

Incorporating barriers restoration and stepping stones establishment to enhance the connectivity of watershed ecological security patterns

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ABSTRACT

Enhancing the connectivity of watershed ecological security patterns (ESPs) is increasingly emphasized for preserving ecological processes. Yet the importance of small-scale conservation and restoration was ignored and few studies have quantitatively compared the contribution of barriers restoration and stepping stones establishment to landscape connectivity. In this study, taking Dongting Lake Basin as an example, a watershed ESP was constructed based on the minimum cumulative resistance model and optimized through graded barriers restoration and different stepping stones establishment. Then the enhancement effects of landscape connectivity were compared to identify the most cost-effective optimization scheme. The results showed that the average of six schemes only protected and repaired less than 1% of the total area, which could enhance corridor connectivity by about 12% and 16% for average corridor length and corridor cumulative resistance respectively. For the optimal ESP, establishing natural patches near the midpoint of longer corridors as stepping stones, increased the probability of connectivity by 21.05%, and reduced the average corridor length and corridor cumulative resistance of corridor connectivity by 17.99% and 15.48% respectively. It also increased network circuitry index of network connectivity from 0.541 to 0.570, compared with the original ESP, indicating the possibility of successful ecological flow increased effectively. It can be concluded that the connectivity enhancement of stepping stones approach was better than barriers restoration approach. This study highlights the importance of small-scale barriers restoration and stepping stones establishment in enhancing landscape connectivity.

1. Introduction

Human activity and climate change lead to landscape fragmentation, thereby exacerbating the decline in ecosystem services and biodiversity (Haddad et al., 2015; López-Sánchez et al., 2024; Ren et al., 2022). The conflicts between social and natural systems threaten regional sustainable development (Fu et al., 2023; He et al., 2014). Conservation planning is crucial to restoring degraded habitats and achieving landscape sustainability (Fu et al., 2023). The Kunming-Montreal Global Biodiversity Framework highlights the importance of increasing the area, connectivity, and integrity of ecosystems (CBD, 2022). However, it is impractical to achieve biodiversity conservation and landscape

sustainability by increasing ecological space without limits. Therefore, it is necessary to construct and optimize an ecological security pattern (ESP) to achieve maximum ecological connectivity with minimum ecological investment from a spatial perspective, which has become an effective strategy for coordinating regional ecological protection and economic growth in the context of China's ecological civilization concept (Dong et al., 2021; Peng, Liu, et al., 2024; Peng, Pan, et al., 2018). ESP is a network structure compounding ecological sources interconnected through ecological corridors to facilitate ecosystem integrity and ecological processes which can restore connections between fragmented landscapes to safeguard biodiversity, enhance ecosystem services, and ensure regional ecological security (Peng, Pan,

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et al., 2018; Peng, Yang, et al., 2018; Yu et al., 1996). It is necessary to briefly explain the connection and differences between ESP originating from China and ecological networks originating from Europe (Dong et al., 2021). Both focusing on landscape connectivity, the former emphasizes comprehensive ecological security (i.e. the integrity and health of the ecosystem) (Liu et al., 2022; Peng, Pan, et al., 2018), while the latter is often designed for biodiversity conservation.

The key steps to identify ESPs are generally to identify ecological sources, construct ecological resistance surfaces, and extract ecological corridors. Ecological sources provide ecological space for the survival and reproduction of wildlife and undertake imperative ecological functions, which are mainly identified based on ecosystem service hot-spots or protected areas (Jiang et al., 2022; Mu et al., 2022). The ecological resistance surface represents the difficulty of ecological flow traversing specific landscape elements, which is mainly constructed by assigning values to natural factors and social factors (Brennan et al., 2022). Ecological corridors are strips of landscape connecting ecological sources for materials, energy, and information flow, such as species movement, which are mainly extracted by the minimum cumulative resistance (MCR) model and the circuit model using the resistance-based approach (Knaapen et al., 1992; McRae et al., 2008; Yu, 1996). However, some studies indicate that ecosystem connectivity for biodiversity conservation and ecological processes still needs to be further enhanced (Huang et al., 2021; Xu et al., 2024). ESP optimization is a pivotal process to facilitate landscape connectivity, conservation effectiveness, and ecosystem resilience from a network perspective (An et al., 2021; Fan et al., 2022), which is imperative to promote ecosystem health and ecological processes such as species movement to further safeguard biodiversity and enhance ecosystem services.

Previous studies often emphasize the importance of large-scale conservation and restoration, leading to neglecting the potential of small-scale conservation and restoration, which can not only serve as habitats but also increase connectivity of larger patches (Volencic & Dobson, 2020). Barriers and stepping stones are typically small-scale areas of ESPs and are easily disturbed, which are also crucial network elements that directly affect connectivity and facilitate the successful probability of dispersal among isolated ecological sources, in addition to ecological corridors (Herrera et al., 2017; Peng, Yang, et al., 2018), requiring focal conservation and restoration. Yet there is a lack of comparative research on enhancing landscape connectivity by barriers restoration and stepping stones to optimize ESPs. Barriers are the most effective areas where restoration can reduce ecological resistance and enhance landscape connectivity between ecological sources (Branco et al., 2014; Peng, Yang, et al., 2018). Most existing studies only propose that barriers should be regarded as restoration priority areas (Peng, Yang, et al., 2018), but there are few studies on the quantitative evaluation of barriers restoration effects (Fan et al., 2022). Stepping stones are resting places for long-distance migratory species, such as small green patches (Herrera et al., 2017; Mueller et al., 2014; Wu et al., 2022). Different from barriers, the land use type of stepping stones is mainly natural land. The research that quantitatively analyzed the connectivity relationship between stepping stones and ecological sources and screened stepping stone establishment approaches is insufficient (Dickson et al., 2019; Wimberly et al., 2018). Enhancing landscape connectivity through network-based approaches sustains ecological processes and is crucial to maintaining biodiversity and ecosystem functions (Hartfelder et al., 2020; Herrera et al., 2017; Poli et al., 2020). Therefore, it is necessary to identify critical ecological conservation and restoration areas, and compare the enhancement effects of landscape connectivity using different ESP optimization approaches, i.e. barriers restoration and stepping stones.

