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# Revealing the dynamic biological flow between eastern and western China from the perspective of ecological network

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## ABSTRACT

China is one of the most biodiversity-rich countries, yet the ecological gap between its eastern and western regions, driven by geographical barriers, restricts species migration and disrupts ecosystem connectivity. However, the potential of biological flow to bridge this divide remains poorly understood. To address this, we developed a dynamic biological flow framework, combining ecological networks with two new tools, Ecological Linkage Tool Direction and Biological Flow, to quantify species migration directions and intensities across the Middle Spine of Beautiful China. Within and beyond ecological sources, we analyze dynamic biological flow and network structure at node, link, and graph levels. We also simulate changes in network efficiency under various corridor and habitat degradation scenarios. Among the 13,800 ecological corridors, 27 % are oriented east-west (EW), yet the region exhibits a net negative habitat inflow, with 48 % of migrating species potentially failing to reach target habitats. Biological flows outside habitats follow west-to-east (21 %) and north-to-south (18 %) patterns, with the highest migration losses occurring in the north-to-south direction. The regional network efficiency is 0.053. The failure of ecological network in the Inner Mongolia Pastoral Area reduces efficiency by 24 %, intra-patch EW corridors by 57 %, and inter-patch west-to-east corridors by 13 %. Species-specific analyses of the red panda (*Ailurus fulgens*) and Chinese horseshoe bat (*Rhinolophus sinicus*) reveals that habitat distribution determines dynamic flow direction, while species-specific adaptability influences flow intensity. This study quantifies dynamic biological flow patterns, overcoming the limitations of widely used static distribution-based conservation planning, more accurately reflecting species migration traits.

## 1. Introduction

Since the onset of the Anthropocene, global biodiversity has been in steady decline due to climate change and increasing human pressures (Frans and Liu, 2024; Johnson et al., 2017). Species migration, a critical component of biological flows, underpins the maintenance of diminishing genetic diversity and ecosystem resilience (Brennan et al., 2022; Moore and Schindler, 2022). Yet, with only 10 % of global protected areas effectively connected, inadequate ecological connectivity remains a bottleneck for biodiversity conservation (Ward et al., 2020). In response, the Global Biodiversity Framework (Target 3) urges member states to enhance ecosystem connectivity within their conservation

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strategies (Watson et al., 2023). Nowadays, ecosystem connectivity is seen as a critical factor for global biodiversity conservation, vital for maintaining species diversity and the continuity of ecosystem services (Brodie et al., 2025; Roy et al., 2023). As the global sustainable development agenda advances, integrating regional coordination with ecological security has become an urgent international priority (Fuso Nerini et al., 2024; Wu et al., 2023). Within this context, ecological gap analysis, a key tool advocated by the Convention on Biological Diversity (CBD), identifies the specific ecological conditions required for species migration and long-term survival, providing a scientific foundation for achieving conservation goals (Dissanayake et al., 2024; Pressey et al., 2021).

Globally, numerous initiatives have been launched to enhance ecological connectivity. The Pan-European Ecological Network (PEEN), initiated by the European Environment Agency, exemplifies how transboundary ecological networks can enhance species flow and ecological security (Jongman et al., 2011). In contrast, despite being one of the world's most biodiverse nations, China's biodiversity conservation efforts remain largely confined to spatial planning, with evident deficiencies in designing connectivity (Mu et al., 2024; Yue et al., 2024). Strengthening ecological networks has thus emerged as a pivotal strategy for preserving biodiversity and mitigating further losses (Doherty et al., 2023; Peng et al., 2024a). The well-documented Hu Line, a major geographical and ecological divide shaped by climatic and topographic gradients, severely constrains species migration, disrupts ecosystem services, and endangers regional ecological integrity (Guo et al., 2016; Hu, 1935). Western China plays a crucial role in water conservation, carbon sequestration, and windbreak-sand fixation, providing potential habitats for species movement while serving as an ecological buffer for the densely populated eastern areas (Feng et al., 2022; Fu et al., 2023). With the advancement of the Beautiful China Initiative and high-quality ecological development efforts in the Yellow River Basin (Fang et al., 2020; Fu et al., 2022), constructing an east-west ecological network from the perspective of biological flows to bridge regional ecological gaps has emerged as a valuable scientific challenge.

Despite significant differences in topography, climate, and land use between the eastern and western China (Li et al., 2024; Yang et al., 2021), there is a need for continued ecological connectivity across the Hu Line, offering potential habitats for species migration and climate adaptation (Xu et al., 2024a). Nowadays, ecological networks and corridors are recognized as effective strategies for balancing conservation and development (Cosmo et al., 2023; Jin et al., 2020). Ecological networks, consisting of interconnected habitats, support species movement and gene flow, while corridors, whether natural or man-made, facilitate biological migration and sustain ecosystem connectivity (Zhang et al., 2025). However, limited ecological connectivity restricts species migration, disrupts ecosystem services, and weakens regional ecological stability (Geng et al., 2025; Mu et al., 2025a). In response to climate challenges and biodiversity conservation goals, establishing an east-west ecological network is essential to facilitating species migration and enhancing ecological connectivity. In this context, the Mid-Spine Belt of Beautiful China (MSBBC) has been proposed as a national ecological security barrier, highlighting the need for an intact ecosystem (Du et al., 2023; Wang et al., 2021). However, a systematic framework for quantifying ecological network structures and their impact on species migration remains underdeveloped. Developing scientific methodologies for quantifying biological flows is crucial for advancing conservation, supporting sustainable development, and bridging the ecological gaps along the Hu Line (Fu et al., 2023; Peng et al., 2024a).

An ecological network is a dynamic system of interconnected ecosystems that supports species migration, energy transfer, and genetic exchange (Opdam et al., 2006; Peng et al., 2018). Beyond spatial connectivity, these networks enable directional species movement, which is critical for maintaining ecosystem functionality (Lu et al., 2024; Shen et al., 2024). However, widely used ecological network models, such as the minimum cumulative resistance (MCR) and circuit theory models, focus primarily on static spatial relationships while assuming uniform biological flow (McRae et al., 2008; Mu et al., 2022a; Xu et al., 2025). These approaches overlook key ecological processes, including directional species migration and dynamic biological flow (Keeley et al., 2021). In reality, ecosystems are continuously influenced by environmental changes, species behavior, and human activities, resulting in variations in the number of species migrations (Mu et al., 2022b; Saura et al., 2014). As a result, traditional ecological network models struggle to capture the complexity of ecological processes (Peng et al., 2024a; Xu and Peng, 2022). This limitation reduces their applicability in conservation planning, making it difficult to identify critical migration corridors or predict species movement. There is an urgent need for more advanced biological flow modeling approaches to account for ecological processes and to improve network functionality (Fig. S1).

According to island biogeography theory, biological flow is influenced by habitat biodiversity, area, and quality, which shape species migration pathways and flow intensity, ultimately determining ecological network connectivity (Lu et al., 2024; MacArthur and Wilson, 1963). Therefore, ecological networks should be seen not as static structures of habitats and corridors but as dynamic systems where species migration, ecological interactions, and environmental changes continuously reshape connectivity and function (Assis et al., 2023; Shen et al., 2024). However, current ecological network analysis often overlooks biological flow, particularly how species movement, genetic exchange, and ecosystem interactions influence network structure and resilience over time (Bianco et al., 2024). Most studies focus on optimizing the spatial arrangement of habitats and corridors, prioritizing ecosystem services while assuming static connectivity patterns (Xu et al., 2024b). This approach neglects key factors such as migration directionality, flow intensity, and variations in dispersal, limiting its ability to capture the true dynamics of ecological networks (Felipe-Lucia et al., 2022; Peng et al., 2024b). To address these gaps, next research should integrate biodiversity data, including species-specific ecological requirements, dispersal traits, and habitat preferences, to refine ecological network models. Moving beyond broad spatial models toward species-specific, process-based approaches is essential for improving conservation planning and ecological network management.

This study investigated the ecological gap between eastern and western China from the perspective of dynamic biological flows, exploring the role of ecological networks in promoting regional coordination and sustainable development. Focusing on the MSBBC, this study addresses three interconnected questions: (1) the spatial structure of regional ecological corridors and networks, clarified in section 4.1; (2) the quantification of dynamic biological flows to reveal the direction and intensity of species migration, presented in section 4.2; and (3) the influence of ecological source areas and biological flows on the efficiency of ecological networks under different disturbance scenarios, analyzed in section 4.3. By addressing these questions, this research aims to refine biological flow models and provide scientific insights for integrating ecological networks into conservation strategies. The findings will offer empirical support for regional sustainable development and advance the spatial planning practice of ecological networks.

