plains. The primary topography consists of mountainous landscapes dominated by the Changbai Mountains in the southeast and expansive plains represented by the Songnen Plain in the central and western regions. Given its importance in China's "Northeast Revitalization" and "the Belt and Road" projects, the HCUA faces mounting environmental pressures and resource constraints. Therefore, a comprehensive analysis of ES supply–demand relationships and resource allocation through integrated management zoning is urgently needed.

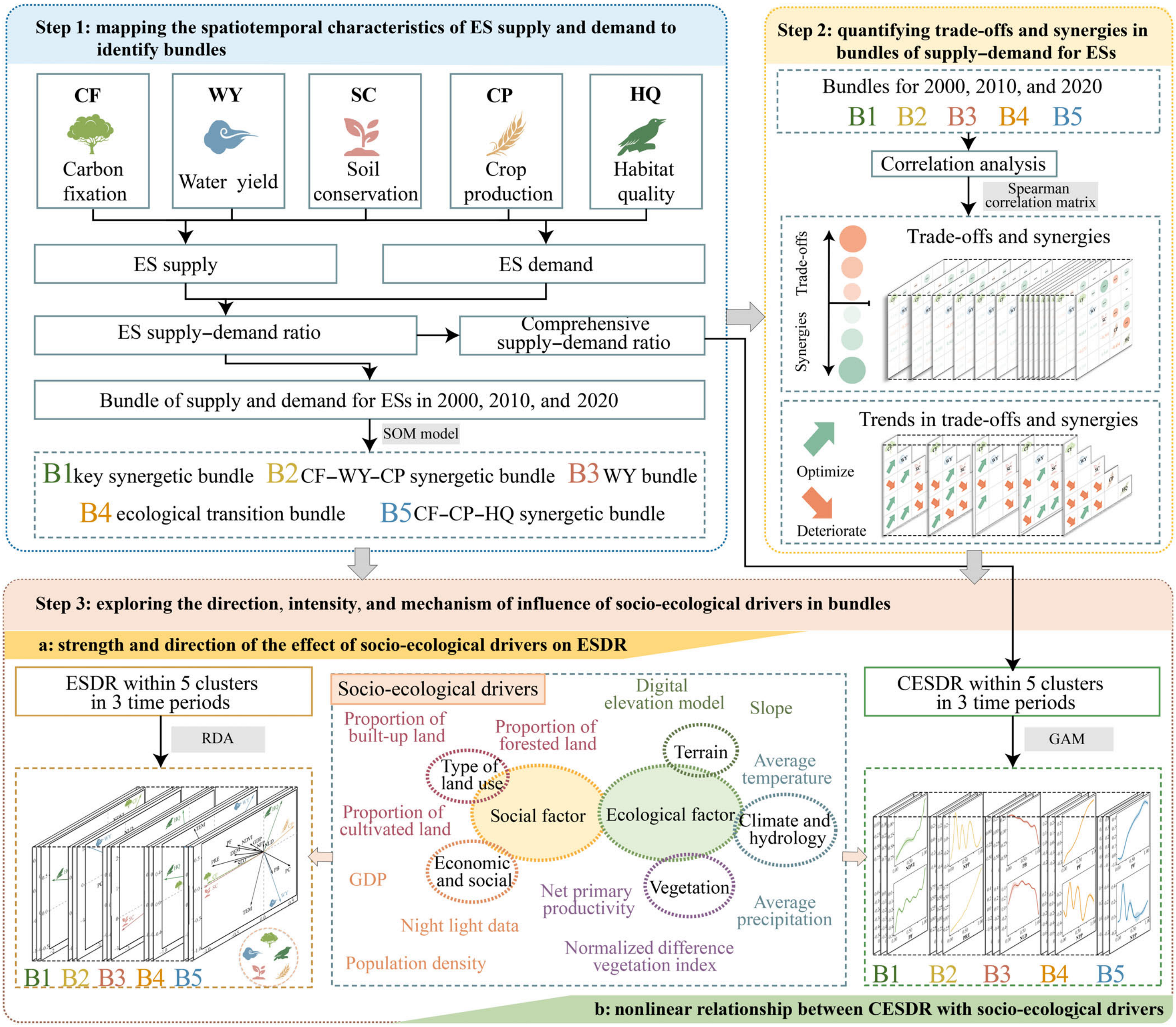


**Fig. 1.** The framework and procedures of this study. ES, ecosystem service; SOM, self-organizing map; B1 to B5, bundles 1 to 5; RDA, redundancy analysis; GDP, gross domestic product; CESDR, comprehensive ecosystem service supply–demand ratio; GAM, generalized additive model.



## Data sources

This study presents the data sources and their descriptions in Table S1. The data sources underwent preprocessing, and the coordinate system and the resolution were standardized.

## Evaluation of the supply–demand relationships for ESs

### *Evaluation of ES supply and demand*

The research evaluated 5 essential ES supply and demand factors: (a) The study area possesses abundant wildlife resources, serving as a habitat and migration point for numerous rare species. (b) Saline and alkaline lands, along with soil salinization and desertification, are notably severe in certain areas of the urban agglomeration, resulting in substantial water loss and soil erosion issues. (c) As a key food supply region in China, the food production capacity of northeastern China is essential. (d) In alignment with China's carbon peaking and neutrality goals, CF represents a key ES function. In light of the aforementioned conditions and the current ecological status of the HCUA, the spatial and temporal distribution of ES supply and demand alignment is elucidated through 5 primary service functions: CF, WY, SC, crop production (CP), and habitat quality (HQ) [21]. The primary formulas and references are provided in the Supplementary Materials, Section S2: "Methods for measuring ecosystem service supply–demand".

### *Evaluating the ratio of supply and demand for ESs*

The ESDR is a core indicator for evaluating ecosystem health. It quantifies the proportional relationship between ES supply and demand, reflecting the balance within a specified region or time period. The ESDR has been widely used to analyze supply–demand dynamics [22]. To capture the overall balance across multiple services, we further propose a CESDR, derived by spatially overlaying individual ESDR layers with equal weighting across the study area [23]. This composite metric offers a holistic assessment of the supply–demand equilibrium. The CESDR is computed as follows:

