





Long-Distance Corridors Facilitate Asian Elephant Adaptation to Climate Change

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ABSTRACT

Amid ongoing habitat degradation and fragmentation, along with the disruption of traditional moving routes, the Kunming-Montreal Global Biodiversity Framework underscores the urgent need to enhance species connectivity to improve their adaptability to climate change. Recent instances of long-distance movements by Asian elephants (Elephas maximus) have raised concerns about the potential for such events to become more frequent under future climate scenarios. A landscape adaptation strategy is urgently needed to improve the connectivity and integrity of Asian elephant habitats to meet their long-distance movement requirements. However, large-scale ecological networks for Asian elephants that incorporate long-distance corridors remain lacking. This study employs species distribution models and minimum resistance models to construct current and future multi-scenario ecological networks, aiming to elucidate key features of climate adaptability and priority corridor strategies for Asian elephants. Our findings indicate that long-distance corridors identified under future climate scenarios play an integral part in maintaining connectivity within the priority network. The study identifies 162 priority long-distance corridors, accounting for 25.5% of the overall network, whose lengths and importance are expected to increase. Additionally, 37.2% of these priority corridors pass through protected areas, providing guidance for optimizing existing reserves and addressing conservation gaps that cover 61.2% of the study area. The study highlights the need for habitat conservation strategies for Asian elephants to fully consider the uncertainties of dynamic spatiotemporal changes. It emphasizes the global significance of macro-scale ecological network design and the critical role of constructing long-distance corridors. Furthermore, the integration of protected areas with long-distance ecological corridors is identified as a key measure to address future uncertainties and achieve lasting biodiversity conservation.

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Summary

Asian elephants are increasingly moving into areas with human activity, raising significant concerns about humanelephant conflict and related conservation challenges. These long-distance movements, combined with the impacts of future climate change, highlight the pressing need to upgrade habitat connectivity. While ecological networks are effective for habitat and species conservation, how to design long-distance corridors for Asian elephants in the context of changing climates remains unclear. In this study, we propose a macro-scale priority ecological network under multiple climate scenarios to improve the species' climate adaptability and inform conservation strategies. Our findings show that long-distance corridors are vital for connecting habitats and exhibit strong climate resilience. Over one-third of these corridors overlap existing protected areas, addressing 61.2% of conservation gaps and providing guidance for optimizing future conservation systems. Coordinating protected areas and long-distance corridors is key to ensuring biodiversity conservation amid future environmental uncertainties.

• Practitioner Points

- Asian elephant habitats are undergoing ongoing degradation, impacting connectivity and posing challenges to species conservation and survival.
- Under future climate change scenarios, differences in habitat quality may drive population shifts from lower to higher latitudes, affecting species distribution and adaptability.
- Long-distance ecological corridors are imperative for improving connectivity and climate resilience, highlighting their strategic importance in addressing future conservation challenges.

1 | Introduction

In May and June 2021, a herd of wild Asian elephants (Elephas maximus) left a low-altitude nature reserve in Xishuangbanna, Yunnan, China, and embarked on a long-distance journey, roaming over 500 kilometers northward and approaching the outskirts of the provincial capital, Kunming, which is situated at a much higher latitude (Campos-Arceiz et al. 2022). Although such long-distance movements have not always occurred, they are not unprecedented. Historically, Asian elephants ranged across higher-latitude regions, including extensive areas of West Asia and the plains of China (Sukumar 2003). However, habitat destruction and the rapid expansion of human activities have substantially reduced their geographical range, which is now restricted to 13 countries at lower latitudes (Sukumar 2006; Prakash et al. 2020). Furthermore, global warming is causing species to shift toward higher latitudes at an average rate of 16.9 km per decade (Chen et al. 2011). Large herbivores are particularly vulnerable, as vegetation changes drive their distribution patterns (Butt et al. 2015; van Beest et al. 2023). The potential for future longdistance movements of Asian elephants is a significant issue that warrants further investigation. However, our current understanding of this trend and strategies to mitigate the impacts of future climate change are insufficient.

Under the dual pressures of climate change and intensified human activities, Asian elephants face habitat degradation and fragmentation. Their traditional migration routes are increasingly disrupted (Luo et al. 2022; Torres et al. 2016; Hankinson et al. 2020), leading to significant and unavoidable consequences. First, connectivity between elephant populations is likely to weaken or even break, potentially accelerating population isolation (Hilty et al. 2020; Haddad et al. 2015). Such isolation can hinder gene flow, hastening the loss of genetic diversity and leading to population decline (Prugh et al. 2008). Furthermore, the inherent subjectivity in Asian elephants' spatial behavior means that their search for new habitats may become erratic, increasing the likelihood of human-elephant conflicts (Wall et al. 2021; Goswami et al. 2015; Sukumar 1989). If not addressed, these ongoing changes will exacerbate the complexity of human-elephant coexistence (Simkin et al. 2022). Previous studies have indicated that other large vertebrate species are also likely to seek new habitats or food sources when faced with climate change and human-induced habitat destruction (Shen 2020). In response to this concerning outlook, the Kunming-Montreal Global Biodiversity Framework emphasizes the importance of strengthening habitat connectivity and integrity for all species. One study suggests that large-scale elephant migrations between southern and northern China likely occurred repeatedly with cyclical climatic variations (Wang et al. 2021). This situation necessitates the immediate development of a practical strategy for conserving Asian elephant habitats to support gene flow among populations and mitigate the unpredictability and potential conflicts associated with changes in their movement patterns due to climate change (Synes et al. 2020).