## 2. Study area and materials

### 2.1. Study area

This study focuses on the Mid-Spine Belt of Beautiful China (MSBBC) to explore ecological pathways for coordinated east-west development amid regional imbalances (Fig. 1). The concept of MSBBC originates from the Hu Line, which delineates China's southeastern densely populated region from its northwestern sparsely populated region based on county-level population distribution (Hu, 1935). The MSBBC region spans from 23°37′14″ − 50°58′53’’N, 97°31′44″ − 133°27′11″E, characterized by a gradual increase in elevation from northeast to southwest. It encompasses diverse ecological conditions, ranging from boreal and

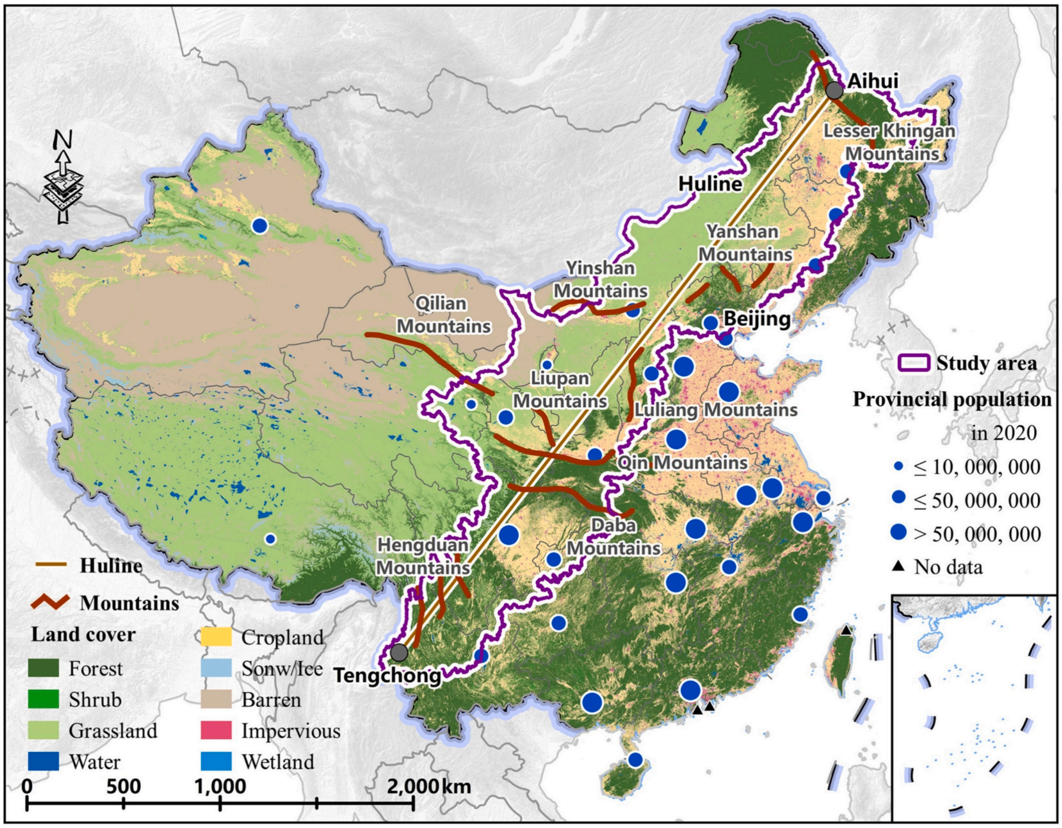

**Fig. 1.** The study area of the Mid-Spine Belt of Beautiful China (MSBBC). Land cover data are derived from China land cover dataset (CLCD) (Yang and Huang, 2021), population data are obtained from the Seventh National Population Census of China, and the vector of the MSBBC is sourced from the International Research Center of Big Data for Sustainable Development Goals.

temperate mountain forests to semi-humid temperate grasslands and semi-arid steppes (Fig. S2). This division not only reflects significant spatial disparities in natural environments and socio-economic development but also serves as a major ecological boundary influencing species migration and resource distribution (Fu et al., 2025). The establishment of MSBBC aims to mitigate regional disparities through optimized territorial spatial planning, playing a key role in advancing national ecological security and the "Beautiful China" initiative (Guo et al., 2016; Wang et al., 2021). Therefore, MSBBC has become a strategic region for enhancing ecological connectivity, providing a critical foundation for ecological network optimization and sustainable regional development.

### 2.2. *Materials*

We utilized the following datasets: (1) the 2020 landscape elements and omnidirectional connectivity dataset (Mu et al., 2025b), providing connectivity metrics at a 300 m resolution; (2) the 2020 high-resolution China Eco-environmental Quality (CHEQ) (Xu et al., 2021), assessing eco-environmental quality via remote sensing at a 500 m; (3) the 2020 habitat quality dataset (Mu et al., 2024), mapping habitat suitability at a 300 m; (4) Digital Elevation Model (DEM) data from the SRTM (Farr et al., 2007), used to derive slope data at a 30 m; and (5) the mammal distribution data were obtained by combining occurrence records with MaxEnt modeling (Xu et al., 2024a), using records of 158 terrestrial mammal species, including the red panda (*Ailurus fulgens*) and Chinese horseshoe bat (*Rhinolophus sinicus*), with AUC accuracies of 0.959 and 0.969, respectively. These datasets provide the foundation for biodiversity assessment in analyzing dynamic biological flows (Table 1).

The data were primarily used for constructing the ecological network (including delineating ecological sources and resistance surfaces) and for calculating dynamic biological flows. Specifically, the CHEQ and slope data used to determine the ecological resistance surface were resampled to a 300 m resolution using average resampling to ensure spatial consistency with the base landscape data and network analysis outputs (i.e., the Albers equal-area conic projection). The species distribution data were overlaid with the ecological source vectors to characterize the biodiversity attributes of each source area and to serve as input for subsequent dynamic biological flow calculations. These preprocessing steps ensured resolution consistency and spatial comparability among different data sources, providing a foundation for

**Table 1**
The adopted datasets in our study.

| Data | Resolution | Application | Source |
|---|---|---|---|
| Landscape elements | 300 m | Delineation of ecological sources | (Mu et al., 2025b) |
| Omnidirectional connectivity | 300 m | Delineation of resistance surface | (Mu et al., 2025b) |
| China Eco-environmental Quality (CHEQ) | 500 m | Delineation of resistance surface | (Xu et al., 2021) |
| Habitat quality | 300 m | Delineation of resistance surface and calculation of dynamic biological flow | (Mu et al., 2024) |
| Digital Elevation Model (DEM) | 30 m | Delineation of resistance surface | (Farr et al., 2007) |
| Mammal distribution | 1000 m | Calculation of dynamic biological flow | (Xu et al., 2024a) |
| Red panda distribution | 1000 m | Calculation of dynamic biological flow | |
| Chinese horseshoe bat distribution | 1000 m | Calculation of dynamic biological flow | |

ecological network analysis and species migration modeling.

## 3. Methods

This study presented a dynamic biological flow assessment framework in ecological networks, elucidating the impacts of species migration direction and flow intensity on network efficiency through three key steps (Fig. 2). First, ecological sources are identified and resistance surfaces are constructed by classifying landscape elements and integrating omnidirectional connectivity, CHEQ, and slope data (Fig. 2a). Second, dynamic biological flow is quantified using two newly developed tools: Ecological Linkage Tool-Direction (ELT-Direction) and Ecological Linkage Tool-Biological Flow (ELT-Biological Flow). ELT-Direction determines the directionality of all ecological corridors, while ELT-Biological Flow estimates the intensity and direction of species flows between ecological sources based on biodiversity, habitat area, and quality (Fig. 2b). Finally, network performance is evaluated across three levels, include nodes (habitat importance), links (corridor importance), and graph (network efficiency). The failure simulations further assess the impacts of directional corridor loss and habitat degradation on network efficiency, identifying critical corridors and vulnerable nodes under various disturbance scenarios (Fig. 2c).

### 3.1. Ecological source and resistance surface

Considering that medium-sized felids, such as wild cats, typically require 10 to 100 km$^2$ of habitat (Sunquist, 2002), this study selected landscape core areas larger than 10 km$^2$ as ecological sources. The 10 km$^2$ threshold ensures that the selected patches provide sufficient habitat resources and connectivity potential for species dispersal. To refine ecological source boundaries, morphological erosion and dilation operations were applied, which helped eliminate small fragmented patches and enhance source continuity. As a result, 1825 ecological sources were identified across the MSBBC region. Additionally, to account for landscape connectivity, ecological environmental quality, and terrain variation, ecological resistance surface was adjusted as follows:

$$R_{Con} = Con_{max} - Con \tag{1}$$

$$R = R_{Con} \times \frac{CHEQ_{mean} + 1}{CHEQ + 1} + R_{Con} \times \frac{HQ_{mean} + 1}{HQ + 1} + Slope \tag{2}$$

where $R$ represents ecological resistance; $R_{Con}$ represents connectivity resistance; $Con$ is the omnidirectional landscape connectivity; $CHEQ$ the eco-environmental quality observed by remote sensing; $HQ$ represents habitat quality; $Slope$ refers to the slope of the terrain.

