



## Research article

# Pathways for achieving conservation targets under metacoupled anthropogenic disturbances

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## ABSTRACT

Enhancing connectivity between protected areas stands as a paramount objective in advancing global conservation goals, particularly in coastal regions grappling with escalating human disruptions. However, little attention has been given to quantitative assessment of human-nature interactions within and among protected areas. Here, we endeavored to model the connectivity between protected areas in rapidly urbanizing regions in China, drawing on insights from the framework of metacoupling based on connected corridors at short and long distances. In alignment with the overarching global conservation aim of increasing the overall coverage of protected areas, we found that adding new site to the protected area system yields superior connectivity gains compared to merely expanding the boundaries of the existing sites. Within the connectivity network between protected areas, we discerned specific sites acting as stepping stones, pivotal in enhancing connectivity among the chosen protected areas. Our study propounds a pragmatic methodology for prioritizing local protection initiatives and underscores the criticality of incorporating connectivity conservation strategies. This approach is vital for attaining regional biodiversity targets, given the dual perspective encompassing both human activities and the natural environment, particularly in the face of mounting anthropogenic disturbances.

## 1. Introduction

The primary global threats that decrease biodiversity include habitat degradation and fragmentation caused by anthropogenic activities (Caetano et al., 2023; Chauvenet et al., 2020; Moore and Schindler, 2022). Protected area (PA) downgrading, downsizing, and degazettement (PADDD) has recently gained attention among scientists and policymakers (Golden Kroner et al., 2019). Monitoring the PA coverage established by Aichi Biodiversity Target 11 to halt biodiversity loss is one of the goals in conservation management, with the aim of conserving at least 17 % of land as PAs by 2020 and increasing key biodiversity areas by 2050 (Choi et al., 2022; Gill et al., 2017; IUCN, 2021). However, these global conservation targets were not achieved (Saura et al., 2019), and stabilizing the net loss of biodiversity and achieving recovery and restoration by 2030 remains a difficult challenge.

To reach the target coverage, it may be necessary to not only improve the area of coastal PAs but also the effect of these areas in terms of

increasing well-connected habitats. The establishment of PAs is one of the most fundamental and effective approaches for generating well-connected areas to counterbalance the loss of connectivity caused by human disturbances (Cumming and Allen, 2017). The efficiency of improvements in connectivity varies according to the methods used to increase the area of PAs and thus achieve biodiversity targets; such targets can be achieved either by expanding the original boundary of existing sites or adding new sites. However, it is still unclear which approach is more efficient to achieve such targets and improve regional connectivity under increasing human disturbances. Besides, previous studies have largely concentrated on ecological connectivity evaluated by resistance based on different types of anthropogenic disturbances (Di Marco et al., 2018; Ward et al., 2020). Resistance escalates in correlation with the extent of human disturbance, signifying augmented movement costs. Urban centers specifically impose substantial traversal expenses, while areas with minimal disturbance tend to facilitate easier traversal. But few studies have explored the role of human-nature interactions in connected PAs in terms of balancing anthropogenic disturbances

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(Brennan et al., 2022; Parks et al., 2020). Most studies focus on the connections between PAs from an ecological or natural perspective under the influences of human disturbances (Lü et al., 2017; Tesfaw et al., 2018; Yoon et al., 2022), with limited quantification of the dual interactions between nature and humanity. The framework of meta-coupling helps to assess the interconnections between coupled human and natural systems across short and long distances (Liu, 2017). The human-nature interactions among PAs can be estimated by the connectivity network based on cumulative human influences while migrating in short and long distances. The connection occurs locally through pericoupling connections among habitats over short distances

with minimal resistance and extends to telecoupling connections over long distances with comparatively higher levels of resistance. Integrating metacoupling into connectivity analysis can provide a new perspective for achieving the quantitative targets of biodiversity conservation in coupled human-nature systems (Liu et al., 2007).

To illustrate this method, we estimated the metacoupled connectivity among national PAs (NPAs) in China's coastal provinces based on human-nature interactions. Drawing from the SLOSS debate, which discusses whether a single large reserve is more effective in conserving species compared to multiple small PA (Saura, 2021). We conducted various scenario analyses aimed at augmenting the total area. We