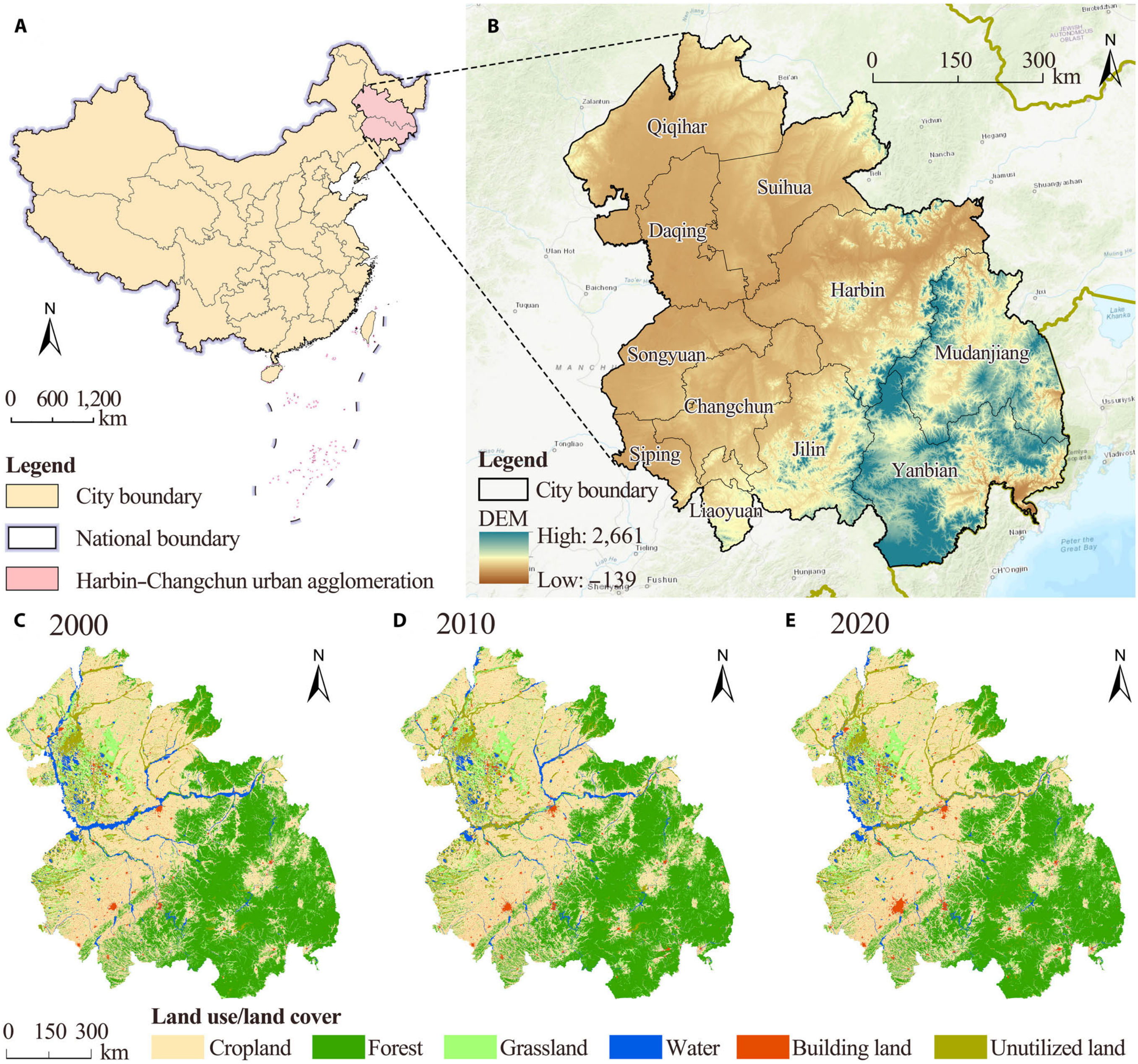


**Fig. 2.** (A) Geographic location and administrative boundaries of the study area. (B) Geographic elevation of the study area. (C) Land use types in 2000. (D) Land use types in 2010. (E) Land use types in 2020. DEM, digital elevation model.

$$ESDR_{xj} = \frac{ES_{xj}^{S} - ES_{xj}^{D}}{\left(ES_{x}^{Smax} + ES_{x}^{Dmax}\right)/2} \tag{1}$$

$$CESDR_{j} = \sum_{x=1}^{n} ESDR_{xj} \tag{2}$$

where $ESDR_{xj}$ is the ESDR type $i$ in grid cell $j$, $ES_{xj}^{S}$ is the supply of ES type $x$ in grid $j$, $ES_{xj}^{D}$ is the demand of ES type $x$ in grid $j$, $ES_{x}^{Smax}$ is the maximum supply value of ES units in the ES region of type $x$, and $ES_{x}^{Dmax}$ is the maximum demand value of ES type $x$ in the study region.

## ES identification of bundles within supply–demand dynamics for ESs

Self-organizing maps (SOMs) are an unsupervised, competitive neural-network approach for data clustering that couples topology-preserving dimensionality reduction with efficient cluster analysis, thereby facilitating the identification of the latent spatial patterns of ES bundles related to supply and demand [24]. This research employed the "kohonen" package in R 4.3.0 to analyze 325,705 grid units, each measuring 1 km$^2$, as samples for SOM bundling for the years 2000, 2010, and 2020 within the HCUA. For parameterization, the SOM lattice adopted a rectangular topology; a seed value of 123 was set to ensure reproducibility, and all remaining hyperparameters were kept at the package defaults during training. Guided by both methodological considerations and research objectives, we compared solutions across alternative numbers of bundles and ultimately selected 5 ES supply and demand bundles. This configuration yields high within-bundle homogeneity, clear between-bundle separability of supply–demand structures, and strong spatial interpretability of the results.

### Investigating trade-offs and synergies within the relationships of ES supply–demand bundles

Correlation matrices were employed to quantify the direction and strength of trade-offs and synergies between ES supply and demand relationships. A positive correlation indicates a synergy, whereas a negative correlation denotes a trade-off [25]. We employed the Spearman correlation matrix to analyze the complex connections between supply and demand for each bundle of ESs over the past 2 decades. Additionally, we employed the "corrplot" package in R 4.3.0 to visualize and assess the synergies and trade-offs within each ES supply–demand bundle.

### Exploration of the social–ecological drivers of the relationships of ES supply and demand bundles

To investigate the factors that contribute to the diversity of ES in various bundles and to enhance ecological management and optimization across regions, we performed redundancy and regression analyses for each group of ES supply and demand bundles. This approach identified the primary drivers within each bundle and clarified the mechanisms linking them to ES supply–demand relationships [26]. Considering the social–ecological and natural environmental context of the study area, we included 12 potential drivers (Table 1) and normalized them. All continuous drivers were standardized to eliminate scale effects and satisfy model assumptions. To minimize collinearity among predictors, we calculated variance inflation factors in R 4.3.0 and retained only variables with variance inflation factor < 5 [27]. RDA is a direct gradient ordination technique that simultaneously reveals the correlations between ES supply–demand and their drivers, as well as the relative influence of each driver. We first performed detrended correspondence analysis. Because the maximum gradient length was less than 3, indicating that ES indicators were continuous with low dispersion, we selected RDA to determine the correlations and relative effect sizes among multiple ES supply–demand scenarios and their driving factors. To evaluate statistical significance, we conducted 999 permutation tests on the constrained axes. To further partition each driver's independent contribution to ES supply–demand dynamics, we employed hierarchical partitioning, which averages model fit across all possible variable subsets to separate a driver's independent explanatory power from overlapping effects produced jointly with other drivers. All analyses were implemented in R 4.3.0 using the "vegan" and "rdacca.hp" packages.

To capture the unknown nonlinear relationships between ES supply–demand and social–ecological drivers, we fitted GAMs. Using nonparametric smoothers such as splines, GAMs flexibly accommodate local data structure and variable relationships [28]. Our study utilized the "mgcv" package in the R 4.3.0 software to investigate the nonlinear correlations between CESDR and 12 drivers in 5 bundles over a 20-year period. These drivers were represented by thin-plate regression spline models with smooth terms corresponding to various social–ecological factors, in order to balance goodness of fit and model complexity [29]. Among the 60 nonlinear relationships obtained, we selected representative based on 2 criteria: a $P$ value <0.001 for the smooth term of the corresponding driver, indicating a highly significant effect on CESDR, and priority to the 2 drivers with the highest goodness of fit (based on the model's $R^2$, i.e., variance explained) in each year and bundle. This ensures that the displayed relationships are statistically robust and capture the dominant mechanisms within each ES bundle.

## Results

### Spatial patterns of supply–demand relationships between ESs

#### *Spatial patterns of ES supply and demand*

The findings indicate that the supply and demand of ES in the HCUA exhibit spatial heterogeneity, although the overall spatial



**Table 1.** Social–ecological drivers of the HCUA

| Type of driver | Potential social–ecological driver | Description | Code |
|---|---|---|---|
| Social factor | Economic and social | Population density (persons/km$^2$) | POP |
| | | Night light data | NLD |
| | | Gross domestic product per unit area (10$^4$ RMB/km$^2$) | GDP |
| | Type of land use | Proportion of cultivated land (%) | PC |
| | | Proportion of forested land (%) | PF |
| | | Proportion of built-up land (%) | PB |
| Ecological factor | Terrain | Digital elevation model (m) | DEM |
| | | Slope (°) | SLO |
| | Climate and hydrology | Average precipitation (mm) | PRE |
| | | Average temperature (°C) | TEM |
| | Vegetation | Normalized difference vegetation index | NDVI |
| | | Net primary productivity | NPP |

HCUA, Harbin–Changchun urban agglomeration pattern remains relatively stable (Fig. 3). More precisely, regarding the supply of ESs, the geographical distribution patterns of CF, WY, and HQ exhibit similarities over the past 2 decades. In particular, the regions with the greatest supply of ESs are located in the mountainous and hilly terrain of the southeastern part of the study area. Although the spatial distribution of WY showed a consistent downward trend from the south-to-north gradient year after year, the areas with the greatest supply of CP were mainly found in the southwestern farmland and grassland region, gradually extending northward. On the demand side of ESs, both the CF and CP show a consistent pattern of spillover from the city center to the urban fringe. High demand in the western and northern regions is concentrated toward the northwest. Demand in urban areas increases year by year as cities expand. In the southern region, the demand distribution mirrors the supply distribution and also increases annually.