The construction of ecological networks centered around charismatic species has emerged as a viable spatial planning approach and a powerful tool for enhancing habitat connectivity (Keeley et al. 2019). However, past research has often been confined to smaller regional scales, primarily focusing on the connectivity of potential habitats for Asian elephants within national or localized areas (Kanagaraj et al. 2019). These studies have provided valuable insights into identifying key resource patches and quantifying landscape connectivity (Liu et al. 2018; Suksavate et al. 2019). Given that Asian elephants can disperse over distances ranging from 30 to 300 km—and up to 500 km for the northward-moving herds studying larger-scale ecological corridors is essential to accommodate potential long-distance migrations (Wang et al. 2021; Fernando et al. 2008). Long-distance corridors are pivotal components of large-scale conservation networks (Dutta et al. 2016), as they maintain connectivity and enable long-range dispersal, making them a key focus in conservation planning (Keeley et al. 2016). Due to the complexity and uncertainty associated with future climate change, there is an urgent need to develop extensive climate-adaptive ecological networks. Such networks not only address the current gap in long-distance corridors but also provide a comprehensive framework for future climate adaptation strategies. Additionally, as a charismatic species with a strong umbrella effect, Asian elephants can attract increased financial support and public engagement for ecological network construction (Keeley et al. 2019). This approach aids in conserving Asian elephants and also enhances pathways for material and energy

flow, supporting broader biodiversity conservation and climate resilience (Stewart et al. 2019; Krogman 2020).

This study addresses the anticipated long-distance movement requirements of Asian elephants in response to future climate change. It involves constructing and assessing an ecological network to facilitate these movements while also considering the impacts of changing climate conditions. The objectives of this research are (1) to identify the characteristics of core ecological source areas for Asian elephants by modeling their habitat distribution using presence data and machine learning models; (2) to construct and assess ecological corridors for Asian elephants, with a particular focus on analyzing the importance and connectivity of long-distance corridors; and (3) to optimize the ecological network based on integrated multiscenario landscape features, thereby developing a climateadaptive priority conservation network. Importantly, this study anticipates future scenarios, offering theoretical support and solutions to address potential challenges and uncertainties. The findings can serve as a scientific reference for conservation decision-making and management of other large mammals with ecological needs similar to those of Asian elephants, offering practical management strategies for adaptive conservation at regional and national levels.

2 | Materials and Methods

2.1 | Study Area and Scenario

The study area (33°17′19" N-1°26′08" N, 68°16′28"-109°46′02" E) encompasses ten land-connected countries in South and Southeast Asia where Asian elephants are frequently active, including India, Thailand, and China (specifically Yunnan Province) (Figure 1). This region is characterized by complex terrain, with elevation differences reaching up to 8000 m. The climate is predominantly tropical rainforest and tropical monsoon, with significant temporal and spatial variability in temperature and precipitation. The average annual temperature is 24°C, and the average annual precipitation is 257 mm (WorldClim Bio1 and Bio12 datasets). Additionally, the study area boasts extensive forest coverage and diverse vegetation types. Despite this, frequent land use changes and selective logging under the economically driven development model have led to the fragmentation and degradation of natural habitats (Edwards et al. 2014). The region has long been recognized as a hotspot for global biodiversity conservation (cop15 2024). However, increasing rates of forest degradation and habitat fragmentation (Ma et al. 2023) pose significant challenges to the conservation of elephant habitats (Luo et al. 2022), emphasizing the need for improved conservation efforts.

The study uses 2015 as the baseline year, with projections made for 2030 and 2050. The climate models selected are the key scenarios recommended in the latest global climate research from the Coupled Model Intercomparison Project Phase 6 (CMIP6). CMIP6 introduces the scientific integration of Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs), which collectively account for the socioeconomic impacts on emission scenarios (Riahi et al. 2017). Accordingly, the study adopts the recommended coupled scenarios: SSP1-RCP2.6, SSP2-

RCP4.5, SSP3-RCP7.0, and SSP5-RCP8.5. These scenarios are among the most commonly used and widely studied (O'Neill et al. 2016; Eyring et al. 2016). They represent a broad range of potential futures, factoring in uncertainties related to socioeconomic and climate scenarios, and ranging from low and medium concentration pathways that involve climate policy interventions to medium and high concentration pathways without such interventions (Details of these scenarios are provided in Supporting Information S1: Table SI-1).

2.2 | Framework Overview

This study examines the construction of a large-scale ecological network for Asian elephants at the landscape level, which incorporates long-distance ecological corridors (Figure 2). These corridors are categorized as long-distance corridors (over 50 km) and ultra-long-distance corridors (over 100 km). The network is developed based on a comprehensive ecological network construction paradigm, focusing on three key components: ecological source selection, ecological resistance surface construction, and ecological corridor extraction. This approach aims to better align with future conservation goals.

The study employs the MaxEnt model for ecological source selection, using the resulting habitat suitability index to identify ecological source areas and resistance surfaces, with the resistance surface incorporating negative exponential functions. Furthermore, the study combines the minimum cumulative resistance (MCR) model with circuit theory to extract ecological corridors and critical nodes for Asian elephants.

Subsequently, the source areas and corridors are analyzed to determine their functional characteristics. Finally, by overlaying the ecological source areas, the study identifies priority sources that remain functionally and spatially stable, as well as high-priority corridors with a high comprehensive ranking, forming a priority network for Asian elephants.