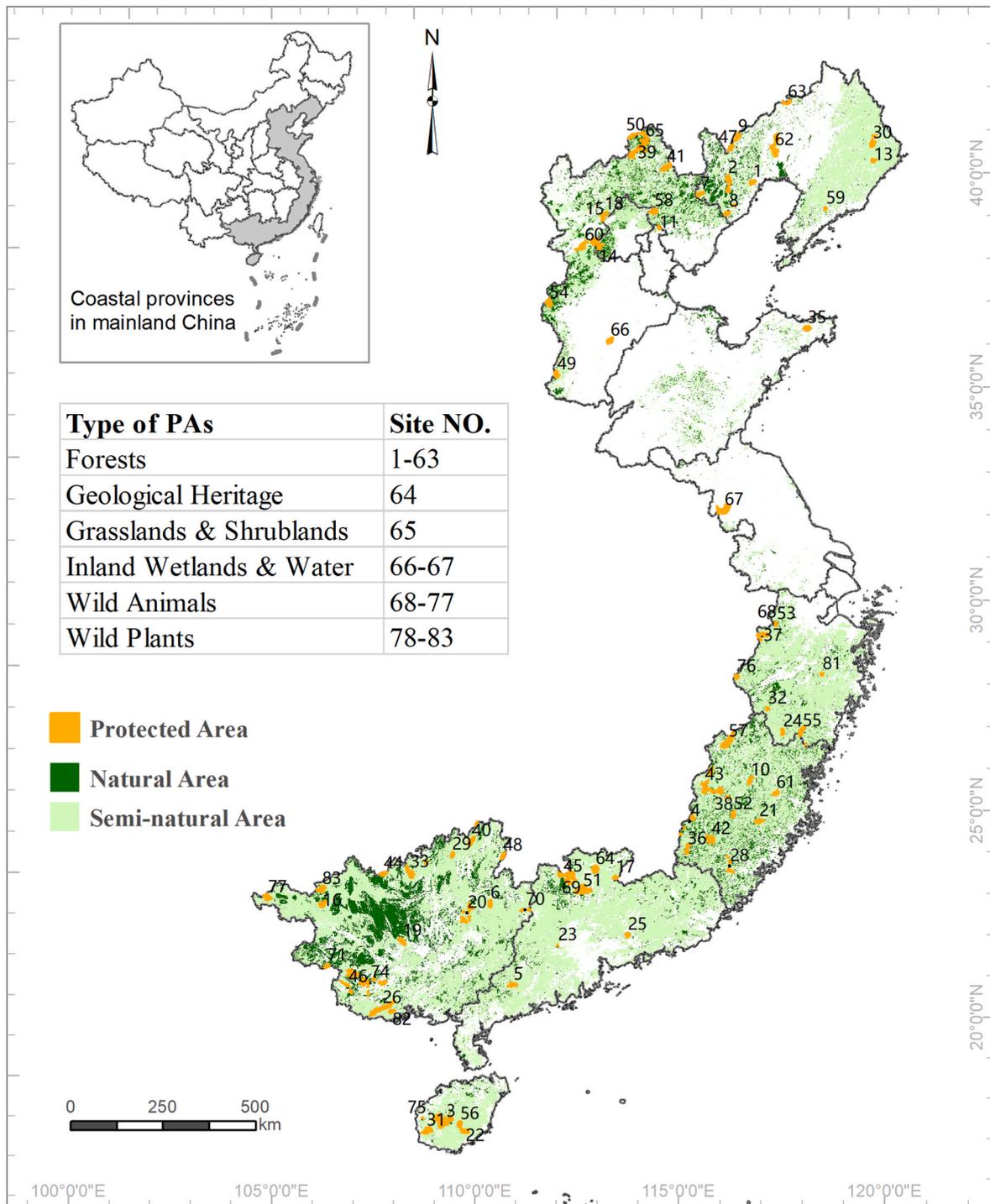


Fig. 1. Distribution of national protected areas (NPAs).

estimated the resulting biodiversity conservation effects in terms of connectivity both before and after expanding the coverage of PAs. This study evaluated the connectivity among PAs under a scenario of expanding the boundary of existing PAs, adding new sites selected among provincial PAs (PPAs), and a combination of expanding boundaries and adding new sites. To meet the Post-2020 Global Biodiversity conservation goals, we determined the most efficient method of enhancing connectivity by increasing the total PA coverage and then evaluated the offset efficiency in enhancing connectivity per km<sup>2</sup> of the updated connectivity network to compensate for key human disturbances (landscape changes and increases in population density). Furthermore, it is particularly important to identify the areas in a metacoupled network that should be prioritized for protection while maintaining resilience. The concept of metacoupling connectivity effectively expands beyond ecological protection in human-influenced environments. It encompasses a dual interaction between nature and humanity. The aspect of connectivity from natural level is represented by the connected areas and corridors in the offset analysis, and the aspect from human level can be addressed by the payments for ecosystem services and ecosystem service values in connected areas and corridors. Maintaining and increasing the metacoupling connectivity among PAs in coastal zones can be used to inform the development of solutions to global challenges related to biodiversity and habitat loss.

## 2. Materials and methods

To estimate the dual interaction between nature and humanity based on metacoupling connectivity, several crucial steps were undertaken: (1) generated input layers of habitat to increase total area of PAs across three scenarios; (2) evaluated connectivity in each scenario based on resistance layers of human disturbance; (3) identified the scenario demonstrating the most effective enhancement in connectivity; (4) modeled the potential adaptation of natural habitats to increasing human disturbance, and estimated the ecosystem services loss within the connected areas to emphasize the influence of connectivity at the human level.

### 2.1. Study area

Our study area encompasses only 13 % of China's total terrestrial land area but accounts for 60 % of China's GDP and 10 % of the global GDP; this area is thus the economic driver of the whole country (Fig. 1). According to the 2017 environmental investigation of coastal areas in China (<http://www.soa.gov.cn/>), large swathes of coastal natural areas have been converted to built-up land in metropolitan regions, such as the Guangdong-Hong Kong-Macao Greater Bay Area, Bohai Bay (Tianjin), Hangzhou Bay (Zhejiang) and Min River Estuary (Fujian). High-intensity human disturbances lead to high vulnerability of habitats and biodiversity loss in coastal areas. In 2017, coastal disasters cost 6398 million RMB, accounting for 1.3 % of the total GDP in coastal provinces.

According to reports from the Ministry of Ecology and the Environment of the People's Republic of China, 983,400 km<sup>2</sup> (10 % of mainland China) of terrestrial area is covered by NPAs (MEE, 2017), which leads to a large gap of 7 % the Aichi Biodiversity Target established by the Convention on Biological Diversity. Most NPAs are located in north-western China (e.g. Qinghai Province and Tibet); thus, most threats to biodiversity occur in eastern coastal areas that experience extensive human disturbance (Xu et al., 2017). Therefore, connecting small or isolated PPAs can conserve biodiversity and improve the management of PAs; this process is critical to achieving the Aichi Biodiversity Targets (Adams et al., 2019; UNEP and IUCN, 2016).

Despite the limited coverage of NPAs and multiple anthropogenic disturbances in coastal areas, well-connected PAs provide benefits to areas beyond their boundaries (Brudvig et al., 2009). Connecting neighboring NPAs through natural and seminatural lands can effectively

eliminate island effects among patches. In the coastal provinces of mainland China, 688,841 km<sup>2</sup> (53.3 % of the total coastal area) is covered by natural and seminatural areas, thus providing sufficient natural patches to connect PAs. However, increasing human disturbances (increased population density and landscape changes) in coastal zones has increased the difficulty of maintaining ecosystem resilience.

### 2.2. Three scenarios of increasing protected areas

The inclusion of additional sites of PA and expanding existed boundary offers increase opportunities for creating alternative corridors. Habitat corridors facilitate movement of species between patches. Consequently, this expansion contributes to a more connected area overall. Three scenarios were considered as the potential approaches to increase the coverage of PA: expanding the boundaries of NPAs, adding new sites selected from PPAs, and both upgraded PPAs and expanding the boundaries of NPAs. By assessing connectivity alterations in these scenarios, we aim to understand the potential impact and efficiency of expanding the total PA coverage on biodiversity conservation.

#### 2.2.1. Scenario 1: expanding the boundaries of existing NPAs

We created buffers around each site to enlarge the total area covered to meet the Aichi Biodiversity Target; in other words, the total area of the 83 selected NPAs was equal to 17 % of the study area. To eliminate the size effect of habitats in modelling connectivity (MacArthur and Wilson, 1967; Saura et al., 2019), all sites were shown with the same size after expanding NPAs by different buffer zones. Then, the selected enlarged NPAs with circular buffer zones were set as key PAs for modelling connectivity conservation among coastal NPAs.