### *Spatial patterns of ESDR*

The analysis of the spatial pattern of ESDR from 2000 to 2020 revealed significant diversity and dissimilarity (Fig. 4). Trend analysis shows that the overall supply–demand ratios for CF and CP showed downward trajectories, with net reductions of 13.6% and 41.5%, respectively; HQ increased by 2% initially but recorded a net decline of 3% by 2020. In contrast, the supply–demand ratio for WY first fell by 10.1% and then rose by 65.2%, yielding an overall increase over the 2 decades. Conversely, the supply–demand ratio for SC, while also declining and then increasing, showed a net decrease of 35.6% over the study period. Analysis of spatial characteristics reveals that the ES surplus areas of CF, SC, and HQ were predominantly located in the southeast. In these areas, the ESDR gradually declined, while the ES deficit in the primary urban areas of each city expanded progressively. Notably, the deficit area of CF substantially influenced urban

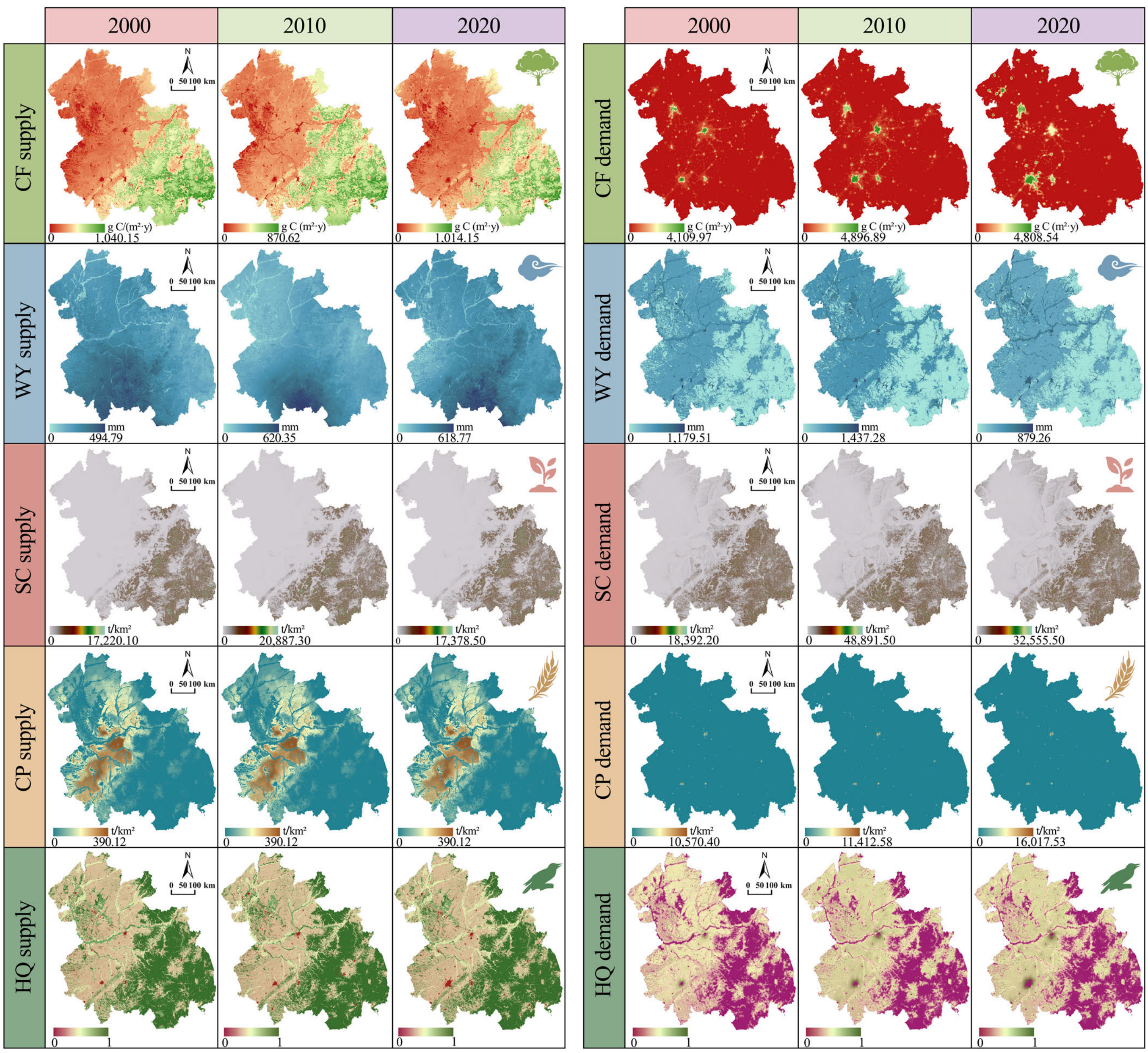


**Fig. 3.** Distribution of ES supply and demand in 2000, 2010, and 2020. CF, carbon fixation; WY, water yield; SC, soil conservation; CP, crop production; HQ, habitat quality.

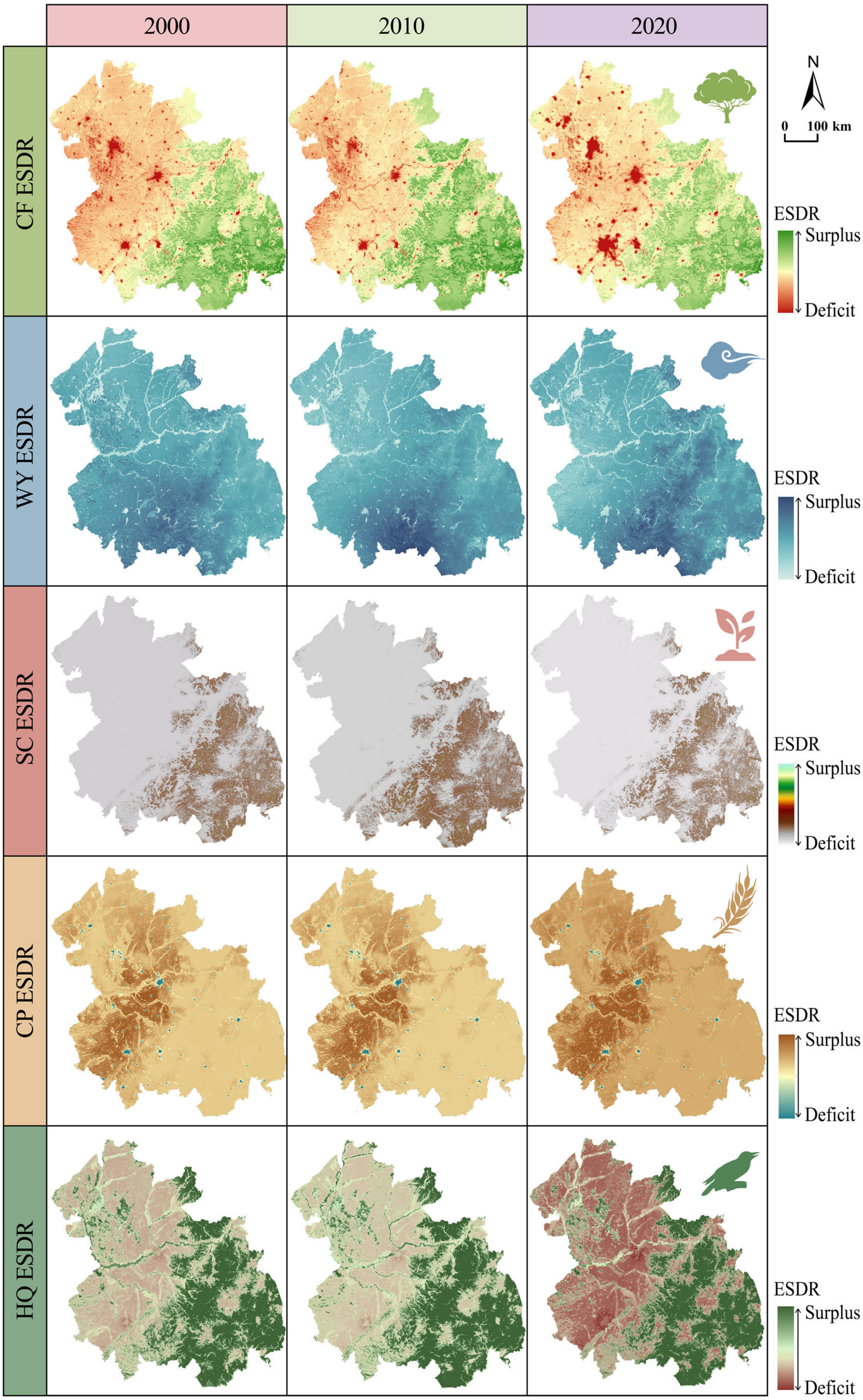


**Fig. 4.** Spatial heterogeneity of supply and demand relationships across ESs in 2000, 2010, and 2020. ESDR, ecosystem service supply–demand ratio.

development. While the surplus areas of WY services were located in the south and showed a gradual increase, the deficit areas in urban centers and along rivers were also expanded. The surplus portion of CP showed a broader distribution and stronger surplus, whereas the deficit areas were more concentrated and exhibited only limited annual expansion. Figure S1 in the Supplementary Materials illustrates the trends in supply–demand relationships for each ES from 2000 to 2020.