Dongting Lake Basin has rich biodiversity and important ecosystem services, which is of vital importance in maintaining ecological security in the Yangtze River Basin, but ecological degradation and landscape fragmentation have gradually intensified (Ning & Ouyang, 2023; Zheng et al., 2023). The scientific questions of this study were as follows: how

can small-scale conservation and restoration contribute to the enhancement of landscape connectivity? What is the most effective way to enhance landscape connectivity in barrier restoration and stepping stone establishment? The main objectives of this study were to: (1) construct a watershed ESP to identify ecological sources and ecological corridors; (2) optimize ESP through small-scale barriers restoration and stepping stones establishment; and (3) evaluate the effects of different optimization schemes on landscape connectivity to identify the optimal scheme of ESP optimization.

2. Materials and methods

2.1. Study area and data source

Located in south-central China, Dongting Lake Basin has a total area of approximately 26×10^4 km², the western region is mountainous, the south-central region is the hilly basin, the northeastern region is plain and the overall terrain is concave (Fig. 1). Dongting Lake is the second largest freshwater lake in China and the most important wintering ground for migratory birds in the middle and lower reaches of the Yangtze River (Cao et al., 2008). The surrounding wetlands and other natural ecosystems provide important and suitable habitats for species (Zhang et al., 2023). Dongting Lake Basin has rich biodiversity and provides prominent ecosystem services such as food supply, habitat maintenance, and water conservation. However, the increasing landscape fragmentation leads to declined ecosystem services, longer movement and greater resistance, further isolating habitats, and hindering species movement, information flow, and other ecological processes (Haddad et al., 2015; Ning & Ouyang, 2023). Therefore, approaches to enhance landscape connectivity are urgently needed to facilitate ecological processes.

The following datasets were used in this study: (1) land use data for 2018 with spatial resolution of 30 m was obtained from Resource and Environment Science and Data Center (<https://www.resdc.cn/>); (2) digital elevation model (DEM) with spatial resolution of 30 m was downloaded from Geospatial Data Cloud (<https://www.gscloud.cn/>); (3) precipitation data for 2018 was obtained from National Meteorological Information Center (<http://data.cma.cn/>), and 67 meteorological stations in Dongting Lake Basin and its surroundings were selected; (4) evaporation data for 2018 with spatial resolution of 500 m (MOD16A3) was downloaded from NASA-Earth data platform (<https://search.earthdata.nasa.gov/>); (5) normalized difference vegetation index (MOD13A3 NDVI raster data products) for 2018 with spatial resolution of 1 km was obtained from NASA-Earth data platform (<https://search.earthdata.nasa.gov/>); (6) net primary production (MOD17A3 NPP raster data products) with spatial resolution of 500 m was obtained from NASA-Earth data platform (<https://search.earthdata.nasa.gov/>); (7) soil data with spatial resolution of 1 km was derived from the Harmonized World Soil Database provided by Food and Agriculture Organization of the United Nations (<https://www.fao.org/>); (8) road data for 2018 was derived from OpenStreetMap (<http://download.geo.fabrik.de/asia.html>); and (9) protected areas were obtained from World Database on Protected Areas (<https://www.protectedplanet.net/en>) and Resources and Environment Science and Data Center (<http://www.resdc.cn/>). All the data were resampled to spatial resolution of 500 m.

2.2. ESP construction

The purpose of constructing ESP is to conserve biodiversity and enhance ecosystem services in order to ensure ecological security. Priority conservation areas are called upon to strengthen ecosystem service (Zeng et al., 2022). Ecosystem services are an increasingly popular policy framework for connecting ecosystem with human well-being (Peng et al., 2023). Previous studies have shown good spatial consistency between ecosystem regulation services and biodiversity (Le

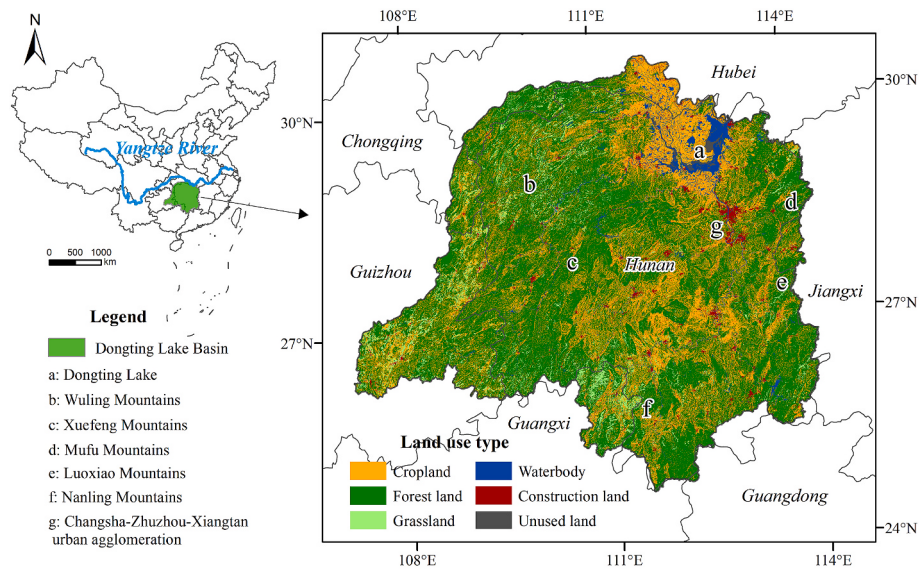


Fig. 1. Geographical location and land use type of the study area.