#### 2.2.2. Scenario 2: adding new sites

To test the direct contribution of only adding new sites, as comparing to the scenario 1 with expanding area, we modeled connectivity with the certain numbers of upgraded PPAs and the original NPAs through the Climate Linkage Mapper (McRae et al., 2013). This part of the analysis was conducted as a control testing for scenario 3 (i.e. upgrading PPAs and expanding NPA boundaries) without considering of the total coverage target. The related results in scenario 2 can be used to answer the question that if the improving connectivity is mainly driven by adding site or the combination of adding site and expanding boundary. As per the PA regulations in China (GB14529-93, revised in 2017), NPAs receive the highest level of protection, strictly enforced by the central government. Following NPAs are the provincial protected areas (PPAs). We reviewed all the recently added NPAs before 2018 and found that all these new sites were upgraded from existing PPAs. Therefore, in this scenario we upgraded PPAs to NPAs to expand the total PA coverage; all 291 PPAs in coastal provinces were listed as potential NPAs. As the PPAs are possessing relative high level biodiversity and natural assets, the magnitude of human disturbance within PPA and surrounding environment becomes the key factor to evaluate the quality of a PPA. Areas with human influence below a given threshold were identified as suitable patches for connecting corridors. We considered the suitability of the surrounding environment and selected only PPAs surrounded by areas with low human disturbance. The human influence value was assigned based on the natural properties of these factors, as evaluated in our previous research (Li et al., 2019). The corresponding threshold was based on the median value of overall human influence in the core area coverage of NPAs, which included half area of the total NPAs. The human influence score was used to present resistance along a migration corridor, and pixels with human influence values exceeding the threshold suggested excessive human disturbance of local habitats. Despite the maintenance of NPA numbers, surrounding landscapes and human disturbances, such as road construction and urban expansion, have escalated. Consequently, certain PPAs are experiencing overwhelming human influences. Application of this selection standard resulted in the removal of a few PPAs due to the excessive human

influence, we then created linkages among island NPAs based on the scenario in 2020. The value range of connectivity was adjusted within 0–200,000 corresponding to the conditions observed in 2020. Ultimately, 89 PPAs were selected for use in the connectivity assessment in scenario 2.

2.2.3. Scenario 3: adding new sites and expanding NPA boundaries

This scenario is conducted based on the selected PPAs in scenario 2, and combined with the buffered NPAs established in scenario 1. The main purpose of this scenario is to enlarge the total area covered to meet the Aichi Biodiversity Target by both adding new sites and expanding boundaries.

2.3. Evaluating connectivity conservation under different scenarios

The impacts of climate change and anthropogenic disturbances were used as inputs to predict connectivity through the Climate Linkage Mapper (McRae et al., 2013). Anthropogenic influence inputs (Process 1 in Fig. 2) included population density, land use and cover change and human access (roads, railways and airports) (Newbold et al., 2015; Theobald, 2010). The Climate Linkage Mapper tool, a common model in landscape connectivity, was used to model conservation connectivity; this tool created climate corridors among original NPAs and upgraded PPAs as core areas along a climatic gradient (McGuire et al., 2016). The pixels encompassed by corridors were identified as connected areas, representing potential migration paths characterized by minimal human influence. The resistance raster (1 × 1 km resolution) used to model landscape connectivity included landscape patterns, human settlements and access in 2020. These inputs were assigned resistance values based on their natural properties according to related research (McRae et al., 2013; Newbold et al., 2015; Theobald, 2010). The resistance indicators

with high human influences, such as urban area in terms of landscape patterns and a high population density in terms of human settlements, were assigned high values. As interconnected corridors consist of habitats with natural properties, landscape patterns were classified into natural (low resistance), seminatural and non-natural land areas (high resistance) based on the magnitude of human impact. To address variations in population density, we rearranged population density values into groups with equal intervals and the same numbers of pixels. The pixels with high density were assigned high values of resistance as they are exposed to high levels of human disturbances; human access was represented by the extents of roads and railways in three different buffer widths (90 m with high resistance and 500 m and 1000 m with low resistance). The sizes of the buffer zones were chosen according to related studies (Li et al., 2019; Woolmer et al., 2008). Given the influence of global warming, the average annual temperature in 2020 was included in a climate raster layer to model migration from high to low temperatures. We assume that habitat temperatures will rise due to climate change, potentially rendering the original habitat unsuitable for local species. Species are forced to shifting their distributions in response to changing climates, the climate gradient corridors allow species dispersal to suitable climates (low temperature). The datasets of surface temperature at 1 km resolution are available from the open source websites (<http://www.climatologylab.org/terraclimate.html> and <http://www.resdc.cn/>). Since the PA data analyzed in the three scenarios changed based on the NPAs in 2020, the connectivity conservation among the original NPAs in 2020 was used as the baseline value for all scenarios to evaluate the effectiveness of upgraded NPAs in enhancing conservation connectivity.