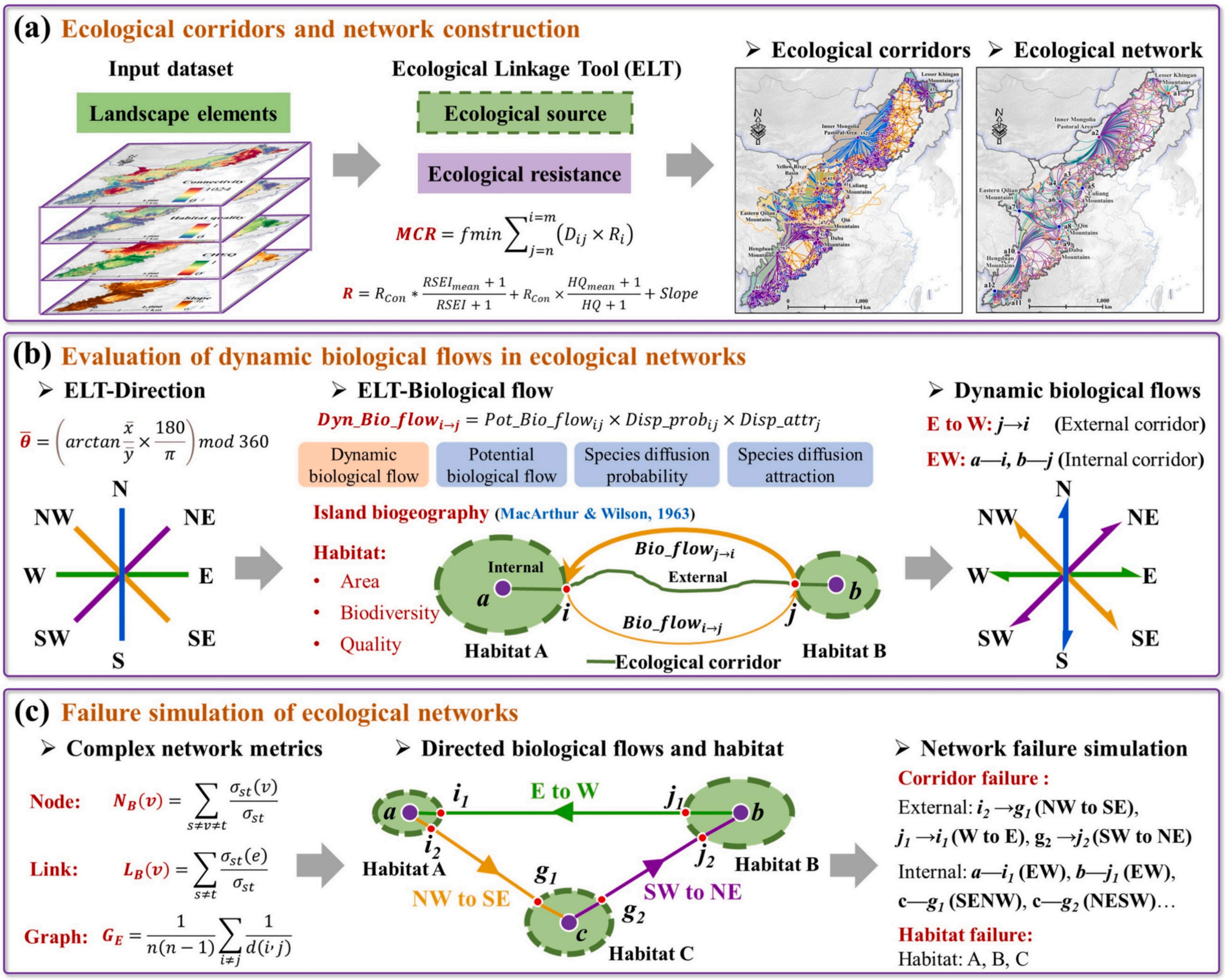

**Fig. 2.** A framework for dynamic biological flow assessment in ecological networks, including ecological corridor and network construction (a), dynamic biological flow computation (b), and ecological network failure simulation considering directional corridor loss and habitat degradation (c).

### 3.2. Ecological corridors and network construction

The Ecological Linkage Tool (ELT) is designed to identify ecological corridors within and beyond irregular ecological sources, activate key nodes and stepping stones, and construct a comprehensive ecological network (Fig. S3). Unlike Linkage Mapper (McRae and Kavanagh, 2011), which relies on ArcPy, ELT is developed using open-source tools such as the Geospatial Data Abstraction Library (GDAL) and supports parallel computing, significantly improving computational efficiency for large-scale ecological network construction. The workflow consists of the following steps: (1) Euclidean allocation is applied to ecological sources. Pixels are assigned to the nearest source region based on Euclidean distance, generating an adjacency table for ecological sources; (2) Neighboring sources are updated by incorporating the nearest neighbor points, refining the adjacency table to ensure more accurate connectivity representation; (3) The minimum cumulative resistance (MCR) model is executed. The execution range of the MCR model is optimized using the nearest neighbor points, generating ecological corridors and activated nodes, which are then converted into an ecological network. The MCR model is expressed as follows:

$$MCR = f \times min \sum_{j=n}^{i=m} \left(D_{ij} \times R_i\right) \tag{3}$$

where *MCR* represents the minimum cumulative resistance for species dispersal from ecological source patch *j* to a given spatial location; *f* is a function of the product of $D_{ij}$ (the spatial distance between source *j* and other patches *i*) and $R_i$ (the resistance coefficient for species dispersal in a specific direction from source *i*); and *min* ensures that each evaluation unit takes the lowest cumulative resistance value among different sources. Corridors connecting the edges of two ecological source patches are defined as inter-patch corridors, while those connecting an edge to the centroid of a patch are referred to as intra-patch corridors.

### 3.3. Ecological linkage tool-direction

ELT-Direction identifies the directionality of ecological corridors by segmenting corridor vertices, computing segment-wise azimuths, and converting them into unit vectors. The average unit vector for all segments is then used to determine the overall direction of the corridor. Given a corridor consisting of n vertices with coordinates $(x_1, y_1)$, $(x_2, y_2)$, …, $(x_n, y_n)$, each segment is formed by two consecutive points $(x_i, y_i)$ and $(x_{i+1}, y_{i+1})$. The azimuth $\theta_i$ of each segment is computed as:

$$\theta_i = \left(arctan \frac{x_{i+1} - x_i}{x_{y+1} - x_y}\right) mod\ 360 \tag{4}$$

where *arctan* is the inverse tangent function, which returns the angle corresponding to the given slope. The *mod* 360 operation ensures that all computed azimuths fall within 0° to 360°, providing a standardized representation of directionality.

Next, each azimuth is converted into a unit vector and averaged across all segments to obtain the mean vector $(\overline{x}, \overline{y})$. The overall mean azimuth $\overline{\theta}$ for the corridor is then calculated as:

$$\overline{x} = \frac{1}{n} \sum_{i=1}^{n} cos\left(\theta_i \times \frac{\pi}{180}\right) \tag{5}$$

$$\overline{y} = \frac{1}{n} \sum_{i=1}^{n} sin\left(\theta_i \times \frac{\pi}{180}\right) \tag{6}$$

$$\overline{\theta} = \left(arctan \frac{\overline{x}}{\overline{y}} \times \frac{180}{\pi}\right) mod\ 360 \tag{7}$$

By computing the mean unit vector instead of directly averaging angles, biases caused by circular averaging are eliminated, improving the accuracy of directionality estimation. Based on the mean azimuth, corridors are classified into four primary categories: east-west (EW), north-south (NS), northwest-southeast (NWSE), and northeast-southwest (NESW) directions. All computations are performed in a projected coordinate system, specifically the Albers equal-area conic projection, which is well-suited for mid-latitude regions as it minimizes area distortion and preserves angular accuracy, ensuring more reliable directional analysis.

### 3.4. Ecological linkage tool-biological flow

Dynamic biological flow represents species migration between habitat patches, influenced by habitat area, biodiversity, and habitat quality (Lu et al., 2024). According to island biogeography theory, large habitat patches function as species pools, supplying biodiversity to surrounding habitats (MacArthur and Wilson, 1963). Habitat biodiversity and habitat quality are key indicators of habitat suitability, as larger and higher-quality habitats offer greater foraging and mating opportunities, increasing their attractiveness for species dispersal (Urban and Keitt, 2001). Building on previous research (Lu et al., 2024), we applied logarithmic corrections to habitat area and corridor length to enhance data comparability in large-scale applications. The calculation process is as follows:

$$Dyn\_Bio\_flow_{i \to j} = Pot\_Bio\_flow_{ij} \times Disp\_prob_{ij} \times Disp\_attr_j \tag{8}$$

$$Pot\_Bio\_flow_{ij} = min\left(Hab_{bio\,i} \times \ln(Area_i),\ Hab_{bio\,j} \times \ln\left(Area_j\right)\right) \tag{9}$$

$$Disp\_prob_{ij} = e^{-k \times ln\left(d_{ij}\right)} \tag{10}$$

$$Disp\_attr_j = Norm_{0 \to 1}\left(Hab\_bio_j \times Hab\_qua_j \times Area_j\right) \tag{11}$$

where $Dyn\_Bio\_flow_{i \to j}$ represents the dynamic biological flow from habitat *i* to habitat *j*, generated by species migration. $Pot\_Bio\_flow_{ij}$ denotes the potential biological flow between habitats *i* and *j*. To account for habitat carrying capacity, $Pot\_Bio\_flow_{ij}$ is determined by the minimum value of the product of biodiversity ($Hab\_bio_i$, $Hab\_bio_j$) and habitat area ($Area_i$, $Area_j$) between habitats *i* and *j*. The dispersal probability $Disp\_prob_{ij}$ from habitat *i* to *j* is modeled as an exponential decay function dependent on dispersal distance $d_{ij}$ and a distance decay coefficient *k*. $d_{ij}$ represents the maximum dispersal distance, and *k* is typically set to 0.05 (Lu et al., 2024; Luo et al., 2021). The dispersal attraction $Disp\_attr_j$ quantifies the attractiveness of habitat *j* as a dispersal destination. For intra-patch corridors (where $i = j$), dynamic biological flow remains undirected. However, for inter-patch corridors (where $i \neq j$), the direction of biological flow is determined based on $Dyn\_Bio\_flow$, ensuring an ecologically meaningful representation of species movement patterns.

### 3.5. Complex network analysis and failure simulation

In ecological network assessment, betweenness centrality quantifies a node's role as a bridge along shortest paths, highlighting its significance in maintaining connectivity and facilitating information transfer (Freeman, 1977). Edge betweenness centrality evaluates the involvement of a specific edge in shortest paths, reflecting its capacity to regulate network structure and material flow (Girvan and Newman, 2002). Global network efficiency, defined as the reciprocal of the average shortest path length, measures the overall efficiency of information and material transfer within the network, serving as an indicator of ecosystem functional stability (Latora and Marchiori, 2001). Higher node and edge betweenness centrality values indicate that the corresponding ecological nodes and corridors play critical roles in enhancing information flow, sustaining connectivity, and preserving network structure, thus acting as key hubs. Furthermore, failure simulations assess the impacts of directional corridor loss and habitat degradation on network efficiency, identifying critical corridors and vulnerable nodes under various disturbance scenarios (Fagan et al., 2023).

The betweenness centrality of a node $v$ is defined as the proportion of shortest paths passing through it relative to all shortest paths in the network, calculated as follows:

$$P_B(v) = \sum_{s\neq v\neq t} \frac{\sigma_{st}(v)}{\sigma_{st}} \tag{12}$$

where $\sigma_{st}$ represents the total number of shortest paths between nodes $s$ and $t$, and $\sigma_{st}(v)$ is the number of shortest paths between $s$ and $t$ that pass through node $v$. The summation is performed over all possible node pairs $s$ and $t$, excluding $v$ itself.