2.3 | Data Sources and Pretreatment

2.3.1 | Species Occupation Data

The species distribution data used in this study comprise two sources: data from the Global Biodiversity Information Facility (GBIF) and field monitoring data. GBIF is the largest and most influential open-access biodiversity information network globally, and its data reliability has been recognized in numerous studies. However, there are fewer records of the increasing Asian elephant population in China (Luo et al. 2021). To supplement this, the study incorporated site information from infrared camera observations conducted over the past decade by the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences.

The study area included 1411 unique data points from GBIF and 1577 infrared monitoring points from XTBG. Since these data points do not reflect actual population sizes, the significant difference in data quantity could affect the Maxent model's habitat gain results or introduce sampling bias into the algorithm. To ensure data

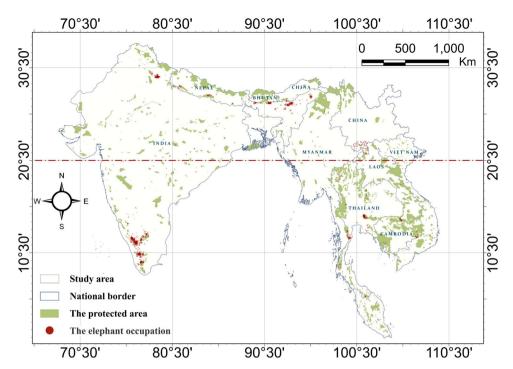


FIGURE 1 | Geographic overview of the study area. The red dashed line indicates the division of the study area into northern and southern parts along the latitude of 20°30′ N.

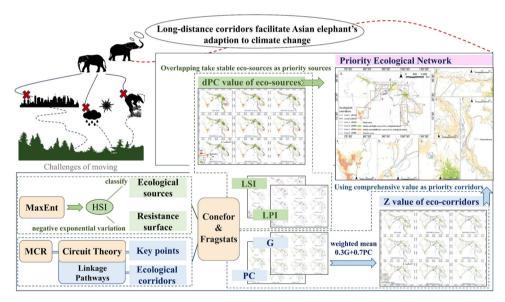


FIGURE 2 | Study framework. The diagram in the upper left corner illustrates the challenges faced by Asian elephants due to human activities, climate change, and human-elephant conflicts, which hinder their movement (black lines: solid lines indicate usable movement paths, while dashed lines represent potential movement paths). As a result of these influences, the elephants divert their movement, seeking distant areas with better habitats. The red dashed lines indicate potential long-distance ecological corridors, illustrating the priority ecological network identified in the study. dPC, distance to protected area centroid; G, value of gravity model; HIS, habitat suitability index; LPI, landscape permeability index; LSI, landscape shape index; MCR, minimum connected resistance; PC, patch core area; Z, composite weighted value.

reliability, a preliminary validation was conducted using the species distribution range provided by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (http://www.iucnredlist.org/). Data points outside this range were excluded as an initial validation step.

To further reduce the impact of spatial autocorrelation caused by data concentration, the following pre-processing steps were performed: (1) Removing blank values and other invalid data, such as geographic information with a value of 0 or repeatedly invalid entries, before inputting the data into the model; (2) Randomly reducing data points in high-density areas (Yunnan, southern India) to match Asian elephant population trends in existing distribution areas (IUCN 2019). Ultimately, a total of 1324 valid data points characterized by completeness and representativeness were obtained for model input, including 54

from China, 149 from Thailand, and 802 from India (Supporting Information S1: Table SI-2).

2.3.2 | Environmental Data

The study uses bioclimatic and human activity data to reflect dynamic changes across future scenarios. It investigates the key environmental variables affecting the distribution of Asian elephants, including topography, vegetation, and foraging resources (Neupane et al. 2022), considering 28 environmental factors. Since the impact of human activities on sustainable development is mainly reflected in land use (Busch and Reisch 2016), human disturbance factors in this study are primarily represented by land use patterns.

Given the distribution correlations among these predictor variables (Kassambara 2020), it is essential to minimize collinearity within the MaxEnt model (Merow et al. 2013). Therefore, IBM SPSS 23.0 was used to calculate Pearson correlation coefficients (Mi et al. 2023) (Supporting Information S1: Table SI–3) to reduce the impact of multicollinearity on the accuracy of the simulation results. This approach ensures that the most significant factors are retained while highly correlated variables are excluded (Sheppard 2013). Specifically, variables with a high correlation coefficient (|r| > 0.85) were removed, retaining only one variable from each correlated group.

Ultimately, 23 environmental factors representing the habitat preferences of Asian elephants were selected as modeling variables (Supporting Information S1: Table SI-4). The analysis revealed that climate change is the primary driver, with climate-related factors contributing significantly to the simulation results (Table SI-5).

2.4 | Identification of Ecological Sources and Ecological Corridors

2.4.1 | Ecological Source Identification and Resistance Surface

This study utilized habitat suitability modeling to determine preliminary ecological sources and conducted area screening based on the minimum habitat range. The MaxEnt model was employed to assess the habitat suitability of Asian elephants (Yang et al. 2021). The MaxEnt model is a machine learning tool commonly used for species distribution modeling (SDM) (Phillips et al. 2017), with the advantage of providing accurate predictions using only presence data. Its effectiveness has been demonstrated in numerous studies (Pearson et al. 2007; Qin et al. 2020; Zahoor et al. 2022). More importantly, the combination of MaxEnt and connectivity models has shown optimal performance in corridor construction (Poor et al. 2012). The model parameters were adjusted according to the study Huang et al (Huang et al. 2020)., while other parameters were set to their default values. The model's performance was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) (Phillips and Dudík 2008). AUC values between 0.7 and 0.9 indicate that the model is acceptable or highly accurate (Swets 1988). The fitting results of the study showed high accuracy, with an average AUC value of 0.9 (minimum 0.8945, maximum 0.9041) (Supporting Information S1: Table SI-6).