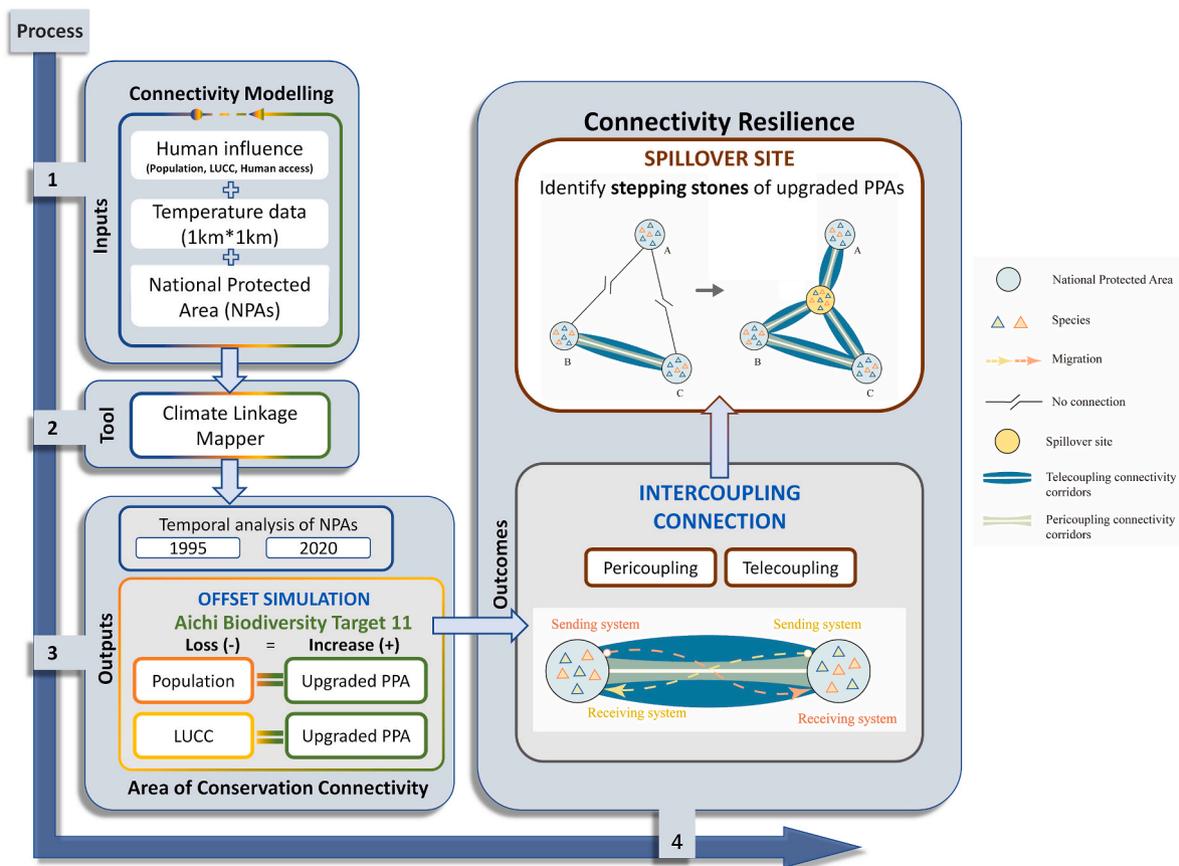


Fig. 2. Key processes involved in simulating connectivity in response to various factors.

#### 2.4. Determining the efficiency of improving connectivity under the three scenarios

The PA connectivity gains were evaluated from two perspectives: the overall connectivity value of the connected area (calculated by cost-weight distance), and the efficiency of improved connectivity. The values of cost-weight distance were presented in resistance-based terms, indicating the level of difficulty for ecological movements between distinct habitats (Nuñez et al., 2013; McGuire et al., 2016). These distances were calculated by summing the overall resistances along delineated corridors. It's important to note that resistance increases in correspondence with the degree of human impact, signifying higher movement costs in these areas. We calculated the overall connectivity value in all connected areas before and after changes in different scenario cases. If the overall connectivity value was unchanged, we assumed that the connectivity gains provided by adding PAs balanced the connectivity loss due to population and landscape change (see details in Section 2.5). The efficiency of enhancing connectivity in the three scenarios was evaluated according to the overall distribution of connectivity. By using a gradient analysis of connectivity improvement per km<sup>2</sup>, we compared the areas with significant change in the three scenarios to baseline values from 2020. The scenario with the greatest increase in connectivity per km<sup>2</sup> was identified as the most efficient method. The efficiency was calculated as follows:

$$E = \frac{\Delta S_{top}}{\Delta S_{total}}$$

where E is the efficiency of increasing connectivity,  $\Delta S_{top}$  represents the area of increased connectivity values (in the top 10 %, 20 % and 50 % with significant increase of connectivity),  $\Delta S_{total}$  is the total area of increased connectivity. The scenario with the highest efficiency in enhancing connectivity was selected for further analysis.

#### 2.5. Modelling changes in key factors

One of the most useful frameworks in conservation biology is the coupling of human and natural systems, which highlights their interconnectivity across space (Liu, 2017). The key factors that influence connectivity conservation are human activities (Peters et al., 2019), which are represented in the present study by human population density and landscape pattern changes. These two factors are critical drivers of landscape connectivity changes based on our previous analysis in the same region (Li et al., 2019). Increases in the human population density and the intensity of landscape conversion from natural to artificial landscapes were the main causes of connectivity degradation (Kühl et al., 2019; Ren et al., 2014; Tucker et al., 2018); therefore, we generated two models of connectivity offset with different levels of these two factors while holding the other factors constant (Fig. 2).

First, we calculated the population growth rate from 2000 to 2020 in each province. Then, we simulated population growth in each province by a serial analysis with a 10 %-gradient increase from 10 % to 100 %. The population density data in 2020 were used as the background value of population growth to conduct population growth analysis. For the serial gradient analysis, we increased the population density by 20 %, 50 % and 100 %. Upon conducting a thorough comparison of the average resistance in each pixel along corridors, we discovered that the cases involving a 20 % and 50 % representation exemplify the typical alterations seen when additional sites are introduced in the gradient analysis. The choice of 100 % was made to depict the highest number in this gradient analysis. To model landscape change according to historical trends, we separated all pixels into three groups: pixels with landscape conversion (increases or decreases in resistance; two groups) and those that remained the same from 2000 to 2020. In converted pixels, human influence values were doubled; in pixels without landscape conversion, human influence values of 0.2, 0.5 and 1 times the previous level were

added, and in pixels with decreased resistance, the values remained the same. The added values were chosen based on a series of tests to predict significant changes, as well as changes in population density. When selecting cases for the landscape change analysis, our guiding principle was to evaluate offset results with an equivalent number of added sites. This approach allows for a comparative assessment of the offset effect in both gradient analyses of population and landscape changes, maintaining a consistent standard across evaluations.

#### 2.6. Simulated offsetting of change factors and ecosystem services in connected area

We aimed to assess the feasibility of maintaining connectivity amidst heightened human disturbances by simulating connectivity offsets based on two factors mentioned above. Offset connectivity represents the restoration of connectivity from adding PPAs. These added PPAs counteract connectivity degradation caused by changes in human population density and landscape changes. Offset connectivity achieved by eliminating human disturbance could help to halt the loss of biodiversity and restoration of habitats, as proposed in the Post-2020 Global Biodiversity Framework. After several rounds of simulations varying in population density and landscape pattern changes, we selected PPAs with low levels of human influence as sites to compensate for connectivity loss in the simulation (details in Section 2.2.2). These selected sites were integrated with the original NPAs as potential connecting habitats in subsequent connectivity modelling to increase connectivity. With the purpose to test the efficiency of selected sites in enhancing connectivity, we conducted connectivity in both gradient analyses of population and landscape changes. All the connectivity values in different offset analysis were grouped with the same interval, and the ratio of change in each interval represents the variation between the two levels.