## Distribution of the spatial and temporal patterns of supply and demand bundles for ESs

We examined the annual fluctuations and spatiotemporal trends of the 5 ES supply–demand bundles obtained from the optimal bundling scenario (Fig. 5). Bundle 1 (B1) represents the key synergetic bundle, predominantly found in the southeast, characterized by forested land where all ESDRs are prevalent, while CP showed lower ESDRs than the other service types. Bundle 2 (B2) represents the CF–WY–CP synergetic bundle, primarily located in the northwestern region of the country, where cropland was dominated by CP, CF, and WY. This cropland serves as the principal supplier of CP and plays a significant role in soil and water conservation, as well as in CF. Bundle 3 (B3) represents the WY bundle, characterized by its diffuse distribution across the city, predominantly consisting of construction and unutilized land. Urban sprawl has had only minimal impact on WY areas. Bundle 4 (B4) represents the ecological transition bundle, primarily located in the interspersed transition zone between forestland and cultivated land. This bundle exhibits significant contributions from WY, CF, and CP surpluses. With the transition from B1, timely control and protection are essential. Bundle 5 (B5) represents the CF–CP–HQ synergetic bundle, predominantly featuring water bodies and grasslands, and was characterized by surpluses in the ES supply and demand for CP, CF, and HQ.

Analysis of the changes in various bundles over the period from 2000 to 2010 (Fig. 5C) indicates that the areas of B3 and B5 expanded by 4,284.1 and 3,303.6 $km^2$, respectively, whereas B1, B2, and B4 contracted by 2,425.9, 2,937.1, and 2,194.0 $km^2$, respectively. Notable changes include the transition of B1 and B2 to B3, amounting to 2,003.3 and 2,128.2 $km^2$, respectively, reflecting a gradual shift from ES supply–demand surplus to deficit areas, along with the movement from B2 and B4 to B5, of 5,438.3 and 4,796.8 $km^2$, indicating an increase in WY deficits within those regions. From 2010 to 2020, the area of B3 expanded by 2,874.0 $km^2$, driven primarily by conversions from B2 totaling 2,343.0 $km^2$, pointing to a growing extent of multiservice deficits. Concurrently, 6,427.5 $km^2$ was transferred from B1 to B4, indicating a shift toward vulnerability in the synergistic surplus across the 5 services, underscoring the need for targeted management interventions.

## Synergies and trade-offs within the supply and demand bundles of ESs

The analysis of the 5 bundles requires a deeper examination of the synergistic relationships between the supply and demand of multiple ESs within these bundles (Fig. 6). The results show the differences in the quantity and types of trade-offs and synergies between the supply–demand linkages of the respective services in each of the 5 bundles. Among the 10 pairwise ES supply–demand correlations examined across the 5 bundles, 3 pairs—CF–SC, CF–CP, and SC–HQ—were consistently significant across years. Additionally, similarities are observed in the performance of the supply–demand relationships of the same group of ESs across different years. The analysis of the supply–demand relationship of ESs across various bundles indicates a predominance of synergistic effects over trade-off effects. Specifically, CF and SC exhibited synergistic relationships across bundles, with the exception of B3, with correlation coefficients ranging from 0.171 to 0.707, suggesting that SC and CF are mutually advantageous across different landscape types. Notably, except for CF and WY in 2000, all elements within B1 demonstrated synergistic relationships, with a maximum correlation of 0.649, underscoring the importance of B1 in the study area; enhancing any service function in this area can yield benefits for the overall ecological function. Furthermore, synergy was observed for WY and CP in B3 with a mean correlation of 0.496, for CF and SC in B4 with 0.594, and for WY and HQ in B5 with 0.300. By contrast, CP and HQ exhibited clear trade-offs in B2 and B4 and mean correlation values were −0.383 for B2 and −0.455 for B4. Additionally, SC and CP in B2, B3, and B4 exhibited trade-offs, with those in B4 being especially notable, showing the strongest negative correlations, reaching −0.301 in 2000 and −0.304 in 2020. Correlation changes indicate that several relationships within each bundle exhibit a clear trend of degradation. Notably, except for the relationship between CF and WY in B2, the absolute value of synergistic relationships declines, and the absolute value of trade-off relationships rises. This shift signifies a weakening of synergistic relationships and an exacerbation of trade-off relationships. Furthermore, both trade-offs and synergistic relationships deteriorate more substantially within B2, B3, and B5.

## Impacts of social–ecological drivers on the relationships between supply and demand for ES bundles

### *RDA of the social–ecological drivers of ES bundle supply–demand relationships*

The supply–demand relationship of ESs across bundles was substantially influenced by both the quantity and diversity of social–ecological factors; across all 15 results, the first 2 constrained axes were significant ($P < 0.001$). The mean total variance explained across the 5 bundles was 10.2% in 2000, 61.2% in 2010, and 53.4% in 2020. The correlation between the supply and demand of ES remained mostly constant in 2010 and 2020, with a noticeable difference between 2000 and both years (Fig. 7). This shows that the relationship between each driver and the ratio of ES supply to demand gradually stabilizes as the years progress. As a whole, the variation in the arrow lengths of drivers within the same bundles across different years shows a pattern of gradual decrease, while the angles of the pinches tend to average out. This suggests a trend toward averaging the influence on the supply–demand ratios of various ESs. Additionally, the drivers exhibit a degree of synergistic effects, with the strength and direction of the impacts of proportion of built-up land (PB) and population density (POP), as well as proportion of forested land (PF) and slope (SLO), converging. This indicates a strong synergistic relationship between population density and built-up land proportion, as well as slope and forestland proportion, with the former correlating substantially with CP and the latter with HQ. The analysis focused on the primary characteristics of each bundle: in B1, B2, and B5, the supply and demand relationships of ESs were predominantly shaped by social drivers such as proportion of

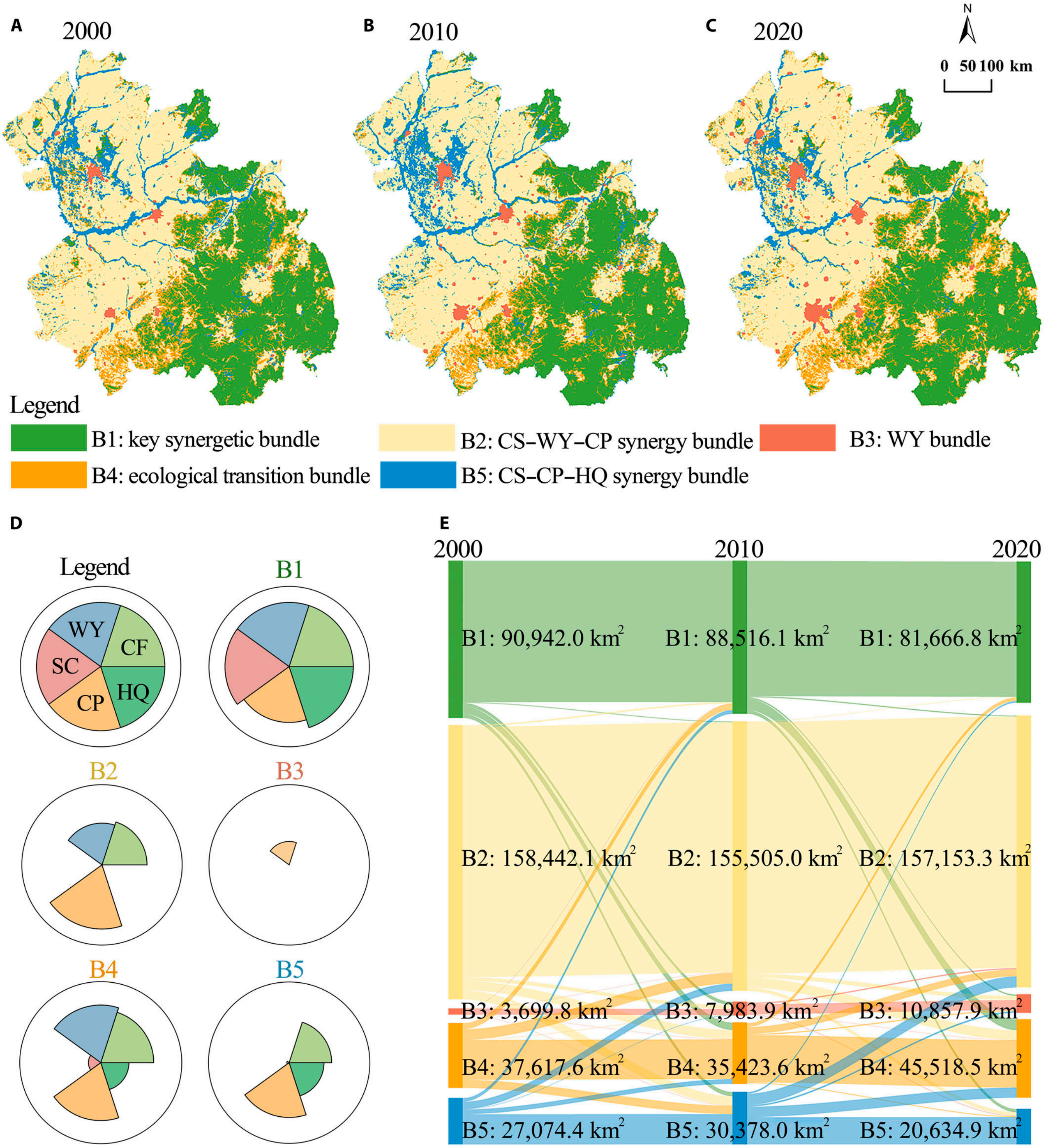


**Fig. 5.** (A) Spatial distribution of ES supply–demand bundles in 2000. (B) Spatial distribution of ES supply–demand bundles in 2010. (C) Spatial distribution of ES supply–demand bundles in 2020. (D) Composition of ES supply–demand bundles and relative sizes of various types of ESDRs, with larger sectors representing higher ESDRs. (E) Interconverted area between different ES supply–demand bundles in 2000 to 2010 and 2010 to 2020.



cultivated land (PC), PF, normalized difference vegetation index (NDVI), and night light data (NLD). Conversely, in B3 and B4, these relationships were primarily influenced by ecological drivers, including average precipitation (PRE), average temperature (TEM), digital elevation model (DEM), and SLO.