Similar to betweenness centrality, edge betweenness is calculated as the proportion of shortest paths that pass through a given edge $e$, expressed as:

$$L_B(v) = \sum_{s\neq t} \frac{\sigma_{st}(e)}{\sigma_{st}} \tag{13}$$

where $\sigma_{st}$ is the total number of shortest paths between nodes $s$ and $t$, and $\sigma_{st}(e)$ is the number of shortest paths between $s$ and $t$ that pass through edge $e$.

Global network efficiency is typically defined as the inverse of the average shortest path length between all node pairs, given by:

$$G_E = \frac{1}{n(n-1)} \sum_{i\neq j} \frac{1}{d(i,j)} \tag{14}$$

where $E(G)$ represents the global efficiency of the network, $n$ is the total number of nodes. $d(i,j)$ is the shortest path length between nodes $i$ and $j$, represent the migration capability of a species within the network, influenced by the maximum dispersal distance of species.

## 4. Results

### 4.1. Directional ecological corridor in MSBBC

The MSBBC ecological network consists of 13,800 corridors, predominantly oriented in the east-west (EW) direction (27 %) and north-south (NS) direction (26 %) (Fig. 3a). Intra-patch corridors constitute 65 % of the total, while inter-patch corridors account for 35 %. Inter-patch corridors primarily facilitate species migration between habitats, while intra-patch corridors serve as pathways for species movement from habitat edges to their cores. Connectivity analysis reveals that low-connectivity corridors are primarily located at the network periphery, particularly in river valleys and transition zones between mountain ranges. Medium-connectivity corridors are concentrated in core ecological source connections, while high-connectivity corridors are predominantly found in mountainous regions with complex terrain, such as the Qinling, Qilian, Daba, and Hengduan Mountains. In the Yellow River Basin, most corridors exhibit low to medium connectivity, forming a linear pattern along the river valleys. The overall connectivity of the ecological network in this region remains weak, indicating that stable connections between ecosystems are at risk.

Overall, intra-patch corridors exhibit higher connectivity and lower ecological resistance, whereas inter-patch corridors, located in peripheral regions, encounter higher ecological resistance due to increased landscape fragmentation and environmental barriers (Fig. 3b). Among inter-patch corridors, NESW-oriented corridors have the lowest

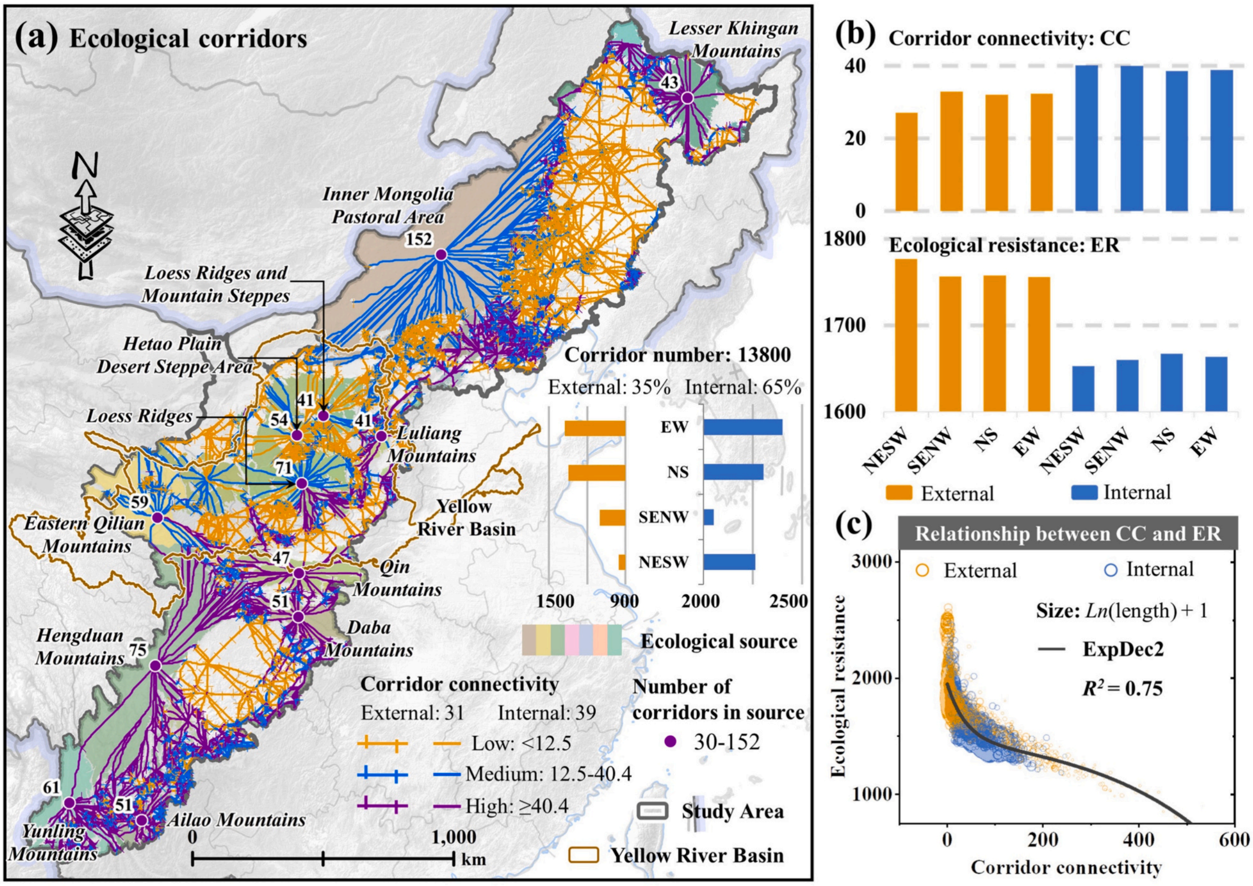

Fig. 3. Spatial distribution of ecological corridors in MSBBC. Connectivity classification of corridors based on network topology (a), connectivity and ecological resistance evaluation of corridors in different directions (b), and the relationship between corridor connectivity and ecological resistance (c). Corridor connectivity is calculated by omnidirectional connectivity data (Mu et al., 2025b).

connectivity (27), whereas among intra-patch corridors, NESW corridors exhibit the highest connectivity (40). The smaller variation in intra-patch corridor connectivity suggests that networks within ecological sources function as stable secondary networks. A strong exponential relationship exists between corridor connectivity and ecological resistance, whereby resistance decreases rapidly as connectivity increases, particularly for corridors with connectivity values below 50 (Fig. 3c). This pattern arises because connectivity serves as a primary factor in the resistance surface design, which also incorporates remote sensing indices, habitat quality, and terrain factors to refine corridor pathways (Fig. S4).

### *4.2. Dynamic biological flow in MSBBC*

During the dynamic biological flow through inter-patch corridors, approximately 48 % of species may fail to reach target habitats, resulting in a net inflow of −573 (outflow: 1199; inflow: 626) (Fig. 4). According to the differential of dynamic biological flows, 21 % of species move from west-to-east, and 18 % from north-to-south (Fig. S5). High biological outflow is concentrated in the Hengduan Mountains, a biodiversity hotspot with widespread species dispersal (Fig. 4a). In contrast, biological inflow sources include both biodiversity hotspots and the Inner Mongolia Pastoral Area, where large habitat size and strong attraction to smaller ecological sources make it a major inflow zone (Fig. 4b). Regionally, net inflow values exceeding 20 are mainly found in the Hengduan, Yunling, and Ailao Mountains, where favorable conditions attract substantial biological flow. Inner Mongolia Pastoral Area has a net inflow above 10, while the Qinling Mountains, Daba Mountains, and Yellow River Basin exceed 2, indicating their role in species dispersal. In contrast, ecological sources with net inflows below 0 are smaller and more scattered, suggesting that weaker ecological conditions limit biological movement.

Dynamic biological outflow follows a clear directional trend, primarily west-to-east, north-to-south, northwest-to-southeast, and southwest-to-northeast (Fig. 4). This pattern aligns with regional ecological conditions, as species migrate toward more favorable southeastern habitats. The north-to-south route experiences the highest species loss, with a minimum net inflow of −16. In high-net-inflow habitats, large patches siphon biological flow from smaller surrounding habitats (Fig. 4c). SENW-oriented corridors show frequent intra-patch biological flow, aligning with the vertical orientation of Hu Line. Larger habitats also exhibit stronger intra-patch movement (Fig. 4d), indicating that