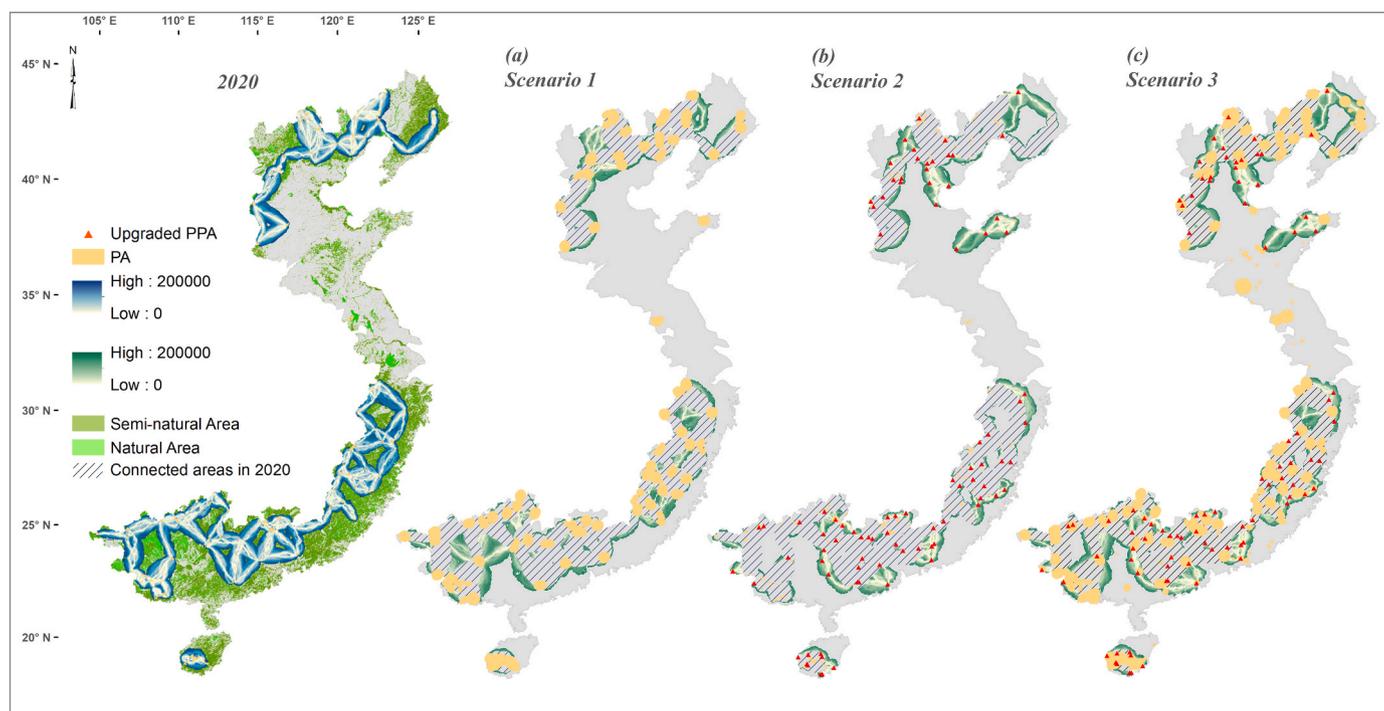
In our landscape connectivity framework, the spillover system represents a stepping stone in landscape connectivity, as it is defined as the system that interlinks other systems in the metacoupling framework (Brudvig et al., 2009; Liu, 2017). These stepping stones not only confer individual benefits but also foster optimal interconnections with other sites (Gill et al., 2017; Brudvig et al., 2009). PAs were categorized as stepping stones if they were connected to at least two other PAs and created a new ecological network that enhances efficiency in both high and low cost distances. Other added PPAs, not classified as stepping stones, merely created corridors connecting neighboring PAs (Fig. 2).

As the offset analysis focuses on connectivity at the natural level, we conducted an assessment of ecosystem services loss within the connected areas to emphasize the influence of connectivity at the human level. To achieve this, we compared the values of ecosystem services in the connected corridors before and after the addition of new sites. The primary types of ecosystem services consist of four categories: Regulating, Cultural, Supporting, and Provisioning services (details in Tables S3–4). The alterations observed in the ecosystem service values within these areas portray the dynamics of local connectivity adapting to escalating human disturbances. To assess the precision of modeled landscape connectivity within PAs, we employed biodiversity maps encompassing amphibians, birds, and mammals, along with GDP data merged with nighttime light and residential density datasets to validate the findings within our designated study area.

### 3. Results

#### 3.1. The efficiency of improving connectivity under the three scenarios

We estimated the area of connectivity under scenario 1 (after expanding the boundaries of all NPAs) (Fig. 3a). The overall connectivity among expanded NPAs was increased significantly compared to that among the original NPAs. Evaluating the areas with large improvements in connectivity indicated that the most notable enhancement in the area of connectivity occurred around small NPAs, with



**Fig. 3.** Changes in the area of connectivity after upgrading NPAs under different scenarios (a: Scenario 1 expanding the boundaries for existing NPAs (yellow area), b: Scenario 2 only upgraded PPAs, c: Scenario 3 adding upgraded PPAs (red triangles) to scenario 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

original areas less than 2 km<sup>2</sup>. Because the original PAs were too small to provide sufficient support for local species, expansion facilitated connection to the wider network. Under scenario 3, we found that some least-cost corridors in 2020 were replaced by longer paths connecting PAs (Fig. 3b). Thus, the most significant improvement in connectivity under this scenario resulted from the ability of local species at these sites to migrate to more suitable PAs over longer distances. In addition, the added PPAs created large areas of well-connected patches in which connectivity was previously low or nonexistent.

By mapping the connectivity under scenario 2 (Fig. 3b), we found that new connections were created between the added sites and existing NPAs, and the results were better than those under scenario 1. The overall network of scenario 2 was almost the same as that of scenario 3 in terms of connectivity, except that some short paths were not connected. Even the scenario of only upgraded PPAs did not reach the total coverage goal of the Aichi Biodiversity Target, with a 69 % gap from the coverage level of the Target; this approach yielded high efficiency in enhancing connectivity without increasing the areas of PAs. According to the gradient analysis of improved connectivity efficiency per km<sup>2</sup> (Table 1), there was a significant increase in connectivity per area (14–22 times that in scenario 3). The most significant improvement occurred in the area of the top 10 % connectivity under scenario 2, indicating that the added sites achieved high efficiency.