Using ArcGIS, the MaxEnt model output for each scenario was classified into five levels of habitat suitability for Asian elephants based on distribution probability. These levels were categorized as follows: Level 1 (< minimum training threshold [Supporting Information S1: Table SI-7]), Level 2 (< = 0.3), Level 3 (< = 0.5), Level 4 (< = 0.75), and Level 5 (> 0.75).

Considering the strong adaptability and capability of Asian elephants to modify their ecological environment (Madhusudan et al. 2015), this study selected areas with a habitat suitability index (HIS) of 0.3 and above (i.e., Levels 3, 4, and 5) as the basis for ecological sources. Subsequently, the area screening process removed regions smaller than the minimum home range of 100 km² (DESAI 1991), resulting in final ecological source maps across multiple scenarios.

The resistance values were determined based on the negative exponential relationship between the values obtained from the MaxEnt model and the ecological resistance, producing the Asian elephant ecological resistance map (Qian et al. 2023; Duflot et al. 2018). Models for identifying long-distance movement areas often rely on estimates of landscape resistance, which are typically derived from habitat suitability. Therefore, SDM's performance is generally sufficient for resistance estimation (Zeller et al. 2018). Additionally, considering the wideranging activity patterns of Asian elephants, the use of a negative exponential function enhances the flexibility of long-distance corridor placement (Keeley et al. 2016). Accordingly, the habitat suitability results were converted into resistance surfaces using a negative exponential function.

2.4.2 | Identification of Important Nodes and Ecological Corridors

The study used circuit theory and the MCR model to identify ecological corridors and nodes. This combination is a recommended and experimentally validated approach, with circuit theory widely recognized for its superior performance in corridor construction (Zeller et al. 2018). The Linkage Mapper tool, which integrates MCR and circuit theory models, was employed to extract corridors and nodes and to map the corridor boundaries (Keeley et al. 2016; Wang et al. 2008). The Linkage Pathways module in Linkage Mapper was used to identify ecological corridors. This module extracts the least-cost paths based on the MCR model, which are considered the most influential ecological corridors for species dispersal across heterogeneous landscapes (Chen et al. 2023).

The study expanded its analysis by assessing the necessary width of ecological corridors for Asian elephants. Circuit theory modeling was used to estimate current density and define corridor boundaries, where higher current density values indicate stronger connectivity. After multiple iterations, it was found

that when the cumulative resistance threshold was set at 200 K, the corridor widths varied mainly between 1 and 10 km—sufficient to accommodate the movement of Asian elephants (Johnsingh and Williams 1999).

Finally, the study mapped the spatial distribution of ecological pinch points and barriers within the corridors that significantly impact connectivity. Ecological pinch points are critical nodes that facilitate connections between ecological sources (Dai et al. 2021), while ecological barriers hinder species migration. Removing or restoring these barriers can reduce ecological resistance and improve connectivity (Peng et al. 2018). The pinch point mapping and barrier mapping modules in the Circuitscape toolbox were used to define ecological corridor boundaries, identify the locations of ecological pinch points, and detect the presence of ecological barriers.

2.5 | Ecological Network Analysis

2.5.1 | Ecological Source Assessment

Based on the filtered core habitats of Asian elephants, Confer software was used to calculate connectivity between ecological source areas and to evaluate and classify these sources according to their dPC values (Bodin and Saura 2010). The ecological source areas were ranked by dPC value from highest to lowest and evenly divided into five levels: Level 1 (> 40), Level 2 (30–40), Level 3 (20–30), Level 4 (10–20), and Level 5 (0–10). Level 5 represents the highest level of connectivity.

Additionally, Fragstats 4.2 was used to assess both the independent and interactive effects of these core habitats on ecological processes. The analysis of ecological sources was conducted at the class level, with patch shape complexity representing the land-scape configuration. The Largest Patch Index (LPI) and Landscape Shape Index (LSI) were used to evaluate the shape complexity of core habitats (Frazier and Kedron 2017). LPI measures the proportion of the largest habitat patch within the entire landscape, while LSI represents the geometric complexity of the overall core habitat. Together, these indices indicate whether habitat fragmentation is occurring. In future scenarios, an increase in LSI values combined with a decrease in LPI values suggests a higher risk of core habitat fragmentation.

2.5.2 | Corridor Network Assessment

For corridor assessment, our study focused on evaluating the importance and connectivity of ecological corridors separately. This helps prioritize conservation and restoration measures for connectivity (Chen et al. 2023). A gravity model was used to measure the strength of interactions between ecological sources and assess the importance of ecological corridors (Kong et al. 2010).

To analyze corridor connectivity, the Probability of Connectivity (PC) index was selected. This index, based on a probabilistic model and the concept of habitat availability, is calculated using Conefor software. It is an important indicator of landscape patterns and processes, illustrating the degree to which the

landscape supports or obstructs the movement of ecological elements (Pascual-Hortal and Saura 2006).