Provost et al., 2023; Ricketts et al., 2016). Protected areas are effectively managed areas established to preserve the natural environment, ecosystems, and biodiversity (Brodie et al., 2023). Therefore, ecological sources were identified by combining ecosystem services and protected areas (Ding et al., 2024; Jiang et al., 2022; Tang et al., 2023). According to the natural background characteristics of the Dongting Lake Basin and previous studies, four ecosystem services including habitat maintenance, carbon sequestration, water conservation, and soil retention were selected (Jiang et al., 2022; Ning & Ouyang, 2023; Peng, Yang, et al., 2018). The reasons and evaluation methods were as follows.

Habitat maintenance is the ability of an ecosystem to provide a suitable environment for species, and the Dongting Lake Basin had rich biodiversity, which was assessed using the Habitat Quality module of the InVEST model (Ren et al., 2022; Sharp et al., 2018). Carbon sequestration is a key service in mitigating climate change, which was calculated using the Carbon module of the InVEST model and corrected with net primary production (Jiang et al., 2021; Lal, 2004; Sharp et al., 2018). Dongting Lake Basin is an important area for water resources protection and conservation, and water conservation was assessed using the general water balance equation (Fewkes, 2000; Ouyang et al., 2016). Preventing soil erosion to maintain soil fertility needs to be a key focus in the Dongting Lake Basin, where there are abundant agricultural supplies and rich water resources, and soil retention was calculated by the revised universal soil loss equation (Gaubert et al., 2017; Ouyang et al., 2016). After standardizing the above four ecosystem services, equal weights were assigned to quantify comprehensive ecosystem services. Detailed formulas can be found in the Supplementary Information.

Considering the landscape multifunctionality and the irreplaceability of single ecosystem services, the union of the top 20% of comprehensive ecosystem services and the top 10% of each ecosystem service was used to identify the high ecosystem service area (Liu et al., 2024; Tang et al., 2023). Due to the low ecological value of fragmented landscapes, which are not conducive to the maintenance of biodiversity, patches less than 60 km² were removed considering the relationship between the minimum area threshold and the number and area proportion of patches (Jiang et al., 2021) (the relationship and removed patches were shown in Supplementary Fig. S1 and Fig. S2). Then, for aggregated patches within 1 km, a minimum hole of 5 km² was set, and protected areas were overlaid to obtain ecological sources.

Certain forms of landscape resistance need to be overcome in the process of ecological flow such as species movement. Ecological resistance surface is the basis of ecological corridor extraction. The

ecological flow process is not only related to land use type, but also affected by various factors such as NDVI, topography (slope and relief), and human activities (distance to the railways, motorways, and other main roads) (Brennan et al., 2022; Li et al., 2022). Therefore, ecological resistance was assigned by combining the above natural and social factors. The indicator selection and resistance value assignment referred to related researches (Jiang et al., 2022; Sutcliffe et al., 2003), and the resistance range was [1, 500] (the detailed resistance value was shown in Supplementary Table S1).

The MCR model was used to identify ecological corridor direction to facilitate ecological process dispersal between landscape elements (Ding et al., 2023; Dong et al., 2020; McGuire et al., 2016). The MCR model calculates the cost of species movement from sources to destinations, reflects the potential possibility and directions of species movement, and extracts the low-resistance channels where adjacent ecological sources are easiest to connect as ecological corridors. For the ecological sources connected through ecological corridors, they are not only the service providing areas, but also the benefiting areas. Ecological corridors were extracted by the Linkage Mapper tool of ArcGIS 10.8 software, and the maximum number of connected nearest neighbors was set to 4 (Luo & Wu, 2021). The circuit model is widely used to identify ecological corridor range (Brennan et al., 2022; McRae & Beier, 2007; McRae et al., 2008), which regards ecological sources as circuit nodes, calculates the weighted resistance distance from each grid to the nearest ecological source, and limits the maximum cumulative weighted resistance threshold between ecological sources. The grids within the threshold are the ecological corridor range. Ecological corridors are regarded as conductive surfaces, and the cumulative cost-weighted distance is regarded as the resistance in the circuit branch. The formula is as follows:

$$MCR = f \min \sum_{j=n}^{i=m} D_{ij} \times R_i \quad (1)$$

$$I = \frac{V}{R_{eff}} \quad (2)$$

where MCR is the minimum cumulative resistance; f is the positive correlation function between MCR and ecological process; D_{ij} is the spatial distance from source i to target j ; and R_i is the resistance coefficient of landscape unit i to the movement of specific species. I is current, V is voltage and R_{eff} is the effective resistance.

2.3. ESP optimization

ESP was optimized using barriers restoration and stepping stones, by optimizing resistance surfaces and ecological sources (Fig. 2). Barriers are regarded as ecological restoration priority areas (Peng, Yang, et al., 2018), which can be identified by the Linkage Mapper tool of ArcGIS 10.8 software. The principle of barrier identification is as follows: set a mobile search window with a certain radius, and recalculate the minimum cumulative cost distance between ecological sources according to the new resistance surface constructed by the reduced resistance value assigned in the search window (McRae, 2012). By comparing the ratio of the minimum cost distance before and after barriers restoration, the enhancement effects of landscape connectivity after restoring specific nodes can be assessed (Branco et al., 2014). The larger the ratio, the higher the ecological restoration priority of the node. Using the natural breakpoint method, the barriers restoration priority was divided into five levels: the highest level, higher level, medium level, lower level and lowest level. Then, barriers were restored according to the following three schemes respectively: (1) barriers restored at the highest level and no less than 10 km²; (2) barriers restored at the highest or higher level and no less than 10 km²; and (3) barriers restored at the highest, higher or medium level and no less than 10 km². The restoration measure considered was to restore the non-natural land in the barriers to forest land, and the restored NDVI was set to the average NDVI of forest land (Fan et al., 2022). Finally, ecological corridors were re-extracted based on the new ecological resistance surface produced. The formula for calculating the minimum cost distance of barriers is as follows (McRae, 2012; McRae et al., 2012):

$$LCD' = CWD1_{MIN} + CWD2_{MIN} + L \times R' \quad (3)$$

where LCD' is the minimum cost distance of the best path between the patches passing through the focal grid after barrier removal; $CWDX_{MIN}$ is the minimum cumulative resistance value from patch X within the search window; L is the longest axis length of the search window; and R' is the resistance value of the feature replacing (or cutting through) the barrier.