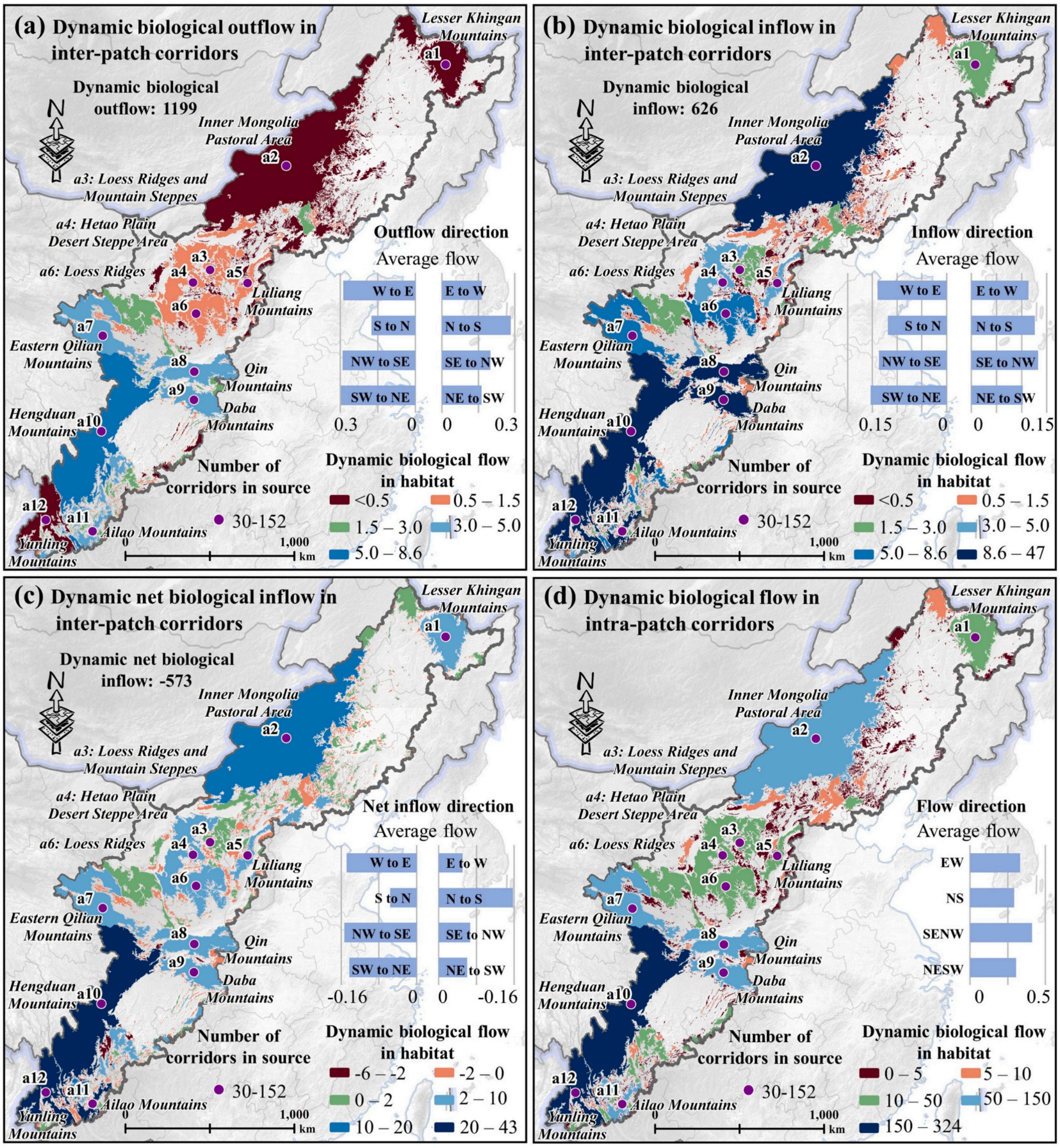

**Fig. 4.** Dynamic biological flow characteristics in MSBBC, including dynamic biological outflow (a), dynamic biological inflow (b), dynamic net biological inflow (c), and dynamic biological flow within ecological sources (d).

biological flow across the Hu Line is more pronounced within well-connected ecosystems. Overall, dynamic biological flow reveals regional ecological complexity and species migration patterns, emphasizing the impact of habitat distribution and biodiversity on flow direction and intensity, rather than solely ecological resistance (Fig. S6). These findings underscore the need to enhance connectivity in areas with negative net inflows.

### 4.3. *Ecological network evaluation and failure simulation*

The MSBBC ecological network has an overall efficiency of 0.053, with core regions such as the Inner Mongolia Pastoral Area (a2), Hetao Plain Desert Steppe Area (a4), Loess Ridges (a6), and Hengduan Mountains (a10) serving as key connectivity hubs due to their high betweenness centrality (Fig. 5). Among intra-patch corridors, EW corridor failure has the greatest impact, reducing network efficiency by 57 %, while failures in other directions cause about a 40 % decline (Fig. 5a). The failure of core habitat nodes (e.g., a2, a10) leads to major efficiency losses, underscoring their critical role in ecological connectivity (Fig. 5b). The failure of a2 (Inner Mongolia Pastoral Area) results in a 24 % efficiency drop, partly due to its high corridor density. Although a10 (Hengduan Mountains) has a similar number of corridors as a6 (Loess Ridges), its impact is 1.8 times greater, suggesting that each corridor in a10 contributes more to network efficiency. Additionally, failures in key habitats along the Yellow River Basin (e.g., a4, a5) trigger cascading effects on primary regional corridors, particularly those with high edge betweenness, potentially fragmenting the network and severely reducing connectivity.

Among inter-patch corridors, the failure of west-to-east corridors causes a 13 % efficiency drop, the highest among all directional failures, reflecting their backbone role in regional connectivity. This is followed by north-to-south corridors, which reduce efficiency by 11 %. Generally, the greater the number of failing corridors, the stronger the negative impact on overall network efficiency (Fig. 5c). Simulating failures at different proportions reveals that when 50 %–80 % of intra-patch EW corridors fail, the efficiency drop is the most significant. For inter-patch corridors, once failures exceed 20 %, the efficiency decline becomes more pronounced. Specifically, failures in west-to-east, north-to-south, northwest-to-southeast, and southwest-to-northeast directions exhibit the sharpest efficiency reductions (Fig. S7), highlighting the importance of maintaining directional connectivity in these critical corridors.

## 5. Discussion

### 5.1. *Dynamic biological flow of species-specific*

To validate the applicability of the dynamic biological flow framework in analyzing species-specific movement, we selected the *Ailurus fulgens* (red panda) and *Rhinolophus sinicus* (Chinese horseshoe bat) as representative species. *Ailurus fulgens* is a flagship species of mountainous regions, with strong habitat specialization, particularly dependent on high-quality, continuous forest habitats, and has limited migration and dispersal abilities. In contrast, *Rhinolophus sinicus* is a habitat generalist, highly adaptable, and able to utilize various forest and cave environments. *Ailurus fulgens* is an endangered species, while *Rhinolophus sinicus* is a sensitive species and a natural host of the SARS virus, making them important representative species in this study (Ge et al., 2013; Thapa et al., 2018).

Despite similar number of corridor directions, *Ailurus fulgens* and *Rhinolophus sinicus* show significant differences in dynamic biological flow, indicating species influence flow intensity more than direction (Fig. 6). Both migrate west-to-east, north-to-south, northwest-to-southeast, and southwest-to-northeast, with populations decreasing along the way (Fig. 6ab). *Ailurus fulgens* has a net inflow of −0.13 along

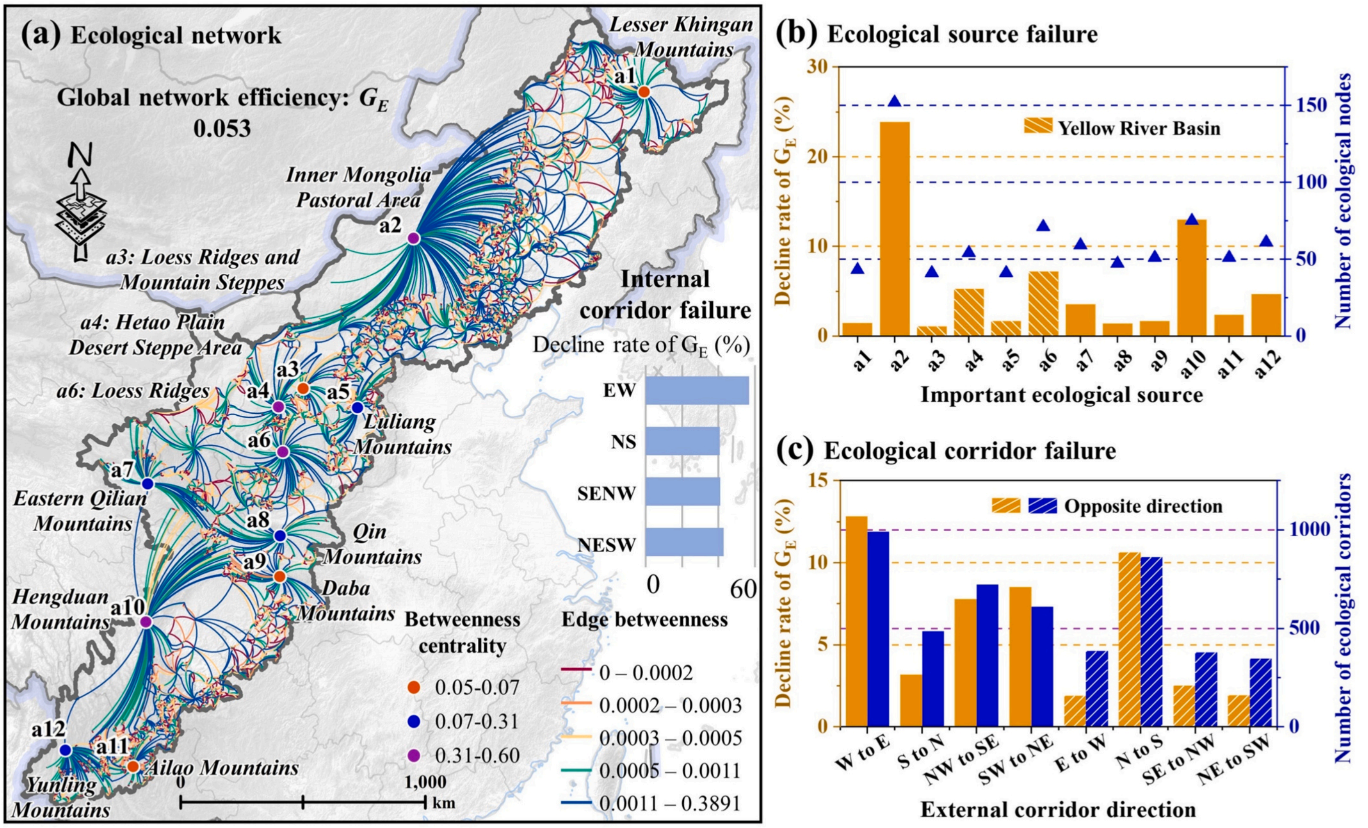

**Fig. 5.** Ecological network efficiency evaluation in MSBBC, including (a) spatial distribution of betweenness centrality, edge betweenness, and overall ecological network efficiency, (b) network efficiency assessment under key habitat failures, and (c) network efficiency assessment under directional corridor failures.