Subsequently, the importance and connectivity indicators were weighted to obtain a composite score (Z), with the connectivity indicator assigned a weight of 0.7 and the importance indicator a weight of 0.3. The weighted results were normalized for data visualization purposes.

In the analysis of barriers and pinch points, our study focused on identifying key areas and their ecological composition, which helps to improve the efficiency of ecological network protection (Xu et al. 2024). The top 20% of areas characterized by their significance as key barriers and pinch points were identified and extracted. Following this identification, the land use composition within these key areas was analyzed across various scenarios.

2.6 | Identifying Priority Areas for Ecological Conservation and Restoration

To identify priority areas within the ecological network that are adaptable to future climate change, priority ecological source areas were selected based on integrated spatiotemporal characteristics and all priority corridors across nine scenarios. The selection process for ecological source areas entailed overlaying regions from these nine different scenarios to distinguish between stable and unstable areas. Stable regions were classified into high-connectivity areas (dPC value > 30) and mediumto-low connectivity areas (dPC value \le 30). This classification helps to identify areas with the capacity to sustain ecological functions across diverse scenarios.

Given the unpredictability of future developments, corridor selection focused solely on temporal changes, ranking them based on their composite scores. Priority corridors, along with key ecological pinch points and barriers, were identified across all scenarios. The 2015 scenario served as the baseline for the study, and ecological sources were classified into three categories based on changes in connectivity levels and spatial distribution: (1) stable regions that maintain high connectivity, (2) stable regions that maintain medium-to-low connectivity, and (3) unstable regions.

Priority corridors for 2015, 2030, and 2050 were selected based on the top 30% of corridor composite scores, classified as level 1, and the next 30%–60% as level 2, with level 1 corridors representing higher quality. By integrating key ecological pinch points and barriers within these priority corridors, a complete ecological network for Asian elephants was established.

In the classification of ecological corridors, higher values consistently indicate higher levels of functionality, with level 1 denoting the highest level. These values include connectivity (PC), importance (G), and composite weighted results (Z). Finally, to further assess the effectiveness of protected areas for conserving Asian elephant ecological sources, the proportion of ecological sources that overlap with protected areas was calculated. This proportion serves as an indicator of the degree to which protected areas prioritize specific species, such as the Asian elephant.

3 | Results

3.1 | Changes in Connectivity Levels Caused by Fragmentation of Asian Elephant Ecological Patches

The findings of this study reveal significant future fragmentation and decline in ecological source areas for Asian elephants. Initially, 62 source areas covered $9.04 \times 10^5 \, \mathrm{km^2}$, with an average area of $0.15 \times 10^5 \, \mathrm{km^2}$ each. By 2030 and 2050, fragmentation increases the number of source areas to 83.4 and 72, respectively, while the total area shrinks by 38.0% and 53.9%. Under the extreme SSP5-8.5 climate scenario projected for 2050, the largest source area experiences a dramatic decline, shrinking by as much as 72.2% (Supporting Information S1: Table S1). Additionally, regions exhibiting high ecological resistance values were predominantly found in the northern mountainous areas and central India. Resistance values increase with the growing distance from ecological source areas (Figure 3).

The study area was divided into northern and southern regions using the latitude of $20^{\circ}30'$ as the dividing line (hereafter referred to as the northern/southern regions). The analysis highlights a significant difference in connectivity between the northern and southern habitats (Figure 3). The north region maintained a high level of connectivity, with an average dPC value of 39.5 ± 2.98 . Even under the extreme SSP5-8.5 scenario in 2030, the lowest connectivity level was 34.1. In contrast, the southern region showed a marked decline and fluctuation in connectivity levels in the future, with an average dPC value of 12.1 ± 6.20 (Supporting Information S1: Table S2).

Additionally, the LPI and LSI metrics were spatially consistent with the connectivity levels of the source areas. High (or low) LPI and LSI values correspond to landscape loss and fragmentation, directly influencing connectivity levels. The highest values for LPI and LSI were observed in the northern region, with average values of 16.1 ± 1.28 and 20.5 ± 1.39 , respectively. The lowest values were located in the southern region, averaging 8.77 ± 2.12 and 12.7 ± 3.04 (Supporting Information S1: Figures S1 and S2 and Table S2).

3.2 | Key Ecological Corridors and Nodes for Asian Elephants Across Multiple Scenarios

The research findings predict an increase in both the number and the length of ecological corridors for Asian elephants within the study area, with a particular focus on the development of long-distance and ultra-long-distance corridors. Initially, 105 ecological corridors were identified, with an average length of 140 km. This number is expected to rise to 131 corridors, with average lengths expanding to 190, 145, 134, and 183 km by 2030 and then further to 169, 203, 196, and 176 km by 2050 across various scenarios (Supporting Information S1: Table S3).

Overall, there was a negative correlation between corridor quality and length. The average length of Level 1 corridors was shorter than that of Level 2 corridors, particularly in 2030, where the average lengths were 43.9 and 81.6 km, respectively (Supporting

Information S1: Table SI-10). However, high-quality long-distance corridors are fundamental for maintaining network connectivity, with 17.1% of long-distance corridors and 8.72% of ultra-long-distance corridors ensuring the spatial integrity of the network (Figure 4, Supporting Information S1: Table S3).