Long corridors may be not efficient for species' movement and other ecological processes flow, therefore stepping stones should be available for species to rest or ecological processes to readjust and thus enhance source connectivity (Saura et al., 2014). ArcGIS 10.8 software was used to identify stepping stones. Firstly, the patches with land use types of forest land, grassland, and waterbody were extracted as natural patches. Secondly, the Spatial Join tool was used to identify natural patches that were not connected to ecological sources but intersected with ecological corridors. Thirdly, natural patches of less than 1 km² were removed (Luo

et al., 2020). Fourthly, stepping stones were identified according to the following three approaches, respectively: (1) near the midpoint (within 13 km, a clear demarcation) of longer corridors (longer than the average corridor length of 29.46 km), a total of 40 stepping stones were selected; (2) average comprehensive ecosystem service, and ensure that the number of stepping stones was consistent for comparative analysis, the top 40 natural patches were selected as stepping stones; and (3) betweenness centrality (formula see the Supplementary Information), the top 40 natural patches were selected as stepping stones. Finally, stepping stones were added to be new ecological sources, then ecological corridors were re-extracted to establish the dispersal relationships between previous ecological sources and stepping stones.

2.4. Landscape connectivity quantification

In this study, landscape connectivity was quantified from a network perspective consisting of source connectivity, corridor connectivity, and network connectivity (Fig. 2). In details, source connectivity focuses on the area and spatial location of ecological sources. Integral index of connectivity (IIC) and probability of connectivity (PC) (Mueller et al., 2014; Saura & Pascual-Hortal, 2007), are often used for characterizing source connectivity. Conefor Sensinode software (<http://www.conefor.org>) was used to calculate the IIC and PC. Since an ecological corridor is a connecting tool, the average length and average cumulative resistance were chosen to quantify corridor connectivity, focusing on the impact of ecological corridors on species dispersal, information flow, and other ecological processes. Network connectivity focuses on the spatial combination relationship of sources and corridors. Graph theory treats the study area as a graph surface connecting nodes via dispersal routes (Liu et al., 2024; Urban & Keitt, 2001), and the network analysis method is an effective tool for exploring the internal structure of ESPs. This study used graph theory and network analysis to evaluate network connectivity (Saura & Pascual-Hortal, 2007), including the network circuitry index (α), connection index (β), and network connectivity index (γ) (Cook, 2002; Wang, Wu, et al., 2021). The calculation formulas are as follows.

$$IIC = \frac{\sum_{i=1}^n \sum_{j=1}^n \frac{a_i a_j}{1 + n_{ij}}}{A_L^2} \quad (4)$$

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}}{A_L^2} \quad (5)$$

$$\alpha = \frac{l - n + 1}{2n - 5} \quad (6)$$

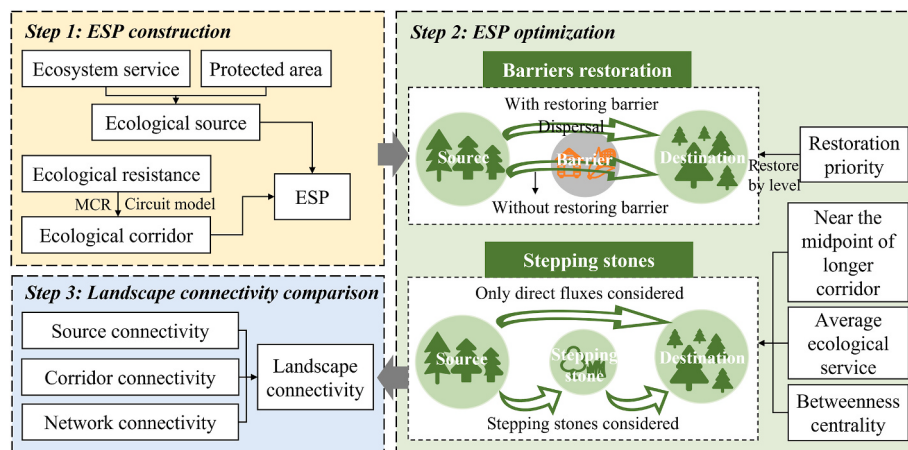


Fig. 2. Research framework of ESP construction and optimization (ESP: ecological security pattern; MCR: minimum cumulative resistance).

$$\beta = \frac{l}{n} \quad (7)$$

$$\gamma = \frac{l}{l_{\max}} = \frac{l}{3(n-2)} \quad (8)$$

where n is the total number of patches; a_i and a_j are the area of patch i and j , respectively; p_{ij} is the maximum product probability of all possible paths between patches i and j ; A_L is the total landscape area; nl_{ij} is the number of links in the shortest path (topological distance) between patches i and j ; l is the number of ecological corridors, with $l_{\max}$ for the maximum number of potential ecological corridors; α represents the degree of network circuitry, with its range of $[0, 1]$ and the closer the value is to 1, the more loops of the ecological corridor, and the stronger the material circulation and energy mobility; β represents the average number of corridors of a single ecological node, and $\beta < 1$ indicates a tree-like network, with $\beta = 1$ for a single loop network, and $\beta > 1$ for a complex network; and γ represents the degree of interconnection of all nodes in the network, with its range of $[0, 1]$, and the larger the value, the higher the connectivity of ecological nodes.