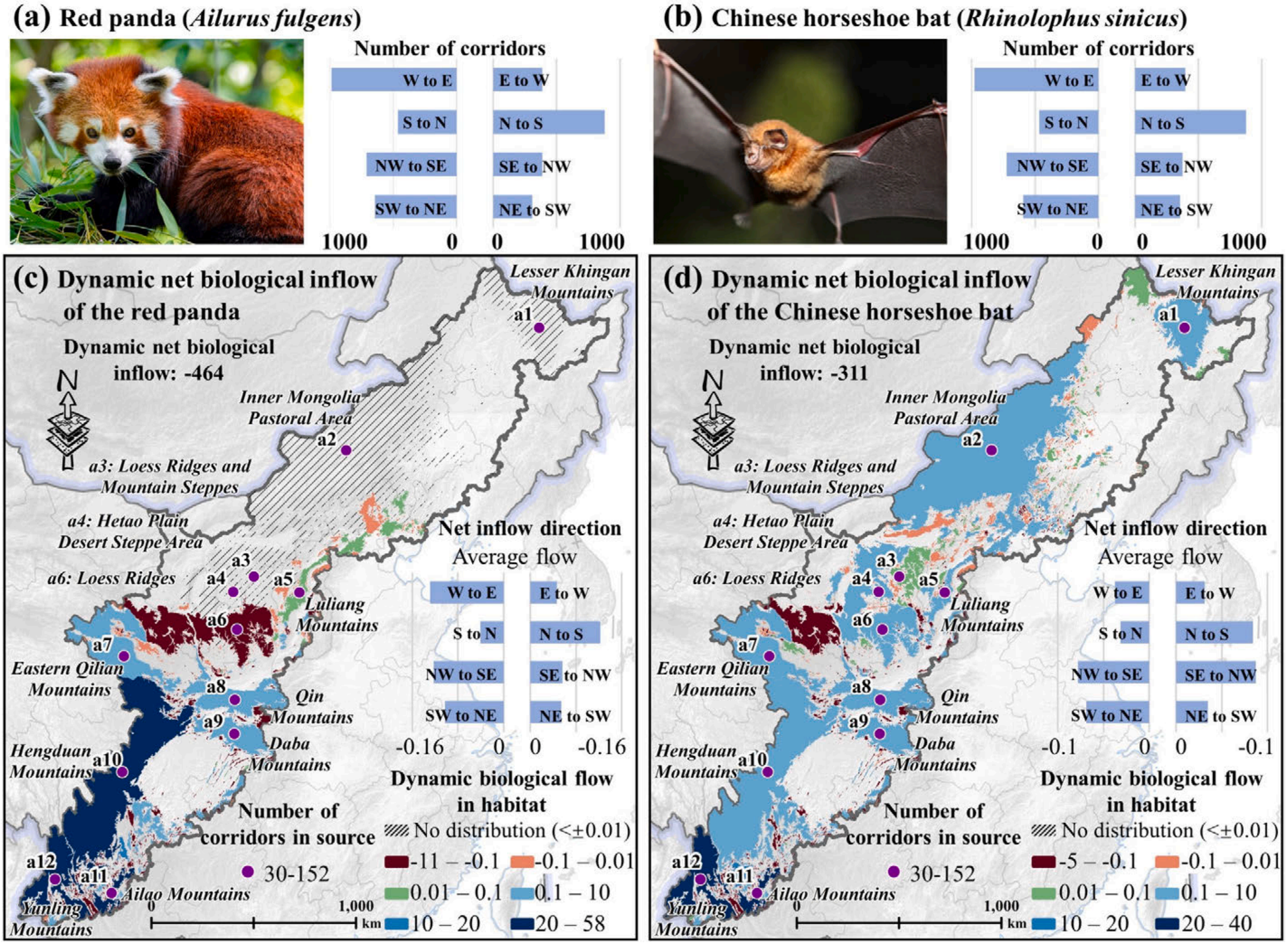

**Fig. 6.** Biological flow characteristics of *Ailurus fulgens* and *Rhinolophus sinicus*, including the number of directional corridors (a, b) and dynamic net biological flow (c, d).

the west-to-east route (outflow: 0.26, inflow: 0.13) (Fig. 6c). Loess Ridges serves as a major outflow region, while Hengduan, Yunling, and Ailao Mountains attract inflows (Fig. S8). Protecting Loess Ridges and maintaining corridor integrity would enhance connectivity and reduce losses. *Rhinolophus sinicus* experiences the highest migration loss (−0.09) in the southeast-to-northwest direction, suggesting significant ecological threats (Fig. 6d), likely due to habitat fragmentation, resource depletion, or environmental barriers. In contrast, west-to-east corridors have more pathways but lower migration losses (−0.03). Its outflow regions, primarily near Loess Ridges, appear highly fragmented, raising concerns about habitat connectivity. Overall, habitat distribution determines dynamic flow direction, while species-specific adaptability influences flow intensity. These findings inform conservation planning: for *Ailurus fulgens*, focus on improving outflow habitats and strengthening connectivity to inflow areas; for *Rhinolophus sinicus*, prioritize reducing fragmentation and mitigating threats along high-loss routes. Such efforts would enhance species survival and network resilience within MSBBC.

### *5.2. Dynamic biological flows and conservation priorities in the MSBBC*

Biological flow has partially mitigated ecological isolation between eastern and western China but has not fully bridged the gap. In some areas, imbalanced flows may even exacerbate habitat degradation. The dominant west-to-east and north-to-south migration patterns remain constrained, resulting in an overall negative net inflow, with approximately 48 % of species failing to reach suitable target habitats, exposing significant migration bottlenecks and connectivity deficits. Regional variations in climate, topography, and human activities further shape species movement and habitat needs (Shrestha et al., 2021; Xu et al., 2024a). For endangered species like *Ailurus fulgens* and sensitive species like *Rhinolophus sinicus*, their strict dependence on habitat integrity and connectivity increases the risks of population extinction and disease transmission.

To address these issues, it is necessary to establish a cross-provincial ecological corridor restoration alliance along the Hu Line. Specifically, priority should be given to restoring east-west corridors with significant efficiency losses (e.g., corridor connecting Inner Mongolia to central-eastern regions) and to reducing high species losses along north–south migration routes (e.g., areas with minimum net inflow reaching −16). From the MSBBC perspective, the Hengduan Mountains have been identified as a hotspot of high biological outflow and a core biodiversity center, where reducing species loss and enhancing the attraction capacity of surrounding source areas should be prioritized. The Inner Mongolia Pastoral Area, due to its large habitat area and strong attraction to surrounding small patches, requires further improvement of habitat quality to consolidate its function as a key sink. The Yellow River Basin has relatively weak overall connectivity, it serves as an important north–south migration bridge, playing a critical strategic role in supporting eastern biodiversity and alleviating western ecological vulnerability (Fu et al., 2022). Strengthening the cross-regional ecological corridor collaboration mechanisms along the Hu Line, unifying critical ecological node planning, and enhancing connectivity of the ecological network to prevent species isolation, reduce landscape fragmentation, and mitigate disease transmission risks caused by human activities.

### 5.3. Dynamic biological flow and sustainable development

Dynamic biological flow is fundamental to maintaining ecosystem stability and biodiversity, shaping species migration, gene exchange, and ecological health. However, uneven regional development disrupts these flows through natural barriers, human activities, and infrastructure expansion, impacting ecological security and sustainability (Jin et al., 2019; Wang et al., 2025). In MSBBC, a well-planned ecological network would connect key habitats, reducing pressure on western ecosystems while supporting eastern biodiversity. Globally, many countries face similar spatial disparities to China's Hu Line, where geographic and demographic imbalances hinder conservation and development (Linard and De Longueville, 2024). In the U.S., population and economic hubs are concentrated on coasts and major river plains, avoiding mountainous and interior regions. In Canada, over 90 % of the population is clustered near the U.S. border due to harsh northern climates. Australia's interior remains largely uninhabited, with settlements concentrated along the eastern coast, mirroring the Hu Line pattern. These patterns reflect challenges in achieving balanced human development and biodiversity conservation across large-scale landscapes.

The MSBBC case study illustrates how enhancing cross-regional ecological connectivity can address such challenges by integrating dynamic biological flows into national spatial planning and conservation strategies. Strengthening ecological corridors, improving habitats quality, and promoting collaborative management across administrative boundaries are key actions to mitigate habitat fragmentation and support ecosystem resilience. The dynamic biological flow framework thus provides a scalable and transferable model for other regions facing similar connectivity constraints. By applying these insights globally, regions can better achieve biodiversity targets, safeguard ecological functions, and promote sustainable landscape development (Blicharska et al., 2019; Jin et al., 2021; Stehfest et al., 2019). Incorporating dynamic biological flow analysis into national spatial planning will help achieve global biodiversity targets (e.g., CBD Target 3), enhance regional resilience, and support sustainable development.

### 5.4. Uncertainty and future research

The directional characteristics of dynamic biological flows observed in this study are consistent with classical biogeographical theories, including island biogeography theory and metapopulation theory (Hanski, 1999; MacArthur and Wilson, 1963). Larger and higher-quality habitats act as critical sinks, attracting more inflow, while smaller and fragmented patches tend to have lower or negative net inflows. The dominant west-to-east and north-to-south flow patterns reflect species' tendency to migrate toward regions with more favorable environmental conditions and richer resources, confirming theoretical predictions from ecological gradient studies (Fox et al., 2011). Habitat size and connectivity significantly influence species migration flows, with stronger flows observed in high-quality habitats such as the Hengduan and Yunling Mountains, while flows are significantly reduced in areas heavily disturbed by human activities, such as the Yellow River Basin. This supports the "habitat area effect" in island biogeography theory. The reliability of our findings is supported by the integration of multi-source datasets (e.g., habitat quality, connectivity, biodiversity) and the newly developed ELT-Direction and ELT-Biological Flow tools, which together improve the accuracy of directional flow and network efficiency assessments.