In terms of corridor importance, critical corridors are typically shorter in length, with significant length differences between Level 1 and Level 2 corridors, ranging from 18.7 and 57.8 km, respectively. These corridors are primarily distributed around the edges of ecological source areas. In contrast, the connectivity index for ultra-long-distance corridors shows smaller differences on average lengths between Level 1 and Level 2 corridors, with average lengths of 106 and 120 km (Supporting Information S1: Figures S3 and S4 and Table S4).

Regarding the key ecological nodes within the study area, 90% of the ecosystem consists of forests and croplands, which are relatively dispersed and primarily located within long-distance corridors. Ecological barriers comprise 19.1% forest and 74.1% cropland, with croplands being the main obstacle to corridor connectivity. In contrast, ecological pinch points are made up of 54.3% forest and 38.3% cropland, with both forest and cropland types facilitating species movements and energy flow (Supporting Information S1: Figure S5).

3.3 | Asian Elephant Ecological Network and Conservation Priority Areas

This study has established a climate-adaptive ecological network designed specifically for Asian elephants (Figure 5A), strategically accounting for alterations in source areas and ecological corridors, as well as the anticipated need for long-distance movements. Within this framework, there is limited alignment between the priority network components and the designated protected areas. Notably, there are distinct differences in the source areas between the northern and southern regions, delineated by the reference latitude. The stability of these source areas plays an integral role in determining the layout and distribution of ecological corridors, affecting the overall effectiveness of the network in facilitating elephant movements and conservation efforts.

In the priority network, $1.64\times10^5\,\mathrm{km^2}$ (18.1% of the sources) of stable sources maintain high connectivity, with 7.49% under protection, all located north of the reference latitude. In contrast, the southern region is divided into two types of sources: (1) stable sources with medium-to-low connectivity, covering only $0.58\times10^5\,\mathrm{km^2}$ (6.40% of the sources), with a protection rate of 31.4%, concentrated in the southeastern area, and (2) a large number of unstable sources in the southwestern area (Supporting Information S1: Table S5).

The distribution of ecological corridors between stable sources is relatively regular and exhibits significant aggregation across different scenarios, while corridors between unstable sources lack such regularity. The study findings identified 635 priority corridors, with 37.2% passing through protected areas (Supporting Information S1: Table S6). Of these, 162 are long-distance

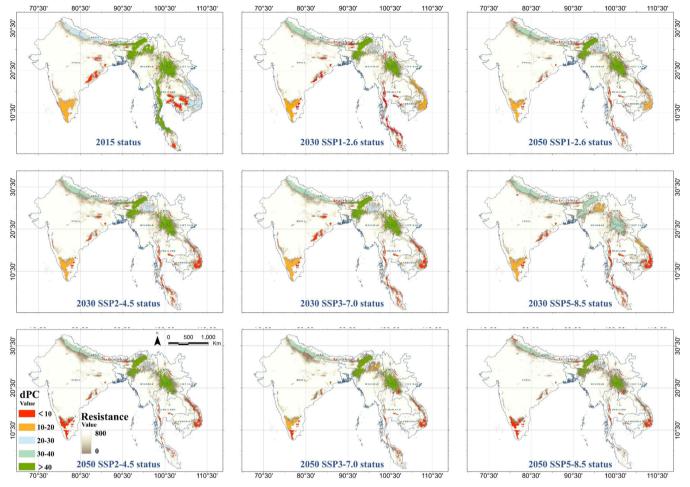


FIGURE 3 | Ecological sources, resistance surfaces, and connectivity levels of Asian elephant habitats under different scenarios. Higher dPC values indicate a higher connectivity of ecological source areas.

corridors, with 51 classified as Level 1 and 111 as Level 2 (Supporting Information S1: Table S3). These long-distance corridors, mostly passing through protected areas, are vital for north-south connectivity (Supporting Information S1: Figure S6). They also demonstrate relative regularity and significant aggregation in future scenarios (Figure 5a,b,f). In contrast, the distribution of short-distance corridors is primarily between unstable sources driven by fragmentation, lacking significant regularity and aggregation characteristics. However, many are of the highest priority level, which aids in connecting fragmented habitats within the region (Figure 5c-f). There are two notable exceptions: (1) in southern India, regular short-distance corridors connect fragmented habitats within stable source areas (Figure 5a), and (2) in Thailand, significant high-aggregation ecological corridors are present within unstable sources (Figure 5f).

4 | Discussion

4.1 | Habitat Changes and Ecological Network Characteristics of Asian Elephants

Based on our results, future climate change is expected to cause a noticeable shift in Asian elephant habitats from lower to higher latitudes. Overall, the northern habitats within the study area exhibit greater spatial stability and functional importance compared to southern habitats. While the southern regions currently represent the primary distribution areas for Asian elephants, they are projected to experience significant spatial contraction, structural fragmentation, and a continued decline in functionality. Over time, intensifying changes in climate patterns—specifically in the Thailand region—are likely to result in unstable habitat patches, transitioning from high to extremely low connectivity levels (Figures 3 and 5f). In southern India, the low connectivity levels may be attributed to the region's relative geographical isolation, but by 2050, the area is projected to experience increased fragmentation and further reduced connectivity at the regional scale (Figures 3 and 5a).