3. Results

3.1. Spatial distribution of ESP

The spatial patterns of habitat maintenance, carbon sequestration, water conservation, soil retention and comprehensive ecosystem service in Dongting Lake Basin are shown in Fig. 3. The low-value areas of habitat maintenance were mainly concentrated in the east of Dongting Lake Basin, especially the cropland around Dongting Lake. Carbon sequestration capacity was directly related to vegetation type and NPP, and low-value areas were mainly distributed in Dongting Lake, urban centers with low vegetation coverage, and cropland with low net primary productivity. The high-value areas of water conservation were mainly distributed in the northwest of Dongting Lake Basin, i.e. the northeast of Wuling Mountains and Xuefeng Mountains, which were significantly higher than other areas. The spatial distribution of soil retention was discrete, and the low-value areas were concentrated in Dongting Lake and its surrounding cropland. The comprehensive ecosystem service was high and contiguous in the forest land and grassland in the northwest, and low in the eastern cropland and urban centers.

A total of 81 ecological sources were identified, covering an area of 73146.93 km², accounting for 27.93% of the total area (Fig. 4). The land use type was mainly natural land, accounting for 85.76%, of which the largest proportion was forest land. Ecological sources were mainly concentrated in the northwest, scattered in the south, and less in the northeast. The ecological sources of the Wuling Mountains and Xuefeng Mountains in the northwest were highly contiguous and well connected. Ecological sources in the south were mainly located in the Nanling Mountains. Ecological sources of Changsha-Zhuzhou-Xiangtan urban agglomeration and its surrounding areas were fragmented, indicating that the ecological background in the eastern region was poor and human interference was strong.

The average ecological resistance in Dongting Lake Basin was 19.59. The overall resistance was higher in the east and lower in the west, because there was a lot of construction land and cropland in the east and forest land in the west. The high resistance was concentrated in Changsha-Zhuzhou-Xiangtan urban agglomeration and other urban centers. A total of 165 ecological corridors were extracted, with a total area of 27836.00 km², accounting for 10.62% of the total area, of which natural land accounted for 83.15%. The statistics of the length and resistance of the ecological corridors are shown in Supplementary Table S2. Ecological corridors in Dongting Lake Basin were mainly distributed in forests with high vegetation coverage, which generally avoided the areas with high resistance. The ecological corridor width in the red area with high current was narrow, and ecological corridors with low current were mainly located in Xuefeng Mountains. It is worth mentioning that the average length of the four ecological corridors connected to Dongting Lake (41.36 km) was about 1.40 times that of all ecological corridors (29.46 km), and the average resistance (1.53×10^5) was about twice that of all ecological corridors, indicating that species in Dongting Lake had longer dispersal distances and higher dispersal difficulty.

3.2. ESP optimization based on barriers restoration

The total area of barriers was 32046.25 km², mainly composed of forest land (62.59%), cropland (27.55%), and grassland (6.58%). The area of the highest level, higher level, medium level, lower level, and lowest level accounted for 1.69%, 5.23%, 16.48%, 35.74%, and 40.86%, respectively. The barriers with high priority and large areas were mainly distributed in the cropland between Datong Lake and Dongting Lake (Fig. 5). As shown in Table 1, the original α , β , and γ were 0.541, 2.037,

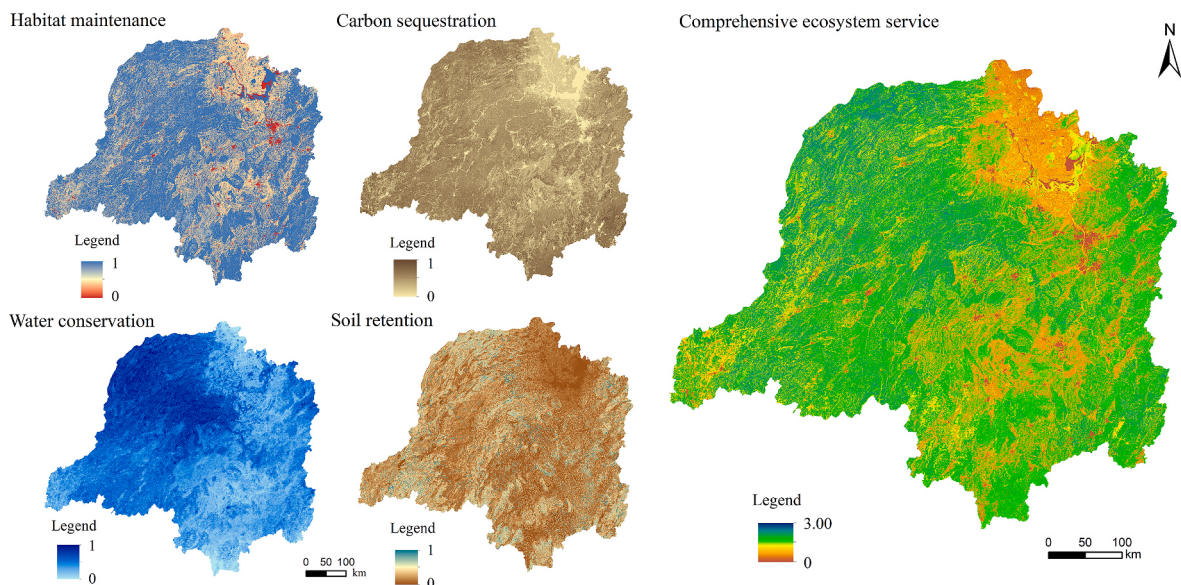


Fig. 3. Spatial patterns of ecosystem services in Dongting Lake Basin.