This study has several limitations. First, there may be differences in the delineation of ecological sources and resistance surfaces. We selected landscape core areas larger than 10 $km^2$ based on structural integrity and species requirements, but other methods of delineation may affect the results. Second, the movement parameters of mammals (such as maximum dispersal distance and migration trends) were mainly derived from existing literature (Sunquist, 2002). While these parameters effectively reflect the characteristics of certain species, extrapolating them across different spatial and temporal scales may introduce uncertainty. Therefore, future research should calibrate these parameters using more extensive field data or long-term monitoring data. The current model also does not account for seasonal migration patterns or interannual variations in habitat suitability, which may lead to errors in estimating migration direction and flow intensity. Future studies should incorporate seasonal variations and consider the seasonal changes in habitat suitability to improve the model's dynamics and accuracy. Furthermore, while the relationship between network efficiency and species flows has been analyzed, the coupling between ecosystem services (such as water regulation, pollination, etc.) and network efficiency has not been explored. Future research should further investigate the long-term effects of species migration on ecosystem services. Lastly, data resolution and scale uncertainty may affect the assessment of ecological network efficiency in the application of protected areas, particularly at the provincial, basin, and specific protected area scales. The integration of high-resolution remote sensing data will help improve the consistency and accuracy of network characteristics at different scales and provide support for precise conservation planning.

## 6. Conclusions

This study developed a dynamic biological flow framework to elucidate ecological gap between eastern and western China. The framework focuses on the MSBBC ecological network and quantitatively reveals species migration patterns and network efficiency. The analysis integrates complex network metrics and dynamic biological flow simulations to identify critical corridors and vulnerable habitats under different corridor and habitat degradation scenarios.

The findings address three central questions posed in this study. First, the current state of regional ecological corridors reveals a network efficiency of 0.053, with intra-patch corridors exhibiting higher connectivity and lower resistance, particularly in core regions like the Qinling, Qilian, Daba, and Hengduan Mountains, whereas the Yellow River Basin shows weaker, fragmented connectivity due to human disturbances. Second, the quantification of dynamic biological flows indicates strong west-to-east (21 %) and north-to-south (18 %) migration trends; however, a net outflow persists, with 48 % of species failing to reach target habitats, especially along north-to-south routes where losses are most severe due to latitudinal barriers. Third, ecological source areas and biological flows significantly influence network efficiency: failures in Inner Mongolia reduce efficiency by 24 %, intra-patch east-west corridor disruptions cause a 57 % decline, and inter-patch west-to-east corridor losses lead to a 13 % drop, with cascading effects most pronounced in Inner Mongolia and the Hengduan Mountains. These results highlight the urgent need to strengthen corridors in vulnerable regions, mitigate migration barriers, and enhance flow driven by species-specific adaptability and habitat distribution. Therefore, it is essential to establish cross-regional corridor alliances (especially along the Hu Line), prioritize the restoration and reinforcement of east-west corridors with significant efficiency losses, and improve the area and quality of habitats in key outflow and inflow zones to enhance ecological resilience and promote sustainable development in both eastern and western China.

## CRediT authorship contribution statement

**Haowei Mu**: Data curation, Investigation, Methodology, Visualization, Writing – original draft. **Shanchuan Guo**: Writing – review & editing. **Kaixuan Pan**: Writing – review & editing. **Bo Yuan**: Writing – review & editing. **Zhou Fang**: Writing – review & editing. **Xuecao Li**: Formal analysis, Writing – review & editing. **Peijun Du**:

Conceptualization, Data curation, Funding acquisition, Validation, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.eiar.2025.108138.

## Data availability

Data related to ecological sources, ecological networks, dynamic biological flows and the vector boundary of the Middle Spine Belt of Beautiful China are available on Zenodo: https://doi.org/10.5281/zenodo.15163034. The analysis code is openly accessible on GitHub: https://github.com/HaoweiGis/Ecological-Linkage-Tool.

## References

Assis, J.C., Hohlenwerger, C., Metzger, J.P., Rhodes, J.R., Duarte, G.T., da Silva, R.A., Boesing, A.L., Prist, P.R., Ribeiro, M.C., 2023. Linking landscape structure and ecosystem service flow. Ecosyst. Serv. 62, 101535.

Bianco, G., Manning, P., Schleuning, M., 2024. A quantitative framework for identifying the role of individual species in nature's contributions to people. Ecol. Lett. 27 (2), e14371.

Blicharska, M., Smithers, R.J., Mikusiński, G., Rönnbäck, P., Harrison, P.A., Nilsson, M., Sutherland, W.J., 2019. Biodiversity's contributions to sustainable development. Nat. Sustain. 2 (12), 1083–1093.

Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N., Kremen, C., 2022. Functional connectivity of the world's protected areas. Science 376 (6597), 1101–1104.

Brodie, J.F., Gonzalez, A., Mohd-Azlan, J., Nelson, C.R., Tabor, G., Vasudev, D., Zeller, K. A., Fletcher Jr., R.J., 2025. A well-connected earth: the science and conservation of organismal movement. Science 388 (6745), eadn2225.

Cosmo, L.G., Assis, A.P.A., de Aguiar, M.A., Pires, M.M., Valido, A., Jordano, P., Thompson, J.N., Bascompte, J., Guimarães Jr., P.R., 2023. Indirect effects shape species fitness in coevolved mutualistic networks. Nature 619 (7971), 788–792.

Dissanayake, I., Piyathilake, V., Sayakkara, A.P., Hettiarachchi, E., Perera, I., 2024. Eloc-web: uncertainty visualization and real-time detection of wild elephant locations. J. Geovis. Spat. Anal. 8 (1), 7.

Doherty, S., Saltre, F., Llewelyn, J., Strona, G., Williams, S.E., Bradshaw, C.J., 2023. Estimating co-extinction threats in terrestrial ecosystems. Glob. Chang. Biol. 29 (18), 5122–5138.

Du, Z., Yu, L., Chen, X., Li, X., Peng, D., Zheng, S., Hao, P., Yang, J., Guo, H., Gong, P., 2023. An operational assessment framework for near real-time cropland dynamics: toward sustainable cropland use in mid-spine belt of beautiful China. J. Remote Sens. 3, 0065.

Fagan, B., Pitchford, J.W., Stepney, S., Thomas, C.D., 2023. Increased dispersal explains increasing local diversity with global biodiversity declines. Glob. Chang. Biol. 29 (23), 6713–6726.

Fang, C., Wang, Z., Liu, H., 2020. Beautiful China initiative: human-nature harmony theory, evaluation index system and application. J. Geogr. Sci. 30, 691–704.

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., 2007. The shuttle radar topography mission. Rev. Geophys. 45 (2).

Felipe-Lucia, M.R., Guerrero, A.M., Alexander, S.M., Ashander, J., Baggio, J.A., Barnes, M.L., Bodin, Ö., Bonn, A., Fortin, M.-J., Friedman, R.S., 2022. Conceptualizing ecosystem services using social–ecological networks. Trends Ecol. Evol. 37 (3), 211–222.

Feng, Q., Bai, G., Li, Z., Wang, B., Chen, L., Wang, P., Yu, T., Meng, H., Liu, W., Lu, Z., 2022. Accelerate construction of new pattern of ecological protection in Northwest China. Bull. Chin. Acad. Sci. (Chinese Version) 37 (10), 1457–1470.

Fox, G.A., Scheiner, S.M., Willig, M.R., 2011. Ecological gradient theory: a framework for aligning data and models. Theory Ecol. 283–308.

Frans, V.F., Liu, J., 2024. Gaps and opportunities in modelling human influence on species distributions in the Anthropocene. Nat. Ecol. Evol. 8 (7), 1365–1377.

Freeman, L.C., 1977. A set of measures of centrality based on betweenness. Sociometry 35-41.

Fu, B., Wu, X., Wang, Z., Wu, X., Wang, S., 2022. Coupling human and natural systems for sustainability: experiences from China's loess plateau. Earth Syst. Dynam. 2022, 1–22.

Fu, B., Liu, Y., Meadows, M.E., 2023. Ecological restoration for sustainable development in China. Natl. Sci. Rev. 10 (7), nwad033.

Fu, J., Su, B., Qin, J., Hu, Y., 2025. Mid-Spine Belt of beautiful China: future reversal of increasing vegetation greening in response to an evolving environment. Int. J. Digital Earth 18 (1), 2449183.

Fuso Nerini, F., Mazzucato, M., Rockström, J., van Asselt, H., Hall, J.W., Matos, S., Persson, Å., Sovacool, B., Vinuesa, R., Sachs, J., 2024. Extending the sustainable development goals to 2050—a road map. Nature 630 (8017), 555–558.

Ge, X., Li, J., Yang, X., Chmura, A.A., Zhu, G., Epstein, J.H., Mazet, J.K., Hu, B., Zhang, W., Peng, C., 2013. Isolation and characterization of a bat SARS-like coronavirus that uses the ACE2 receptor. Nature 503 (7477), 535–538.

Geng, H., van Vliet, J., Albert, J., Zhang, L., Qu, Y., Huang, K., 2025. Rural development outpaces urban expansion in threatening biodiversity in China, *resources*. Conservation and Recycling 215, 108176.

Girvan, M., Newman, M.E., 2002. Community structure in social and biological networks. Proc. Natl. Acad. Sci. 99 (12), 7821–7826.

Guo, H., Wang, X., Wu, B., Li, X., 2016. Cognizing population density demarcative line (Hu Huanyong-line) based on space technology. Bull. Chin. Acad. Sci. (Chinese Version) 31 (12), 1385–1394.

Hanski, I., 1999. Metapopulation Ecology. Oxford University Press.

Hu, H., 1935. Distribution of China's population: attached statistical table and density chart. Acta Geograph. Sin. 2, 33–74.