### *Nonlinear effects of social–ecological drivers revealed by GAMs*

We examined the degree to which each factor affects the CESDR through a GAM, developed incrementally to pinpoint the primary drivers and to analyze the temporal and spatial variations

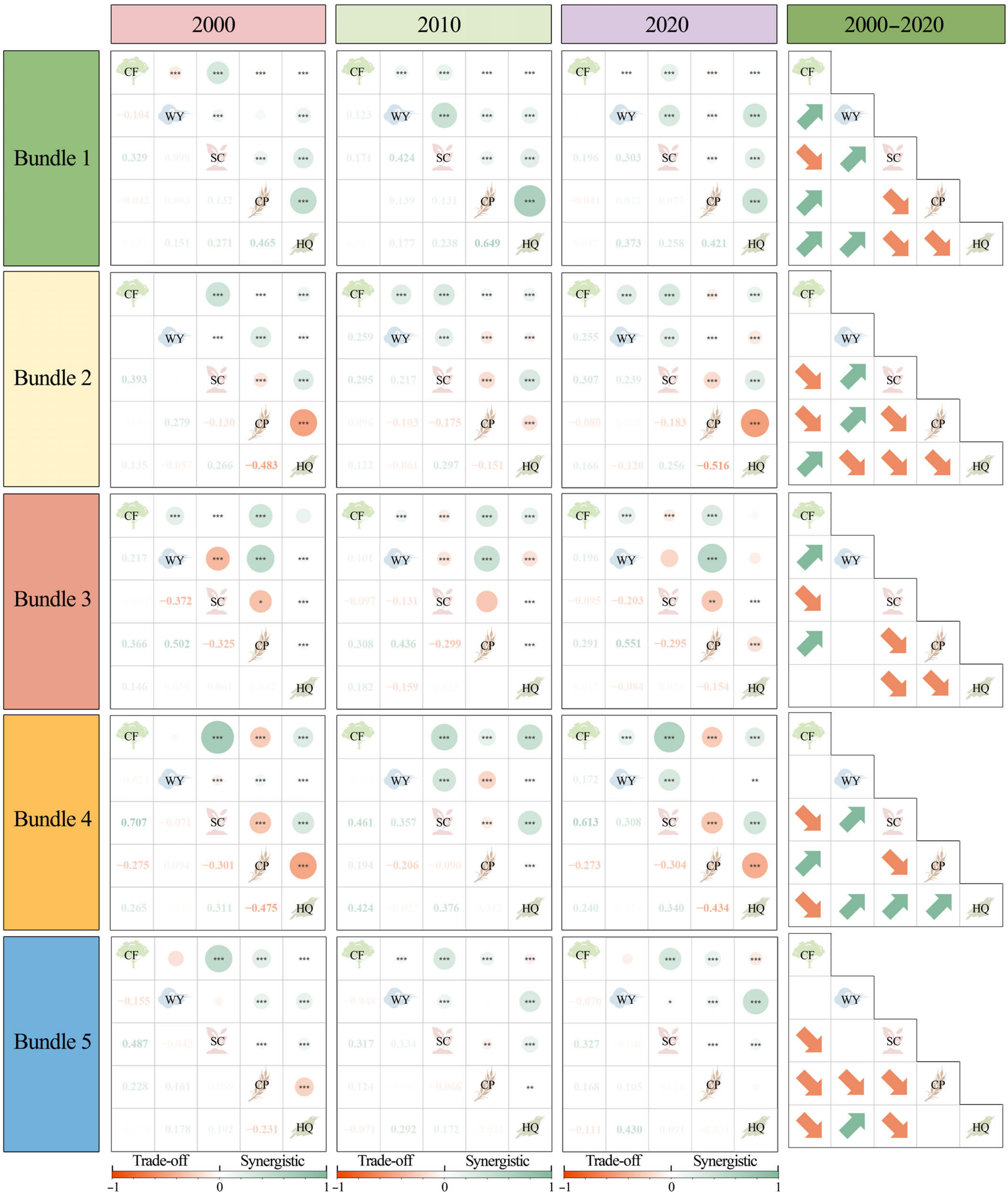


**Fig. 6.** Correlations and changes in correlations (*$P$ < 0.05; **$P$ < 0.01; ***$P$ < 0.001) between ESDRs within the 5 bundles for the years 2000, 2010, and 2020 (red arrows show that relationships are deteriorating in the trade-off direction; green arrows show that relationships are optimized in the synergistic direction).

and the impact in the CESDR corresponding to each social–ecological driver (Fig. 8). According to the analysis, ecological variables show a steady decline in their impact on CESDR changes between 2000 and 2020, with social factors taking center stage. The examination of the internal structure indicates that the response variations of the driving factors display

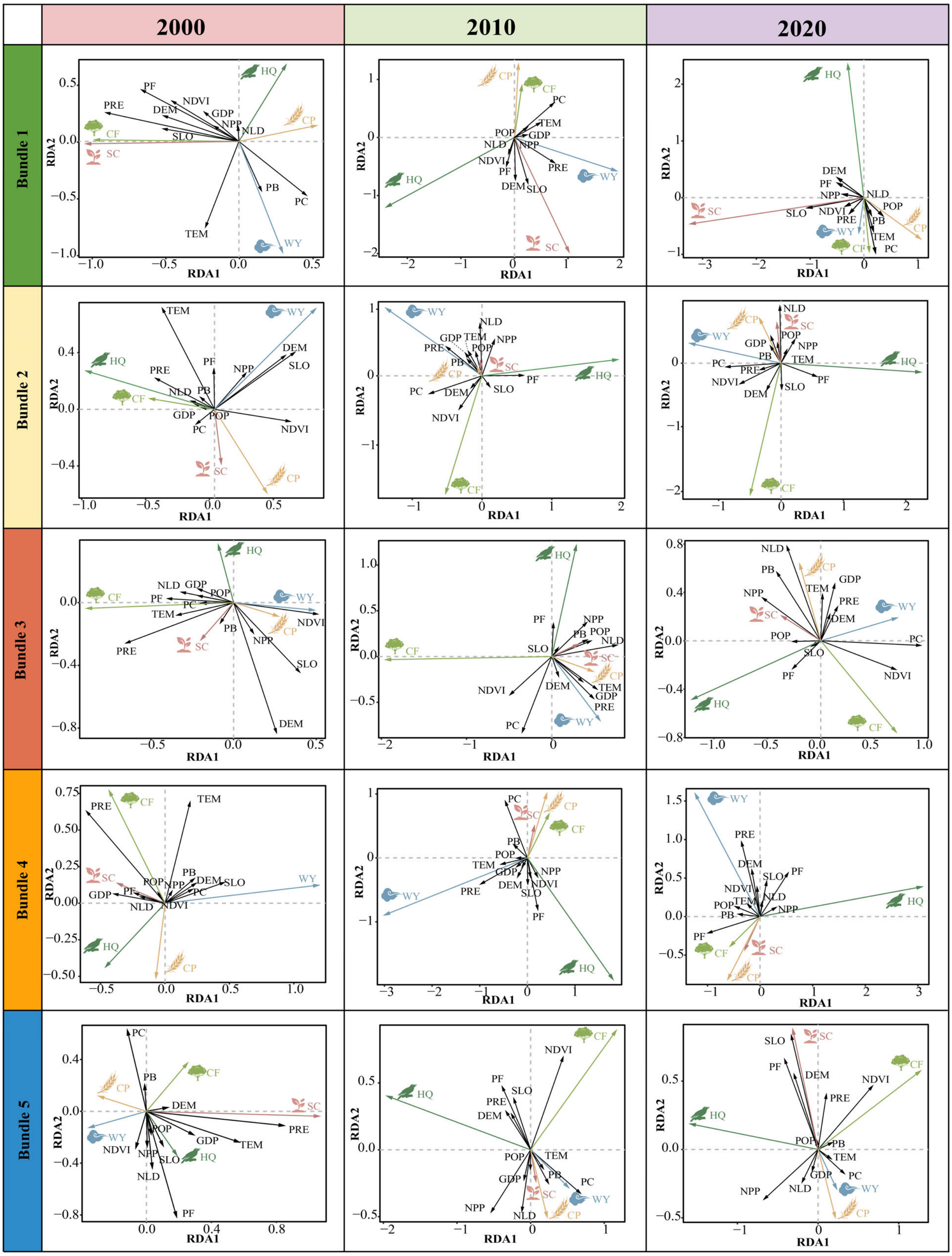

Fig. 7. Impacts of social–ecological drivers on the supply and demand of ESs in 5 different bundles in 2000, 2010, and 2020. (The length of the arrows of the drivers indicates the strength of their impacts on the supply and demand of ESs, and the angle between the drivers and the various types of ESDRs represents the strength of the correlation between the ecosystem service and the social–ecological driver. The same direction of the arrows between the supply and demand of each type of ES and the driver represents a positive correlation, while opposite directions of the arrows represent a negative correlation.)