As seen from the overall distribution of connectivity areas for conservation (CAC) under different scenarios (Table 1), the most significant improvement in connectivity occurred in areas with 21–50 % CAC values (except under Scenario 2). The areas of well-connected habitats (values within the top 10 % of CAC in 2020) considerably increased in scenarios 2 and 3 compared to the baseline and scenario 1, as did areas with the top 20 % and 50 % CAC values. Compared to CAC in all scenarios, the overall CAC in scenarios 2 and 3 exhibit significant improvements in connectivity. If we estimate connectivity without considering the Aichi Biodiversity Target, the efficiency of improving connectivity (per km<sup>2</sup> of added area) was highest under scenario 2 (upgraded sites only without expansion of boundaries). In general,

**Table 1**  
Areas of connectivity conservation (ACC) under different scenarios.

Scenarios	2020	Aichi Biodiversity Target11		Scenario 3 (upgraded PPAs)
		Scenario 1 (expanded boundaries)	Scenario 2 (upgraded PPAs and expanded boundaries)	
<b>Top ACC</b>	<b>0–10 %</b>	130,955	129,254	180,868
	<b>11–20 %</b>	81,484	108,622	118,532
	<b>21–50 %</b>	142,783	185,482	197,096
<b>Efficiency (per km<sup>2</sup>)</b>	<b>0–10 %</b>	/	0	0.22
	<b>11–20 %</b>	/	0.13	0.16
	<b>21–50 %</b>	/	0.21	0.24

adding new NPAs was highly efficient in enhancing conservation connectivity. Upgrading PPAs to enhance conservation connectivity is a national conservation measure that provides resilience to increasing human influence.

### 3.2. Offset analysis of the population density

Metacoupling connectivity among PAs reduces internal and external disturbances to biodiversity; this approach maintains the critical functionality of a system and strengthens ecosystem resilience in rapid urbanizing areas. Analysis of the three scenarios revealed that adding new NPAs was highly efficient in enhancing conservation connectivity (Fig. 3 and Table 1). Upgrading PPAs to NPAs (i.e. adding new NPAs) enhanced the conservation connectivity of NPAs and can be utilized at the national level to improve conservation in response to increased human influence.

Thus, we selected several PPAs as core areas to generate connected PAs and restore degradation of connectivity caused by increases in human population density (Fig. 3). The selected PAs were identified as areas exposed to low human influence and were considered suitable habitats for the migration of local species. Thus, these new NPAs increased the numbers of connecting sites in the network of NPAs, which provided more corridors (e.g. green corridors in Fig. 4). In turn, these newly added NPAs led to an increase in connectivity of the local network within the potential migration distance. The areas of increased connectivity (shown in green) differed from the areas of decreased connectivity (red), indicating that the offset effect occurred in terms of distant connectivity compensation.

Within a certain range, increases in human population density resulted in corresponding increases in the resistance of the local network. The increased resistance led to the loss of connecting corridors (e.g. red corridors in Fig. 4), which led to degraded connectivity in the local network. Therefore, greater increases in population density will necessitate higher numbers of added NPAs. We found that adding 24 PPAs (covering 3553.42 km<sup>2</sup>) to the NPA network compensated for the loss of connectivity caused by a 20 % increase in the population density from that in 2020; adding 35 PPAs (covering 4920.21 km<sup>2</sup>) compensated for a 50 % increase in population density, and adding 41 PPAs (covering 5243.21 km<sup>2</sup>) compensated for the connectivity loss due to an 100 % increase in population density. The zonal analysis of offset efficiency conducted in ArcGIS indicated that the offset effect (per km<sup>2</sup>/%) for a 20 %-population-increase case was 177.67 km<sup>2</sup>/%, which required more added areas than those for the case of 50 % (98.40 km<sup>2</sup>/%) and 100 % (52.43 km<sup>2</sup>/%). The offset efficiency achieved by adding each unit (km<sup>2</sup>) of PA in the last case (i.e. 100 % population increase) to restore connectivity loss caused by a percentage of population increase is three times that in the first case (i.e. 20 % of population increase). In other words, the required increase in PA area per percent population decreased continuously in these three cases (20 %, 50 % and 100 % population increase), which suggests that there is an increased cumulative offset per km<sup>2</sup> of PA when improving metacoupling connectivity. Our results suggest that the effectiveness of offsets from upgraded sites increased as the total number of core areas increased.

### 3.3. Offset analysis of landscape changes

The overall degradation of connectivity was maintained at a stable rate as the landscape pattern exhibited increasing changes, represented by the increased total human impact of land-use types (Fig. 5). Fewer sites were added to restore the loss of connectivity due to landscape changes. We found that areas without landscape change from 2000 to 2020 contributed more to connectivity loss than areas with landscape changes. Even though most of the changed areas were saturated with high levels of human influence, the increased influence of landscape changes was not significant in these changed areas relative to that in the original unchanged areas. The original unchanged areas were more sensitive to external disturbances than changed areas (which experienced continuous disturbances). Overall, the connectivity loss caused by landscape changes was less sensitive to an increase in population density. This result suggests that landscape changes lead to relatively low efficiency, as the landscape changes typically involve irreversible conversion from natural to artificial landscapes.

The addition of NPAs improved the connectivity of networks within areas around the sites (green areas in Figs. 4 and 5) and provided more options in disconnected areas impacted by increases in population density or landscape changes (red areas in Figs. 4 and 5). The disappearance of connecting corridors (red areas in Figs. 4 and 5) represents a typical transition in connectivity with upgraded PAs. Connected NPAs may become isolated, because the increased magnitude of resistance from increases in population density and landscape changes, which exceeds the adaptive capacity of the local network. With extremely high levels of cumulative resistance (>200,000 as the threshold in the connectivity model), the original corridors that experienced high levels of human disturbance became unsuitable for local migration. These areas were of low possibility to recover connectivity as before. Instead, alternative pathways with relatively low levels of human disturbance were formed to reconnect local sites after adding upgraded PAs. The disappearance of connecting paths was mostly observed in areas with significant population density and landscape changes. For example, with the continuous increase in population density in metropolitan areas in coastal regions, such as the Guangdong-Hong Kong-Macao Great Bay Area, Yangtze River delta, and Bohai Rim, significant changes in the