Jin, G., Chen, K., Wang, P., Guo, B., Dong, Y., Yang, J., 2019. Trade-offs in land-use competition and sustainable land development in the North China plain. Technol. Forecast. Soc. Chang. 141, 36–46.

Jin, G., Shi, X., He, D., Guo, B., Li, Z., Shi, X., 2020. Designing a spatial pattern to rebalance the orientation of development and protection in Wuhan. J. Geogr. Sci. 30 (4), 569–582.

Jin, G., Chen, K., Liao, T., Zhang, L., Najmuddin, O., 2021. Measuring ecosystem services based on government intentions for future land use in Hubei Province: implications for sustainable landscape management. Landsc. Ecol. 36 (7), 2025–2042.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356 (6335), 270–275.

Jongman, R.H., Bouwma, I.M., Griffioen, A., Jones-Walters, L., Van Doorn, A.M., 2011. The pan European ecological network: PEEN. Landsc. Ecol. 26, 311–326.

Keeley, A.T., Beier, P., Jenness, J.S., 2021. Connectivity metrics for conservation planning and monitoring. Biol. Conserv. 255, 109008.

Latora, V., Marchiori, M., 2001. Efficient behavior of small-world networks. Phys. Rev. Lett. 87 (19), 198701.

Li, C., Xu, H., Du, P., Tang, F., 2024. Predicting land cover changes and carbon stock fluctuations in Fuzhou, China: a deep learning and InVEST approach. Ecol. Indic. 167, 112658.

Linard, C., De Longueville, F., 2024. World population distribution today. In: Global Settlement Dynamics: How People Inhabit the World, 33-61.

Lu, Y., Huang, D., Tong, Z., Liu, Y., He, J., Liu, Y., 2024. A conceptual framework for constructing and evaluating directed ecological networks: evidence from Wuhan metropolitan area, China. Environ. Impact Assess. Rev. 106, 107464.

Luo, Y., Wu, J., Wang, X., Zhao, Y., Feng, Z., 2021. Understanding ecological groups under landscape fragmentation based on network theory. Landsc. Urban Plan. 210, 104066.

MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. Evolution 373-387.

McRae, B.H., Kavanagh, D.M., 2011. Linkage Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle WA.

McRae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89 (10), 2712–2724.

Moore, J.W., Schindler, D.E., 2022. Getting ahead of climate change for ecological adaptation and resilience. Science 376 (6600), 1421–1426.

Mu, H., Li, X., Ma, H., Du, X., Huang, J., Su, W., Yu, Z., Xu, C., Liu, H., Yin, D., Li, B., 2022a. Evaluation of the policy-driven ecological network in the three-north shelterbelt region of China. Landsc. Urban Plan. 218, 104305.

Mu, H., Li, X., Wen, Y., Huang, J., Du, P., Su, W., Miao, S., Geng, M., 2022b. A global record of annual terrestrial human footprint dataset from 2000 to 2018. Sci Data 9 (1), 176.

Mu, H., Guo, S., Li, X., Zhou, Y., Lü, Y., Du, X., Huang, J., Ma, C., Zhang, X., Xia, Z., 2024. Quantifying landscape connectivity gaps between protected area and natural habitat. J. Clean. Prod. 437, 140729.

Mu, H., Guo, S., Zhang, X., Yuan, B., Li, C., Du, P., 2025a. Quantifying the anthropogenic sensitivity of ecological patterns in arid urban agglomeration. Appl. Geogr. 178.

Mu, H., Guo, S., Zhang, X., Yuan, B., Xia, Z., Tang, P., Zhang, W., Zhang, P., Li, X., Du, P., 2025b. Moving in the landscape: omnidirectional connectivity dynamics in China from 1985 to 2020. Environ. Impact Assess. Rev. 110, 107721.

Opdam, P., Steingröver, E., Van Rooij, S., 2006. Ecological networks: a spatial concept for multi-actor planning of sustainable landscapes. Landsc. Urban Plan. 75 (3–4), 322–332.

Peng, J., Yang, Y., Liu, Y., Du, Y., Meersmans, J., Qiu, S., 2018. Linking ecosystem services and circuit theory to identify ecological security patterns. Sci. Total Environ. 644, 781–790.

Peng, J., Xu, D., Xu, Z., Tang, H., Jiang, H., Dong, J., Liu, Y., 2024a. Ten key issues for ecological restoration of territorial space. Natl. Sci. Rev. 11 (7) nwae176.

Peng, J., Zhang, Z., Lin, Y., Tang, H., Xu, Z., Zheng, H., 2024b. Unveiling decoupled social-ecological networks of great lake basin: an ecosystem services approach. Earth's Future 12 (11), e2024EF004994.

Pressey, R.L., Visconti, P., McKinnon, M.C., Gurney, G.G., Barnes, M.D., Glew, L., Maron, M., 2021. The mismeasure of conservation. Trends Ecol. Evol. 36 (9), 808–821.

Roy, H.E., Pauchard, A., Stoett, P., Truong, T.R., Bacher, S., Galil, B.S., Hulme, P.E., Ikeda, T., Sankaran, K., McGeoch, M.A., 2023. IPBES Invasive Alien Species Assessment: Summary for Policymakers (IPBES).

Saura, S., Bodin, Ö., Fortin, M.J., 2014. EDITOR'S CHOICE: stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. J. Appl. Ecol. 51 (1), 171–182.

Shen, Z., Yin, H., Kong, F., Wu, W., Sun, H., Su, J., Tian, S., 2024. Enhancing ecological network establishment with explicit species information and spatially coordinated optimization for supporting urban landscape planning and management. Landsc. Urban Plan. 248, 105079.

Shrestha, N., Xu, X., Meng, J., Wang, Z., 2021. Vulnerabilities of protected lands in the face of climate and human footprint changes. Nat. Commun. 12 (1), 1632.

Stehfest, E., van Zeist, W.-J., Valin, H., Havlik, P., Popp, A., Kyle, P., Tabeau, A., Mason-D'Croz, D., Hasegawa, T., Bodirsky, B.L., 2019. Key determinants of global land-use projections. Nat. Commun. 10 (1), 2166.

Sunquist, F., 2002. Wild Cats of the World. The University of Chicago Press.

Thapa, A., Hu, Y., Wei, F., 2018. The endangered red panda (Ailurus fulgens): ecology and conservation approaches across the entire range. Biol. Conserv. 220, 112–121.

Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82 (5), 1205–1218.

Wang, X., Guo, H., Lou, L., Chang, R., 2021. From Hu Huanyong line to mid-Spine Belt of beautiful China: breakthrough in scientific cognition and change in development mode. Bulletin of Chinese Academy of Sciences (Chinese Version) 36 (9), 1058–1065.

Wang, X., Zhou, L., López-Carr, D., Song, Y., Gao, H., Che, T., Liu, Z., Wei, W., 2025. Urban grey-green scales: a new perspective for assessing dynamic spatial trade-offs. Int. J. Appl. Earth Obs. Geoinf. 142, 104708.

Ward, M., Saura, S., Williams, B., Ramírez-Delgado, J.P., Arafeh-Dalmau, N., Allan, J.R., Venter, O., Dubois, G., Watson, J.E., 2020. Just ten percent of the global terrestrial protected area network is structurally connected via intact land. Nat. Commun. 11 (1), 4563.

Watson, J.E., Venegas-Li, R., Grantham, H., Dudley, N., Stolton, S., Rao, M., Woodley, S., Hockings, M., Burkart, K., Simmonds, J.S., 2023. Priorities for protected area expansion so nations can meet their Kunming-Montreal global biodiversity framework commitments. Intgr. Conserv. 2 (3), 140–155.

Wu, X., Fu, B., Wang, S., Song, S., Lusseau, D., Liu, Y., Xu, Z., Liu, J., 2023. Bleak prospects and targeted actions for achieving the sustainable development goals. Sci. Bull. 68 (22), 2838–2848.

Xu, Z., Peng, J., 2022. Ecosystem services-based decision-making: a bridge from science to practice. Environ. Sci. Pol. 135, 6–15.

Xu, D., Yang, F., Yu, L., Zhou, Y., Li, H., Ma, J., Huang, J., Wei, J., Xu, Y., Zhang, C., 2021. Quantization of the coupling mechanism between eco-environmental quality and urbanization from multisource remote sensing data. J. Clean. Prod. 321, 128948.

Xu, D., Peng, J., Dong, J., Jiang, H., Liu, M., Luo, Y., Xu, Z., 2024a. Expanding China's protected areas network to enhance resilience of climate connectivity. Sci. Bull. 69 (14), 2273–2280.

Xu, D., Peng, J., Jiang, H., Dong, J., Liu, M., Chen, Y., Wu, J., Meersmans, J., 2024b. Incorporating barriers restoration and stepping stones establishment to enhance the connectivity of watershed ecological security patterns. Appl. Geogr. 170, 103347.

Xu, D., Peng, J., Liu, M., Jiang, H., Tang, H., Dong, J., Meersmans, J., 2025. Bridging climate refuges for climate change adaptation: a spatio-temporal connectivity network approach. Geogr Sustainability 6 (2), 100235.

Yang, J., Huang, X., 2021. 30 m annual land cover and its dynamics in China from 1990 to 2019. Earth Syst. Sci. Data 2021, 1–29.

Yang, X., Zhou, B., Xu, Y., Han, Z., 2021. CMIP6 evaluation and projection of temperature and precipitation over China. Adv. Atmos. Sci. 38 (5), 817–830.

Yue, W., Xia, H., Liu, Y., Xu, J., Xiong, J., 2024. Assessing ecological conservation redline from element, structure, and function dimensions: a case of Zhejiang Province, China. Environ. Impact Assess. Rev. 106, 107485.

Zhang, L., Wan, Y., Sun, Y., He, G., Lei, X., Wei, X., Jin, G., 2025. Optimizing ecological security patterns in a megacity by enhancing urban-rural connectivity: insights from Wuhan, China. Appl. Geogr. 176, 103535.