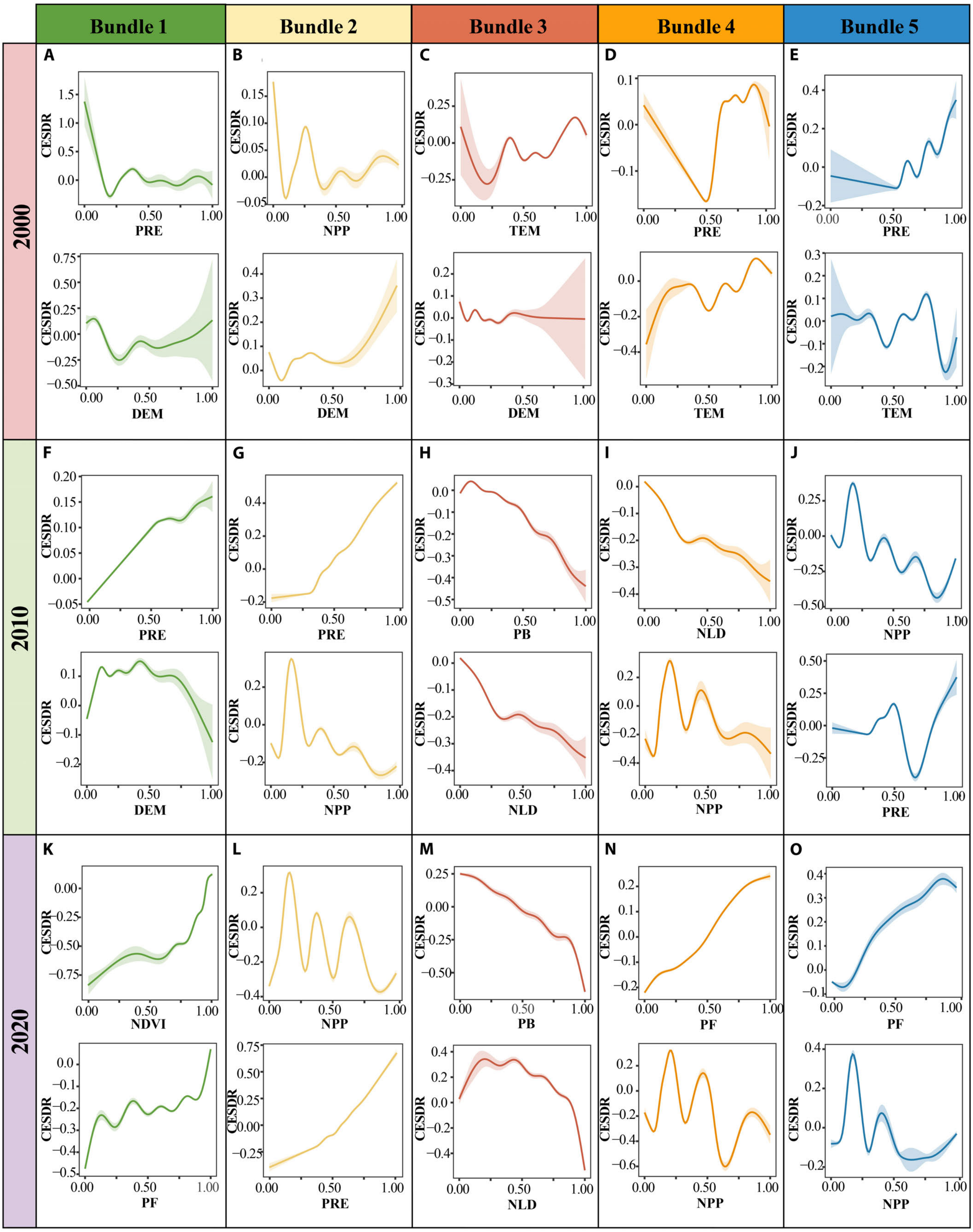


**Fig. 8.** (A to E) Response curves of the 2000 CESDR to major socio-ecological drivers within the 5 bundles of the HCUA. (F to J) Response curves of the 2010 CESDR to major socio-ecological drivers within the 5 bundles of the HCUA. (K to O) Response curves of the 2020 CESDR to major socio-ecological drivers within the 5 bundles of HCUA (the shaded area indicates 2 standard errors for each line with 95% CIs).

nonlinear trajectories, with certain factors demonstrating significant threshold effects and exhibiting multipeak patterns. Particularly, net primary productivity (NPP) serves as a representative case, as its influence on CESDR across B2, B4, and B5 shows nonlinear multipeak declines, with the highest peak of the fit concentrated in the period preceding 0.5. Simultaneously, various drivers exert distinct influences on the CESDR trend across different bundles: the effect of PRE on B1 and B2 shows a relatively consistent upward trajectory, whereas its impact on B4 and B5 indicates a sharp decline mainly below 0.5, necessitating timely monitoring. The influence of DEM in B1 and B2 in 2000 shows an ES surplus with an increasing magnitude, more significant at DEM over 0.5; however, by 2010, there is a downward shift from surplus to deficit, albeit still reflecting a weak surplus relationship within the confidence interval (CI), especially after exceeding 0.75. Furthermore, PB substantially affects B3, amplifying the magnitude of ES deficits over time. In B1, B4, and B5, the impact of PF is particularly evident. In B1, PF slows the rise of CESDR between 0.25 and 0.9, but in B4 and B5, the effect of PF is both continuous and pronounced.

## Discussion

### ES supply–demand imbalance evolutionary features

Due to the complexity and dynamism of ecosystems, supply–demand relationships are perpetually evolving. Dynamic analyses of these relationships can effectively identify potential issues in urban agglomeration development and resource allocation [30]. Further elucidating the temporal evolution of this dynamism deepens our understanding of how urban construction drives ES deficits [31]. ES supply is validated through model measurement (see the Supplementary Materials, Section S3: "Validation of ES supply results"), while demand is assessed using statistical yearbooks and other data to reflect actual conditions. We also compared our findings with similar studies on ES supply–demand assessment and reached largely consistent conclusions [32], thereby confirming the robustness and applicability of the assessment results. It is worth noting that this study emphasizes the delineation of ecological management zones rather than focusing solely on specific absolute values. Bundles are important indicators of supply–demand gaps; their spatial evolution patterns reveal common ES supply–demand contradictions across different development stages, as observed in the Northern Tianshan Economic Belt [33] and the Yangtze River Middle Reaches urban agglomeration [34]. Accordingly, we mapped the spatial trends of ES supply and demand within the HCUA, employing the ESDR to identify critical regions where ES supply–demand heterogeneity converges. Recognizing these areas helps address regional challenges, and monitoring spatiotemporal dynamics facilitates the identification of potential ecological risks.

Among these regions, the B1 region is characterized by a surplus in the supply–demand relationship for all services and underscores the vital role of forests in providing diverse services and functioning as a supply source for the entire urban agglomeration [35],corroborating previous findings [36]. However, the area it occupies has diminished by 0.8% over the past 20 years, particularly along its peripheries, indicating its vulnerability to environmental disturbances. During the first decade, B1 losses occurred in B4, which lies within the transition zone between forested cropland and cultivated land, revealing a marked disparity between supply and demand for SC and HQ. Over the following decade, B4 gradually transitioned into B2, losing both supply and demand surpluses and becoming a region defined by supply–demand deficits. The National Plan for Increasing Grain Production Capacity by 100 Billion Jin, coupled with the region's response, resulted in a pronounced surplus in total grain production. This finding corroborates Peng et al.'s assertion [37] that food production services can intensify trade-offs among other ESs, providing empirical support for cross-sectoral collaborative management. This surplus stemmed from the restoration of arable land and intensified agricultural practices but was accompanied by subsequent decline in SC and HQ [38]. The supply–demand disparity between ESs in B3 escalates along the urban–rural gradient, exhibiting an overall increase of 1.3% over 2 decades. The expansion of urban areas in this region continues to encroach upon critical ecological space, and without regulation, a persistent shortage of ESs is likely to occur. Region B5, which is associated with notable deficits in CF and WY, shifted toward B4 during the past decade. The transition partially replenished WY supply but sustained a persistent deficit in HQ, emphasizing the need for ecological enhancement measures to improve HQ. By integrating multitemporal dynamic analyses, this study not only corroborates the robustness of prior findings but also uncovers deeper mechanisms underlying the evolution of spatial heterogeneity, providing new evidence to support fine-grained ecological governance in high-density regions.