In contrast, northern habitats demonstrate superior functionality, with over three times the dPC value and nearly double the LPI and LSI values compared to southern habitats (Supporting Information S1: Table S2). The aggregation of large, stable source areas in the north (Figure 5A) supports predictions that overall habitat suitability will remain higher in the north. This disparity is likely driven by high population density and frequent human activities in the southern regions, where rapid agricultural expansion has resulted in significant habitat changes, particularly due to economic development (Tan et al. 2022; Di Marco et al. 2018; Coleman et al. 2019). These findings align with research conducted in the India-Nepal region (Kanagaraj et al. 2019), which suggests that under future

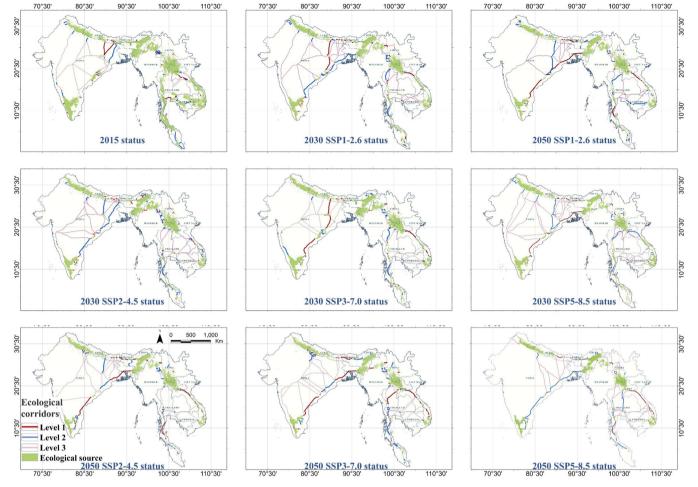


FIGURE 4 | Distribution patterns of Asian elephant ecological sources and corridors under different scenarios, with overall corridor classification.

climate scenarios, lower-latitude areas will experience more severe habitat loss, potentially driving Asian elephants to seek refuge further north along the Himalayas. Consequently, habitat degradation and instability in the southern regions may compel Asian elephants to move beyond their current ranges in search of more suitable habitats in the future (Jakopak et al. 2019). Our results are consistent with earlier predictions that large mammals, such as elephants, would face significant habitat contraction and could be forced to shift to higher latitudes as a response to climate change (Schloss et al. 2012).

In our corridor construction and analysis, we found that (1) ecological corridors constructed based on historical data failed to connect dispersed source areas, and (2) under future scenarios, long-distance corridors were pivotal in maintaining connectivity within the priority network. Our findings show partial consistency with corridor research trends observed in northeastern India and eastern Thailand. However, discrepancies primarily arise from the noncore status assigned to some ecological source areas in our analysis, which results in gaps within ecological corridors. These variations may be attributed to differences in scale and the inclusion or exclusion of future climate conditions in the research methodologies used (Suksavate et al. 2019; Talukdar et al. 2020). Short-distance corridors help mitigate small-scale landscape fragmentation and enhance local ecosystem connections. In contrast, long-distance corridors are necessary for sustaining connectivity across broader

ecological scales. In our study, long-distance corridors compensate for the limited climate adaptability of short-distance corridors and address the potential long-distance movement needs of Asian elephants (Figure 5A). Moreover, these long-distance corridors are projected to continue expanding in the future, with an average extension of 16 kilometers, providing essential support for elephant movements toward higher latitudes (Supporting Information S1: Table S3).

Notably, within our priority network, the regular distribution of corridor clusters between stable habitats provides clear guidance for constructing future conservation corridors. We also identified the composition and locations of key bottlenecks and ecological pinch points, offering valuable insights for enhancing corridor connectivity.

4.2 | Landscape Conservation Strategies for the Protection of Asian Elephants

Maintaining connectivity is essential for protecting biodiversity and sustaining ecological processes amid rapid environmental changes (Keeley et al. 2019). The need to conserve Asian elephants is of paramount importance. Proactive measures are necessary to mitigate issues such as social disruptions (Denninger Snyder and

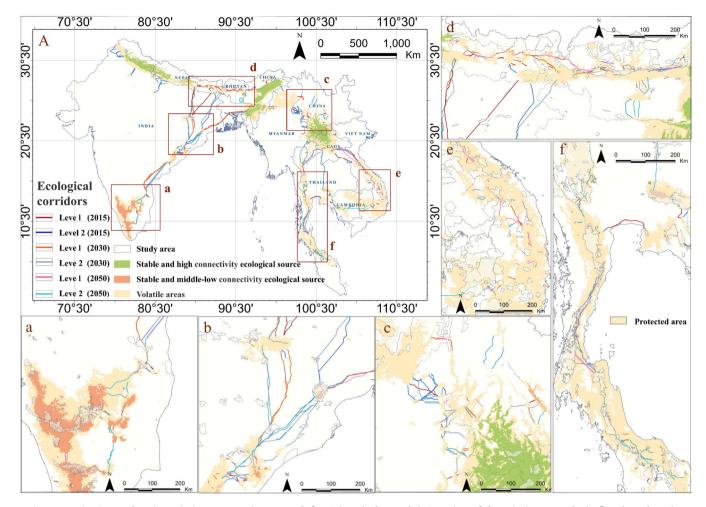


FIGURE 5 | Comprehensive priority conservation network for Asian elephants: (A) Overview of the priority network; (a-f) Enlarged sections, including information on protected areas and key nodes. Note: Not all key nodes are displayed for visualization purposes.