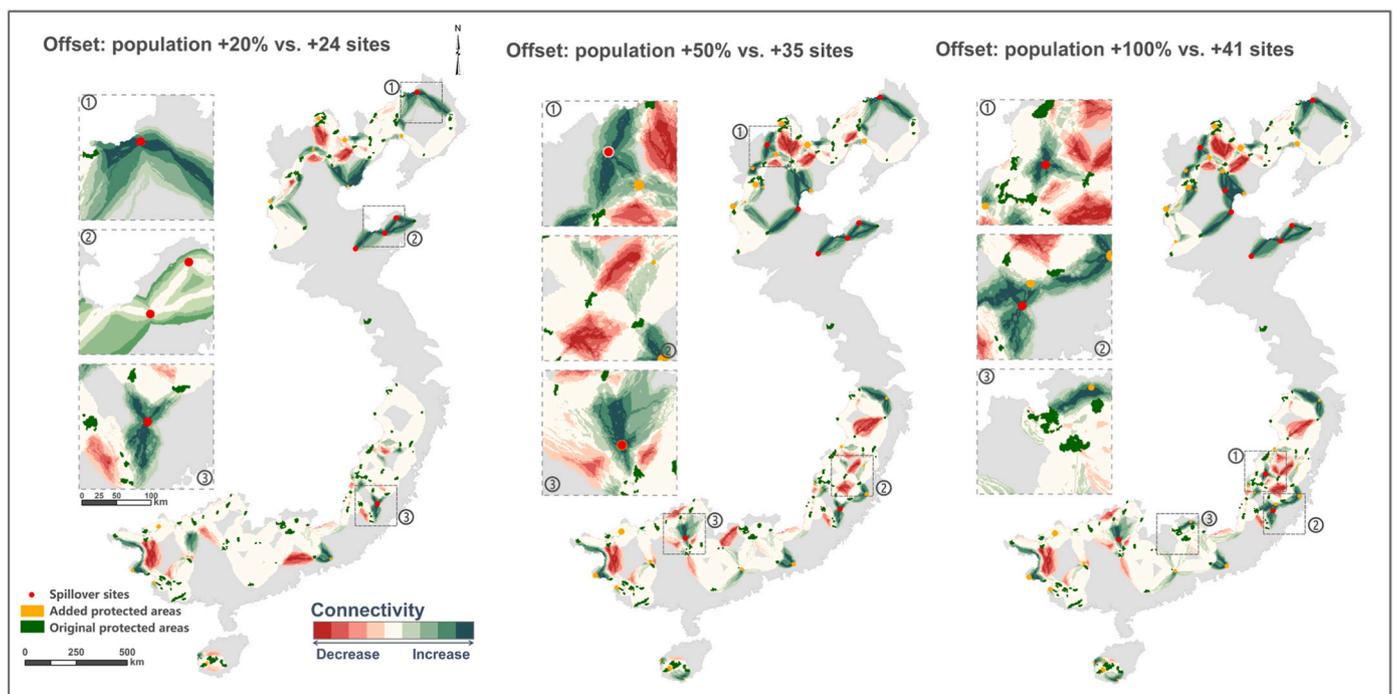


Fig. 4. Simulated offset effect on connectivity due to the addition of new sites under different increases in the population density.

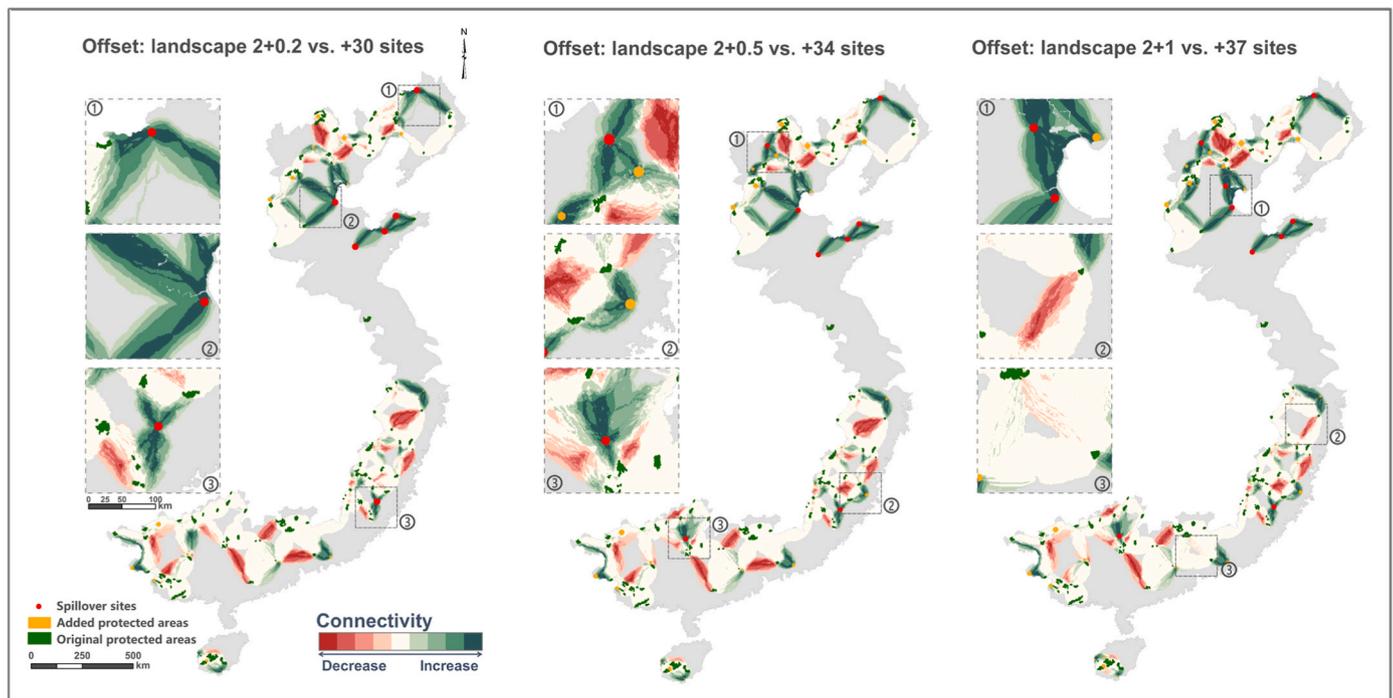


Fig. 5. Offset connectivity simulated by adding protected areas in response to landscape changes.