### Heterogeneous effects of trade-offs between supply–demand relationships for ESs in the city agglomeration and within different bundles

Due to variations in the spatial co-occurrence structure of ES supply and demand relationships across bundles, the direction and intensity of the trade-off and synergies between these relationships across different bundles vary, which corroborates previous findings [7]. This study elucidates the intricate dynamics of ES supply and demand across various bundles and years, highlighting the complexities inherent in regional ES interactions. It thus helps to address the inconsistencies in regional ES development that may arise from overarching trade-off mechanisms and offers a novel perspective for investigating interventions in ES supply and demand within subregions so as to optimize synergistic benefits. It serves as the foundation for effectively enhancing ecological functions and implementing differentiated ES management.

The study shows that the HCUA exhibited a predominantly synergistic relationship between the supply and demand of each ES, which is generally consistent with the results of previous studies involving the region [39]. The trade-offs were mainly observed between CP and HQ as well as SC, and there were significant differences across different ES supply–demand bundles. In the B1 region, which is characterized by significant synergistic advantages, the supply and demand relationships exhibit a synergistic dependence. HQ exerts varying degrees of influence on WY, SC, and CP, implying that enhancing the supply–demand relationship of HQ could yield beneficial and cascading effects across the entire B1 region. Furthermore, the synergistic effects of SC and CP have diminished progressively over time, echoing the co-degradation of ES supply–demand reported by Yang et al. [22] in the Beijing–Tianjin–Hebei urban agglomeration and necessitating the timely upgrading and optimization of HQ's supply–demand structure. In the B2 region, CF exhibits synergistic advantages alongside other supply–demand dynamics; however, the trade-offs between CP and SC, as well as HQ, progressively intensify. Over time, CP also develops trade-offs with CF, a trend that becomes more pronounced in B4, indicating a crisis in the supply–demand equilibrium of other services due to oversupply resulting from an emphasis on CP. This finding is consistent with prior research showing that the overdevelopment of a single service can introduce systemic risks [12,40]. Each ES's supply–demand dynamics shifted from a synergistic to a trade-off relationship in region B3, particularly between SC and CP and between WY and SC. This shift enhanced the synergistic relationship between WY and CP; however, an excessive surplus undermined the original mutual synergy. To manage and address these problems effectively, it is crucial to take into account the stability of the supply–demand relationships of multiple ESs, as well as their spatial and temporal fluctuations. The progressive strengthening of synergistic relationships in the B5 region and the diminishing trade-off between HQ and CP suggest that HQ exerts a beneficial influence in B5.

## Impact of social–ecological drivers on the evolution of the supply–demand relationship for ES bundles

We further clarified that varying social–ecological factors affect distinct ES supply–demand dynamics, highlighting the necessity of accounting for regional particularities when formulating recommendations for regional ES management and optimization based on such studies [41]. This understanding aids in pinpointing the specific temporal and regional conditions under which social–ecological drivers exert influence and provides a theoretical basis for designing management interventions that alleviate ES supply–demand imbalances and promote ecosystem rebalancing.

### *Temporal dynamics of social–ecological driver effects*

The dynamics of ES demand and supply in urban agglomerations are increasingly influenced by social disturbances, as shown by the observation that the drivers of CESDR in 2000 were primarily natural variables, whereas in 2010 and 2020, they were mainly social factors. This pattern is consistent with findings from mountainous regions in northwestern China, which likewise highlight temporal shifts in the dominant roles of social versus climatic drivers [42]. Urban development cannot avoid this issue, but compared with urban agglomerations characterized by more intense socioeconomic activity (e.g., the Beijing–Tianjin–Hebei region), the HCUA shows relatively stronger influences of ecological factors on ES supply–demand [12]. This shift is attributed to relatively modest changes in ecological factors over the past 2 decades, in contrast to rapid changes in certain socioeconomic variables, which were at times near-exponential [43]. This contrast underscores the distinctiveness of the HCUA: as an urban agglomeration with a relatively young development model and stronger constraints from its ecological baseline, its social–ecological interactions—and the associated response patterns and thresholds—may differ from those observed in more mature, high-density urban agglomerations.

### *Nonlinear thresholds of social–ecological drivers for ES supply–demand*

The responses of ES supply–demand relationships to social–ecological drivers are nonlinear and complex, with clear stage-specific characteristics that cannot be fully captured by a single linear equation. The supply–demand relationship among various ESs is shaped by cascading changes in socioeconomic dynamics such as human activities and gross domestic product, which are mutually reinforcing, and is simultaneously weighed against ecological factors including temperature and vegetation cover. In this context, the dynamics of supply–demand relationships are often uncertain, implying the presence of threshold effects. Our results confirm this pattern: social–ecological drivers exert substantive yet uneven threshold effects on CESDR. This finding further indicates that multiple drivers can activate intrinsic threshold mechanisms in CESDR through aggregation effects while also highlighting the severe challenges to ecosystem resilience and stability under concurrent natural and anthropogenic pressures [44].

Thresholds mark the critical points at which ES supply–demand dynamics respond to social–ecological factors, and they typically exhibit temporal variability. Prior studies on ES threshold effects have mainly used breakpoint regression analysis or constraint line analyses [22]. While these methods can detect abrupt changes or piecewise relationships, they are limited in capturing complex nonlinear dynamics, particularly the continuous variation in threshold responses driven by multiple factors. The GAM not only detects multiple peaks and abrupt-change intervals but also quantifies the dynamic effects of individual drivers. It is well suited to characterizing common threshold phenomena, such as DEM, PRE, and NDVI showing shifts around 0.5 over the 20-year period, as well as the multi-peak variation patterns observed for NPP and TEM. When these indicators approach 0 or 1, the direction of change in the corresponding CI curves shifts sharply.

When examining the relationship between each driver and CESDR, NPP shows persistent fluctuations over time. This pattern is especially complex in B2 and B4, where variability is most pronounced at values below 0.5, indicating that NPP's role in these 2 bundles warrants close monitoring. Compared with earlier years, PF exerted a markedly stronger influence on ES supply–demand dynamics in 2020. The benefits of large-scale afforestation projects likely contributed substantially, and the urbanization rate in this city agglomeration also declined during this period. Consistent with previous findings [11], larger forest reserves were associated with a significant positive covariance, suggesting that increased forest cover is almost always advantageous. To sustain an overall surplus in ES supply–demand, NDVI should exceed 0.5 and PF should be greater than 0.25, while PB should remain below 0.5 and NLD below 0.75, controlling for other parameters.

No inflection points were observed in certain monotonic relationships (e.g., PRE in B2), underscoring dominant conditions imposed by fundamental biophysical constraints. Notably, enhancing a single factor cannot resolve overall supply–demand imbalances; optimization must occur within a multifactor framework that integrates synergy and threshold management. In some scenarios, increasing individual factor values does not compensate for ES supply–demand deficits, and indiscriminate improvements may intensify disturbances to the eco-social system, as seen in B1 in 2020. Management actions implemented in isolation and detached from inter-cluster synergies not only fail to narrow supply–demand gaps but may also amplify systemic risks. Greater emphasis should therefore be placed on cross-cluster synergistic mechanisms and holistic regulation to achieve structural equilibrium in regional ES supply and demand.