Rentsch 2020) and public safety concerns (Gross et al. 2021) arising from large-scale migrations. Implementing ecological networks would create suitable conditions for long-distance movements, helping to address these challenges. Our study recommends the following actions:

Firstly, it is essential to identify stable ecological sources for elephants and establish connections between these sources and the existing protected area system. Our study found that 61.2% of stable ecological sources are not currently protected, and 75.5% of unstable sources are at risk of disappearing (Supporting Information S1: Table S5). Identifying stable ecological sources aids in expanding protected areas strategically to cover key habitats for Asian elephants, thereby closing the gaps between existing protected areas and priority habitats for their conservation. Our study also revealed that these sources are often linked by relatively consistent and aggregated corridors, guiding the design of ecological pathways that enable safer elephant movement. (Figure 5a,b,f). This approach can improve future corridor construction, reduce resource waste, and enhance the capacity for human-elephant coexistence in unprotected areas.

Secondly, we emphasize the advantages of long-distance corridors in responding to climate change. Based on the limitations observed in short-distance ecological corridors during the baseline year (Figure 5), we believe that priority ecological

networks for specific species must consider future climate change scenarios to develop proactive and feasible plans. Longdistance corridors address the urgent need for "climate corridors," maximizing the dispersal and persistence capacity of vulnerable species like Asian elephants (Heller and Zavaleta 2009). Furthermore, our findings indicate that 37.2% of corridors intersect with protected areas (Supporting Information S1: Table S6). However, the construction of long-distance corridors should not be viewed as an absolute priority in all cases. Instead, future conservation efforts should adopt longdistance corridors as a guiding framework, complemented by short-distance corridors to enhance overall connectivity progressively. Integrating the Asian elephant conservation network with the optimization and expansion of protected areas can further improve connectivity between protected areas and strengthen the conservation system (Hilty et al. 2020).

Finally, our study highlights the importance of critical nodes within the ecological network layout for large vertebrate species. Establishing ecological pinch points has proven more effective for enhancing connectivity than restoring ecological barrier points (Xu et al. 2024). Future efforts should focus on cropland areas, which constitute nearly 40% of the identified pinch points, by implementing afforestation programs to maximize the function of these key nodes. In contrast, for the nearly 80% of cropland areas within ecological barriers, preventive

strategies—such as wildlife warning systems and compensation schemes—are recommended (Supporting Information S1: Table SI-11).

In conclusion, our study highlights the importance of stable ecological sources, long-distance corridors, and key nodes in mitigating the impacts of climate change. Further research and validation are needed to enhance the feasibility of the proposed strategies. Additionally, integrating conservation networks into protected area construction is essential to facilitate species movements in response to habitat changes.

4.3 | Limitations and Future Prospects

Due to resource constraints, this study developed corridors based on a landscape perspective using species distribution models (SDMs) that relied solely on static presence data. However, static data often lack timeliness and accuracy, which may compromise the reliability of the results. In constructing ecological corridors, existing models were used, with parameter settings informed by various studies. Despite this, limitations may still exist. Furthermore, the research did not validate the efficacy of its prioritized corridors, which may impact the practical applicability of its recommendations. The study used wide-ranging criteria to select corridors and source areas, aiming to develop more resilient solutions to unforeseen environmental changes. While this approach may be broadly applicable on a large scale, it falls short in the specificity required for regional or national planning.

We hope that future advances in dynamic monitoring and data accumulation platforms, such as GPS tracking, will provide more comprehensive information, which, in turn, can offer better insights into species movements (Zeller et al. 2018). Improving the accuracy and feasibility of methods for modeling ecological connections is essential (Riordan-Short et al. 2023). However, it is equally important to validate these models to ensure their reliability, acknowledging that such validation can be challenging in ecological network studies (Riordan-Short et al. 2023).

Ultimately, we urge broader participation in Asian elephant conservation research. By continually refining models, controlling data parameters more precisely, and strengthening result validation, we can enhance the general applicability and reliability of our research outcomes. Moreover, long-term studies on the role of long-distance corridors will be key in building a robust knowledge base for addressing future ecological issues.

5 | Conclusions

This study employed SDM and MCR models to design a climate-responsive conservation network for Asian elephants at a landscape scale. By analyzing both the structural and functional characteristics of ecological sources and corridors, the study provides insights into potential habitat changes for Asian elephants. The results indicate a potential shift in elephant

populations from lower to higher latitudes, driven by the divergence in habitat quality between the northern and southern regions under future climate scenarios.

This study also highlights the decisive role of long-distance corridors within large-scale conservation networks, pointing out the shortcomings of relying solely on short-range corridors for climate adaptability. In response, we propose a dynamic approach that integrates functional changes in both source areas and ecological corridors to foster a climate-adaptive network that supports long-distance movements.

Nonetheless, our research identifies a significant misalignment between the constructed ecological network and existing protected areas, indicating a need for improved conservation measures and management strategies. In essence, the ecological network developed in this study contributes valuable insights for the conservation of other large, wide-ranging mammals and supports the objectives of global biodiversity frameworks.

Author Contributions

Xue Lu: conceptualization, methodology, software, data curation, formal analysis, writing–review and editing, writing–original draft, validation, visualization, project administration, resources. Jie Wang: data curation, software, methodology, conceptualization, writing–review and editing. Zhongde Huang: conceptualization, methodology, data curation, supervision, writing–review and editing. Zhou Fang: funding acquisition, conceptualization, methodology, writing–review and editing, supervision. Maroof Ali: writing–review and editing. Anam Ashraf: writing–review and editing. Shengdong Yuan: writing–review and editing, resources. Yang Bai: conceptualization, supervision, resources, funding acquisition, methodology, software, data curation, investigation, project administration, writing–review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the supplementary material of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.