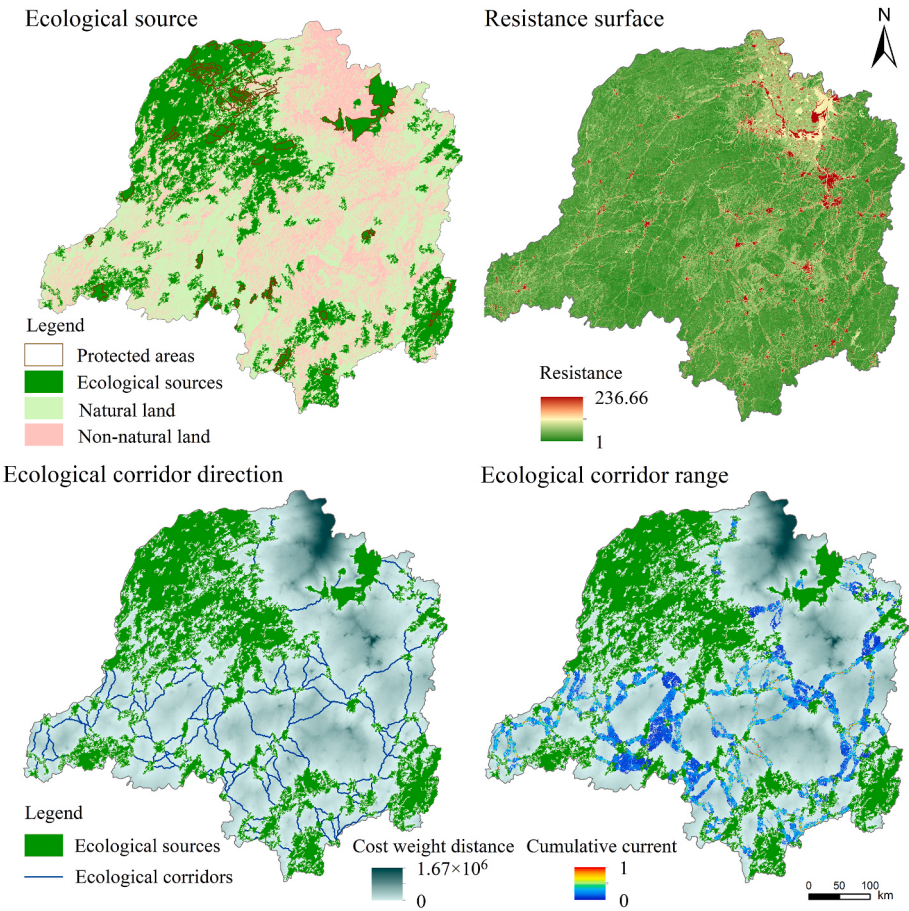


Fig. 4. Spatial patterns of ecological sources, resistance surfaces, and ecological corridors in Dongting Lake Basin.

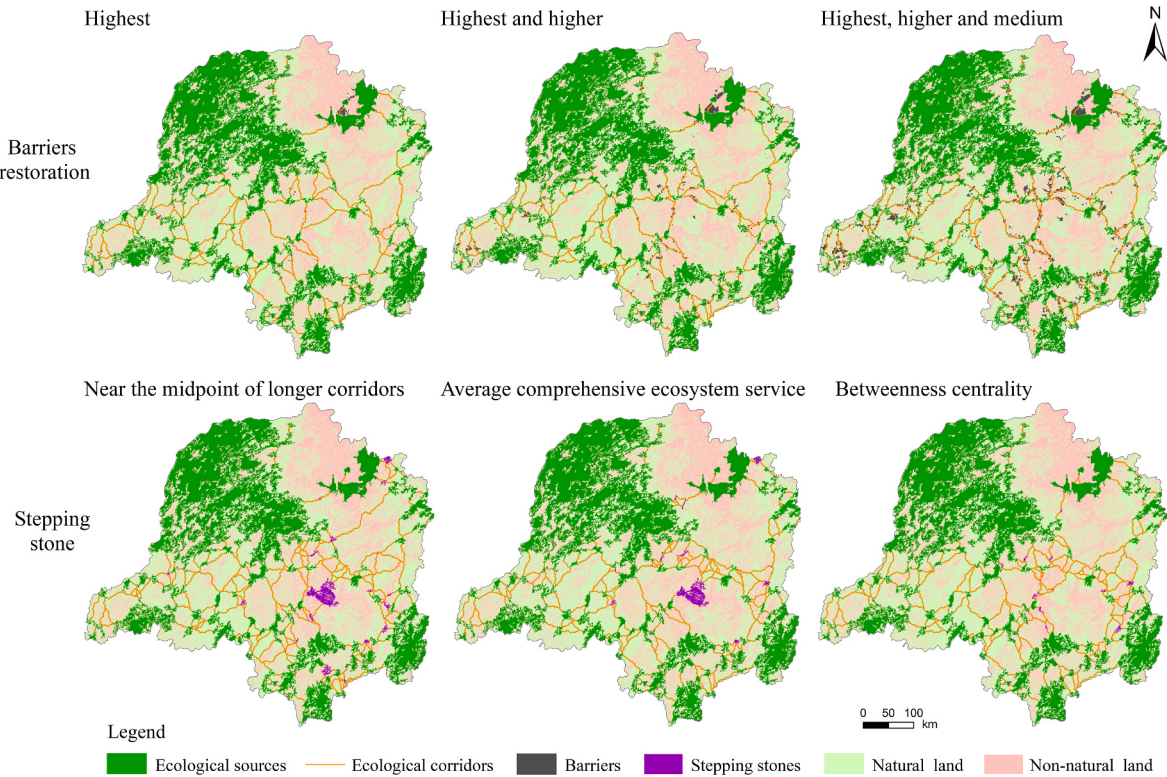


Fig. 5. Optimized ESPs based on barriers restoration and stepping stones.

Table 1

The enhancement in landscape connectivity.