**Table 2.** Key implementation measures and core stakeholders for different ES supply–demand bundles

| Bundle | Key characteristics | Key issues | Management strategies and recommendations |
|---|---|---|---|
| B1 (key synergistic bundle) | This bundle has the highest ES supply capacity, with services that reinforce one another. | Encroachment on ecological land (especially forests) threatens high supply capacity. | • Strictly delineate ecological redlines, prioritize protection of transition zones B1 to B4, and give precedence to restoring forestland lost between 2000 and 2010. Actively develop regional mechanisms to realize the value of ecological products, such as forest carbon sinks.<br>• Enhance synergies among carbon sequestration, soil and water conservation, and related services by maintaining a service surplus: increase PF (keep $>0.25$, ideally $\approx 0.9$) and monitor NDVI (keep $>0.5$).<br>• Implement cross-bundle ecological compensation, leveraging high carbon-sequestration capacity to advance regional carbon neutrality and an ecological–economic balance.<br>• Define core implementing entities—natural-resources and forestry departments, research institutions, and provincial finance departments—responsible for redline supervision, technical support, and design of ecological-compensation mechanisms, respectively. |
| B2 (CF–WY–CP synergetic bundle) | Primary production areas in Jilin and Heilongjiang provinces show a substantial CP surplus. | Persistent SC and HQ deficits, with agricultural expansion intensifying ecological pressure. | • Set production caps where DEM $> 0.5$, and calibrate grain-production intensity in line with adjustments to the "100-Billion-Jin Grain Plan".<br>• Promote land intensification, conservation tillage, and farmland-to-forest conversion while upholding the arable-land protection redline.<br>• Integrate ES indicators into the high-standard farmland construction and evaluation system, and provide subsidies and green-credit incentives for green production technologies.<br>• Balance overall ES supply and demand by monitoring PRE and NDVI, coordinating agricultural economic development with ecological protection.<br>• Define the implementing bodies—the agriculture and rural affairs departments, new-type agricultural operators, and environmental protection authorities—responsible for technology extension, production practice, and environmental supervision, respectively. |
| B3 (WY bundle) | Despite high population density and strong economic development, ES abundance and accessibility remain low. | High PB and NLD coincide with inadequate ecosystem service provision. | • Establish urban growth boundaries, strictly limiting further expansion in areas where PB and NLD exceed 0.75, and advance stock renewal and the ecological decommissioning of low-efficiency construction land.<br>• Curb urban encroachment into natural and seminatural ecosystems, and integrate enhancements to ES functions—such as rainwater resource utilization (WY)—into urban development to reduce flood risk.<br>• Leverage WY–CP synergies to develop peri-urban water-saving agriculture and ease pressure on aquatic environments.<br>• Assign primary responsibilities to territorial/spatial planning authorities, housing and urban–rural development departments, and real-estate enterprises for spatial regulation, project delivery, and ecological-infrastructure construction, respectively. |
| B4 (ecological transition bundle) | The bundle sits at the interface between forestry and agricultural land. | Risk of cropland expansion into forested areas; NPP shows a multipeak decline once above 0.5. | • Designate ecological buffer zones, prohibit the expansion of agricultural land, and phase out cultivation on steep slopes in coordination with the Black Soil Conservation Program.<br>• Steer industrial transformation toward green alternatives such as under-forest economies and ecotourism.<br>• Prioritize and regulate NPP, mitigating post-threshold declines to enhance ES supply–demand synergies.<br>• Define core implementers—local governments, township communities, and ecological/environmental monitoring agencies—responsible for policy formulation, community participation, and dynamic monitoring and early warning, respectively. |

(Continued)

**Table 2.** (continued)

| Bundle | Key characteristics | Key issues | Management strategies and recommendations |
| --- | --- | --- | --- |
| B5 (CF–CP–HQ synergistic bundle) | It contains extensive grassland, wetland, and aquatic ecosystems. | Need to secure water supply while jointly improving WP and HQ. | • Prioritize nature-based solutions (NbSs), with a focus on restoring wetland and lake hydrological functions.<br>• Strictly enforce grass–livestock balance, implement science-based rotational grazing, and curb grassland degradation.<br>• Select plant restoration approaches in line with the nonlinear NPP–CESDR relationship, favoring nature-led interventions for ecological recovery.<br>• Regulate waterfront tourism development, delineate ecological conservation zones, and minimize human disturbance to the greatest extent possible.<br>• Assign primary responsibilities to water resources and forestry–grassland authorities; local communities and herders are the core implementers, and tourism enterprises must operate in strict compliance with ecological protection requirements. |

### Recommendations for spatial planning and management based on the results of the study

Considering the finding that the main social–ecological drivers of ESs and ES interactions vary depending on spatiotemporal and regional contexts, as well as the urgency of ecosystem management, we categorized the 5 ES bundles into 5 ecological functional areas based on ES supply–demand relationships. The core principle is to move beyond one-size-fits-all approaches and allocate management resources and policy instruments differentially, according to the dominant functions of each zone. The proposed classification is compatible with national spatial strategies such as China's Main Functional Zone Planning, translating complex ecological and geographical information into actionable governance units. Accordingly, we propose differentiated, implementation-oriented spatial planning and management strategies (Fig. S2), and we identify key implementation measures and core stakeholders (Table 2). Taken together, this approach seeks to maximize joint benefits for ecological conservation and regional development through coordinated regulation of natural and socioeconomic drivers.

### Limitations and future research

This study has compiled bundles of ES supply and demand regions exhibiting analogous interactions and examined the social–ecological factors that may influence them. While we have identified the most representative drivers and elucidated the mechanisms and functions they serve in the supply–demand dynamics of CESDR and services, the multitude of factors influencing these intricate relationships remains unpredictable, with complex and often nonlinear interactions among drivers. Therefore, in future research, we will attempt to investigate the influence of additional drivers, as well as the external and internal relationships among them.

Concurrently, the link between ESs may be impacted by variations in study scales as well as the division of grids and administrative entities [45]. Since our research focused on urban agglomerations in northeastern China, the findings may differ from those in other regions.

To further clarify the internal mechanisms behind ES supply and demand, future work will continue longitudinal quantification and expand analyses across different spatial scales and regions. This will help ensure the long-term stability of ecosystems and provide a stronger scientific basis for controlling and optimizing the supply–demand balance in urban agglomerations.

## Conclusion

This study quantified the disparity between the supply and demand of 5 ESs in the HCUA using multiple models and methodologies. It identified 5 ES supply–demand bundles across 3 periods within 20 years, analyzed the interactions between ES supply and demand, investigated the mechanisms and nonlinear relationships of social–ecological drivers influencing each bundle, and explored strategies to intervene and monitor the spatial patterns of these drivers to sustain the equilibrium of ES supply and demand. The results indicate that rapid urbanization and excessive population and economic concentration in 2000, 2010, and 2020 have resulted in considerable spatial discrepancies between the supply and demand for all ESs in major urban centers, which have intensified annually. The research identified 5 bundles, each exhibiting numerous synergistic relationships, which suggests a more cohesive development of supply–demand dynamics. However, the overarching trend indicates progressive degradation, except for the relationship between CF and WY in B2, where relatively synergistic bundles progressively transitioned into transitional bundles and ultimately evolved into bundles characterized by disadvantageous synergistic relationships. Furthermore, each bundle is influenced by social–ecological drivers to varying extents, with a temporal shift in primary drivers from ecological to social factors. This is exemplified by NPP, which demonstrates a pronounced threshold effect with a multipeak pattern. Based on these insights, we propose a zoning-oriented spatial planning and management strategy that emphasizes ES intrabundle interactions and social–ecological drivers, thereby ensuring a balanced supply–demand relationship of ESs and promoting the sustainable development of urban agglomerations.

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**Competing interests:** The authors declare that they have no competing interests.

## Data Availability

The data that support the findings of this study are available from the corresponding author (J. Zhang) upon reasonable request.

## Supplementary Materials

Graphical Abstract
Section S2: Methods for measuring ecosystem service supply–demand
Section S3: Validation of ES supply results
Figs. S1 and S2
Table S1
References [46–50]

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# Spatiotemporal Evolution of Ecosystem Service Supply–Demand Shaped by Nonlinear Thresholds in Socio-ecological Drivers

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Improving the zonal management of the ecosystem service (ES) supply–demand balance requires a thorough understanding of its spatiotemporal variability and the nonlinear characteristics of the driving mechanisms. Coordinated social–ecological development at the regional level depends on this understanding. Consequently, we delineated bundles of the ES supply–demand relationship within the Harbin–Changchun urban agglomeration, examined interactions between ES supply and demand across these bundles, and investigated the mechanisms by which social–ecological drivers shape the spatial pattern of this relationship over an extended time series. The findings show that deficit areas for the 5 ESs are concentrated in construction zones and have expanded annually; synergies outweigh trade-offs among the 5 bundles, and the trade-off relationship intensifies markedly over time. Social drivers dominate bundles 1 (key synergetic bundle), 2 (carbon fixation–water yield–crop production synergetic bundle), and 5 (carbon fixation–crop production–habitat quality synergetic bundle), whereas ecological drivers prevail in bundles 3 (water yield bundle) and 4 (ecological transition bundle). The ES supply–demand relationship is increasingly strained by social disturbances over time. A normalized value near 0.5 emerges as a recurrent threshold at which the effects of several metrics such as digital elevation model, average precipitation, and normalized difference vegetation index shift over a 20-year period. Implementing precise optimization and rational planning for bundle-level ecological management benefits sustainable development and human well-being.
Image

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