Optimization approaches		Basic information of optimization		Source connectivity		Corridor connectivity		Network connectivity		
		Number	Area (km ²)	IIC	PC	Average length (km)	Average CWD (× 10 ⁴)	α	β	γ
Original network		–	–	0.043	0.057	29.46	15.25	0.541	2.037	0.696
Barriers restoration	Highest	8	367.25	0.043	0.057	29.33	14.70	0.535	2.025	0.692
	Highest and higher	57	1760.50	0.043	0.057	28.69	13.47	0.529	2.012	0.688
	Highest, higher and medium	167	6051.25	0.043	0.057	27.50	11.71	0.503	1.963	0.671
	Average	–	–	0.043	0.057	28.51	13.29	0.522	2.000	0.684
Stepping stones	Near the midpoint of longer corridors	40	2346.75	0.046	0.069	24.16	12.89	0.570	2.107	0.714
	Average comprehensive ecosystem services	40	1913.62	0.045	0.060	22.03	11.61	0.532	2.033	0.689
	Betweenness centrality	40	495.25	0.043	0.058	23.86	12.56	0.536	2.041	0.692
	Average	–	–	0.045	0.062	23.35	12.35	0.546	2.060	0.698

(IIC: integral index of connectivity, PC: probability of connectivity, and CWD: cost weight distance).

and 0.696, respectively, indicating that the ecological corridor structure was relatively complex and there were numerous circuits. Fig. 5 shows the spatial distribution of ecological corridors after graded barriers restoration. Because barriers restoration only changed the resistance surface without changing habitats, habitat connectivity remained unchanged. In three barrier restoration schemes, the non-natural land area of barriers was 304.39 km², 1184.47 km², and 2979.65 km², respectively.

For the three barrier restoration schemes, the number of ecological corridors decreased from 165 to 164, 163, and 159, respectively. The ecological corridor average length decreased by 0.13 km, 0.77 km and 1.96 km, respectively. The average cumulative resistance of ecological corridors decreased by 3.61%, 11.67% and 23.21%, respectively. All indicated that corridor connectivity was gradually enhanced with the increase of restored area. For network connectivity, the α, β, and γ indices decreased when restoring barriers, and the degree of reduction was the strongest when restoring barriers at the highest, higher and medium levels, which was reduced to 0.503, 1.963, and 0.671, respectively. To compare the restoration efficiency, calculating the change rate of corridor connectivity and network connectivity when every 100 km² non-natural land was restored, the results showed that restoring barriers with the highest and higher levels could facilitate corridor connectivity better, and reduce network connectivity the least.

3.3. ESP optimization based on stepping stones

The distribution of stepping stones was relatively scattered (Fig. 5). The largest stepping stone was located in the mountainous area at the junction of Hengyang City and Shaoyang City. As shown in Table 1, in different stepping stones approaches, source connectivity index IIC and PC were all enhanced, of which near the midpoint of longer corridors had the most effective enhancement, from the original 0.043 and 0.057 to 0.046 and 0.069, respectively. The number of ecological corridors increased effectively from 165 to 255, 246, and 247 respectively, and the ecological corridor average length and average cumulative resistance decreased, indicating that the corridor connectivity was enhanced. Establishing stepping stones based on average comprehensive ecosystem services approach had the greatest enhancement of corridor connectivity, the average length of corridors was shortened by 7.43 km, and the average cumulative resistance of corridors was reduced to 76.13% of the original. The α, β, and γ indices were only increased in the first approach, which increased to 0.570, 2.107, and 0.714, respectively. This was mainly because there were ecological corridors passing through the rings, which made the rings smaller and species dispersal more convenient. In contrast, establishing stepping stone near the midpoint of longer corridors had the best optimization effects on the enhancement of landscape connectivity. Compared with the original ESP, PC increased by 21.05%, the average corridor length and corridor cumulative

resistance of corridor connectivity decreased by 17.99% and 15.48% respectively, and network circuitry index of network connectivity increased from 0.541 to 0.570.

3.4. Comparison of landscape connectivity enhancement

The averages of the three schemes of barriers restoration and stepping stones were calculated respectively, and then the two averages were compared. In terms of source connectivity enhancement, barriers restoration didn't work, and stepping stones approaches had a weak effect on IIC, increasing PC by 8.77% on average. In terms of corridor connectivity enhancement, the enhancement effect of barriers restoration was weak, the average length of corridors was shortened by only 3.22% and the average cumulative resistance of corridors was reduced by 12.85% on average. Stepping stones approaches had an effective connectivity enhancement, the average length of corridors was shortened by 20.74%, and the average cumulative resistance of corridors was reduced by 19.02%, effectively higher than those of barriers restoration approaches, which was about 6.44 times and 1.48 times that of the latter, respectively. The average enhancement effects of network connectivity of barriers restoration and stepping stones were both low (Table 1). Therefore, whether it was a source, corridor, or network connectivity enhancement, stepping stones approach performed better than barriers restoration approach.

4. Discussion

4.1. Importance of small-scale ecological conservation and restoration

With social and economic development, land use conflicts are becoming more and more serious, and effectively enhancing landscape connectivity with limited ecological area has gradually become an effective measure to ensure regional ecological processes and security (Herrera et al., 2017; Puri et al., 2022). Maximizing the benefits at a lower cost of ecological protection and restoration will help the implementation of ecological protection and restoration projects and the realization of sustainable development goals (Dong et al., 2021; Strassburg et al., 2019, 2020). Spatial connectivity is regarded as one of the ten key issues of ecological restoration of territorial space, both large and small patches play important and complementary roles (Peng, Xu, et al., 2024). We found that the average area of ecological sources (903.05 km²) was about 25 times that of barriers and stepping stones (36.75 km²). This may lead to neglect of the importance of small-area conservation and restoration, because larger ecological sources provide the majority of habitats. Volenec and Dobson (2020) found that more than half of global protected areas were less than 100 ha and the median size of added protected areas had continued to decrease over the past 60 years. Small protected areas can not only serve as habitats, but

also enhance the landscape connectivity of large protected areas (Volenc and Dobson, 2020).

Key areas of barrier restoration and stepping stone establishment provide effective approaches to small-scale ecological conservation and restoration and ESP optimization. For example, Fan et al. (2022) proposed to optimize urban ecological space by increasing ecological sources, complicating circle structures, and restoring ecological barriers. Sutcliffe et al. (2003) found that different farmland restoration measures had different potential effects on butterfly movement, indicating that it was necessary to explore the impact of restoring resistance surfaces based on land use type. Luo et al. (2020) compared the impacts of different stepping stone removal approaches on network robustness and found that stepping stones with high centrality were of great significance in maintaining source connectivity. da Rocha et al. (2021) compared the impact of small patches and scattered trees on the success rate of species dispersal and reported that scattered trees had a positive effect while small patches had a negative effect (i.e. ecological traps). The above studies indicate that small critical areas should be included in conservation planning and there is an urgent need to explore the optimal barriers restoration and stepping stones establishment approaches for enhancing landscape connectivity. We found that the average of six schemes only protected and repaired less than 1% of the total area, which could enhance corridor connectivity by about 12% and 16% in average corridor length and corridor cumulative resistance respectively, further confirming the importance of small-scale conservation and restoration.

4.2. Connectivity enhancement differences between barriers restoration and stepping stones

Well-connected conservation priority areas can enhance biodiversity persistence, which has been emphasized in relevant policy targets, such as the Kunming-Montreal Global Biodiversity Framework (CBD, 2022; Magris et al., 2018). Barriers restoration removes barriers in ecological corridors by restoring resistance surfaces, and establishing stepping stones networks shortens one-way ecological corridors by adding new ecological sources, both of which are pivotal approaches to enhance landscape connectivity (Herrera et al., 2017; Mueller et al., 2014; Wimberly et al., 2018). Cost-effective is vital for prioritizing different scenarios. When comparing the investment cost and the optimization effect, on one hand, the investment cost of established stepping stones with all-natural land was lower than that of restoring barriers, because barriers covered a high proportion of non-natural land, especially cropland, posing a threat to food security, while stepping stones involved fewer land use conflicts and were more feasible to implement. On the other hand, stepping stones outperformed barriers restoration in enhancing landscape connectivity. In contrast, the stepping stones network was more effective for ESP optimization.

What needs further explanation is that, in the optimization scheme of barriers restoration, the reason for the reduction of network connectivity was that the reduction of resistance led to some corridors being merged and a reduction in the number of corridors, indicating that some redundant corridors were removed. The removal of redundant corridors had little impact on network function (Luo & Wu, 2021). In the optimization scheme of stepping stones, network connectivity was enhanced only in the first scheme, while in the other two schemes it was both reduced, indicating that the latter two schemes caused some regional node redundancy (Wang et al., 2021) and might instead form ecological traps, which mistakenly lead animals to dead-end routes and prevent species from reaching more habitat patches through leading animals into new but unsuitable places (da Rocha et al., 2021; Pe'er & Kramer-Schadt, 2008).

4.3. Limitations and future research directions

There were also some shortcomings. Firstly, barriers and stepping

stones were distributed within ecological corridors, and more approaches for identifying ecological protection and restoration priority areas need to be further explored. Secondly, the difference between watershed ESP and ESP at national, regional or city scales is that the former focuses more on holistic, systematic, and integrated management of ecosystem. The purpose of constructing and optimizing watershed ESP is to maintain ecosystem functions and services, safeguard biodiversity, and enhance the connectivity and resilience of the watershed ecosystem. As a result, ESP was constructed only within the basin without considering its surrounding environment. However, the ecological process is not limited by the basin boundary (Liu et al., 2024). Thirdly, the stability and effectiveness of the ESP need to be verified. Sensitivity analysis can be explored in future research, such as comparing the impact of different approaches of ecological source identification and different ecological resistance surface construction. Lastly, the combination of barriers restoration and stepping stone establishment can be explored to obtain a better optimization scheme in the future.

5. Conclusions

Enhancing watershed landscape connectivity is conducive to promoting ecological processes and ecological security. Existing studies ignored the importance of conservation and restoration of small-scale areas, and lacked comparative studies on the enhancement effects of barriers restoration and stepping stones establishment on landscape connectivity. This study aimed to quantify the effect of optimizing small critical areas, specifically barriers and stepping stones, on landscape connectivity from a network perspective. The results showed that the average of six schemes only protected and repaired less than 1% of the total area, which could enhance corridor connectivity by decreasing about 12% average corridor length and 16% corridor cumulative resistance. This indicates ESP optimization by small-scale barriers restoration and stepping stones establishment can effectively reduce landscape fragmentation. Comparing the two optimization approaches, stepping stones establishment had lower cost and higher enhancement effects of landscape connectivity than barriers restoration. In barriers restoration schemes, redundant corridors were reduced and connectivity enhancement effects were optimal when restoring the highest and higher level barriers. In stepping stones schemes, establishing natural patches near the midpoint of longer corridors as stepping stones avoided ecological traps and enhanced landscape connectivity best. Compared with the original ESP, the best approach increased PC index by 21.05%, reduced the average corridor length and corridor cumulative resistance of corridor connectivity by 17.99% and 15.48% respectively, and increased network circuitry index of network connectivity from 0.541 to 0.570. In a nutshell, future planning for enhancing landscape connectivity should strengthen attention to the conservation and restoration of small patches, especially the natural patches near the midpoint of longer corridors. This study provides quantitative evidence that ecosystem conservation and restoration of crucial small-scale areas in ESPs can effectively facilitate ecological processes between isolated landscapes from a network perspective.

Data availability

Data will be made available on request.

CRediT authorship contribution statement

Dongmei Xu: Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation, Conceptualization. **Jian Peng:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Hong Jiang:** Writing – review & editing, Methodology, Conceptualization. **Jianquan Dong:** Writing – review & editing, Methodology, Conceptualization. **Menglin Liu:** Writing – review &

editing, Methodology, Conceptualization. **Yiyun Chen**: Writing – review & editing. **Jiansheng Wu**: Writing – review & editing. **Jeroen Meersmans**: 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 information

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