distribution of the connectivity network were observed upon the addition of new NPAs. The substantial loss of the original connecting corridors was balanced by new corridors formed by adding these sites; thus, there was not a net decrease in connectivity. Thus, even a large area of decreased connectivity in this province could be balanced by offset connectivity from the new sites. Despite greater pressure due to rapid urbanization and economic development in this region compared to other coastal areas, sufficient connectivity could be maintained while adapting to increased human influences. One of National innovation-driven demonstration zones in China for implementing the UN's 2030 Agenda for Sustainable Development (United Nations UN, 2015) is located in Shenzhen City of the Guangdong-Hong Kong-Macao Great Bay Area. This national pilot area aims to lead sustainable development of megacities, and increase connections between urban and rural area (Pan et al., 2023). Restoration of connectivity in areas with a high level of disturbance enables local regions to adapt to and mitigate external disturbances via distant compensation. In particular, the identified stepping stone (spillover site in Figs. 4 and 5) has high stability and resilience that enable compensation for anthropogenic disturbances.

## 4. Discussion

### 4.1. Habitat restoration of protected areas under human disturbance

As proposed by the Post-2020 Global Biodiversity Framework, connectivity conservation is essential for halting net biodiversity loss by 2030 and maintaining the resilience of ecosystems. Connectivity provides a practical way to measure biodiversity conservation and habitat restoration at large spatial scales (Hilty et al., 2020). The goals are to facilitate the conservation of PAs and ensure their ability to cope with human disturbance. In the simulations of offset connectivity, we considered two factors that led to degraded connectivity, namely, increases in population density and landscape changes. Comparison of the offset effects of population density and landscape changes, increased population density was the factor that most influenced landscape connectivity. The simulations of offset connectivity under landscape changes and increased population density represent the possibility of restoring and recovering biodiversity to ensure a world of people "living

in harmony with nature".

### 4.2. Effective area-based conservation measures: metacoupling connections

The metacoupling framework includes pericoupling connections in short distance and telecoupling connections in long distance. Metacoupling connections in networks with upgraded PAs can improve the quality of coastal PAs in the context of anthropogenic disturbances (datasets are provided in Figs. S1–S3). The metacoupling connectivity evaluation used in our study is a practical approach to assess global connectivity and achieve the goal of 30% PA coverage of coastal areas. The spillover system of PAs in metacoupling networks acts as stepping stones (details of key concepts are provided in Table S2) (interconnecting habitats) (Mozelewski et al., 2022; Tromboni et al., 2021), generating an alternative way to efficiently connect systems and create better connections in a wide network. Stepping stone sites were identified by the integration of the metacoupling framework to improve the efficiency of connectivity conservation and achieve the target at a large scale. The National Park System in China indicates the need to break through administrative boundaries, consolidating and reorganizing various adjacent and connected protected areas according to the unity of ecosystem integrity and habitat connectivity. Expanding the interconnected network around the national park could offer significant external support by providing a high level of ecosystem services. For instance, Wuyishan National Park (117°24'13"–117°59'19"E, 27°31'20"–27°55'49"N) has become one of the first ten national parks to implement a trial national park system nationwide in 2016. To support this initiative, we commenced species monitoring in 2020 by deploying thermal cameras. The key species include: *Arborophila gingica*, *Arctonyx collaris*, *Capricornis milneedwardsii*, *Dremomys pernyi*, *Melogale moschata*, *Myoponus caeruleus*, *Paguma larvata*, *Sus scrofa* and *Zoothera aurea*. These identified species in our modeled corridors prove the existence of connected area. The interconnected regions rich in ecosystem services surrounding Wuyishan National Park can significantly contribute to creating an extensive ecological network that supports local conservation.

In addition to achieving a specific PA coverage, the Post-2020 Global

Biodiversity Framework also recognizes the importance of habitat quality and the need for conservation at all levels of biodiversity, from the levels of populations to species and ecosystems to large-scale ecological processes. According to our analysis of both spillover (i.e. stepping stones) and non-spillover sites, the ratio of pericoupling to telecoupling connections around stepping stones was more than twice that around other sites. The ability of stepping stones to maintain connectivity was measured in terms of the number and direction of suitable connecting corridors with low-cost distance as well as the interlinkages between neighboring stepping stones. The stepping stones with large numbers and connected corridors in more directions can connect more surrounding habitats than other added sites. The stepping stones are identified as high-priority conservation areas as well as potential priority areas for biodiversity restoration. As one of the important criteria in the National Park System of China, these were identified with high capacity of biodiversity conservation. For every additional high-quality habitat of stepping stone in the offset analysis, it can respectively offset the impact intensity (resistance) of 1.2 % units from population density and 1.3 units land use change. While implementing national park management system, these quantitative results are conducive to guiding the consolidation and reorganization of protected areas with increase of human disturbances, providing a certain reference basis for habitat fragmentation restoration and improving ecosystem services. The identification of stepping stone sites in this study also informs the optimization of sites for monitoring human–nature interactions related to conservation in rapidly developing areas at the global level. This approach provides a method of selecting PAs to facilitate improved connectivity and handling of increasing human disturbances, particularly disturbances that may degrade ecological functions; effective compensation must also consider the socioeconomic elements.

#### 4.3. Evaluation of the role of ecological corridors in supporting human society

To explore the socioeconomic dimensions of ecological connectivity, we further analyzed the conservation investments based on ecosystem service values and payments for ecosystem services (Yang et al., 2013) in the offset simulations. A comparison of the ecosystem service values in the areas of disappeared and newly connected corridors revealed that all eleven key ecosystem service values in the newly connected corridors were lower than those in the disappeared corridors due to the changes in population and landscape patterns (Fig. S4 and Fig. S5, Table S3 and Table S4). The average value of total ecosystem services in the disappeared corridors was nearly 1.5 times that in the areas of newly added corridors. The most significant differences between values were observed in the southern part of our study areas, where the majority of NPAs were located. In particular, the value of cultural ecosystem services (landscape aesthetics) turned out to be dependent on the type of service, with much higher differences between disappeared and newly added corridors. The disappeared corridors with high service values in the southern region were replaced with newly added corridors with relatively low value, and the large gap in cultural services between the two groups of corridors reveals the degradation of cultural ecosystem services from ecological networks to local society. Such degradation between two groups of corridors was mainly caused by the increase in human disturbances and related degradation of the natural ecosystem in the newly connected network. Those newly added habitats and corridors were not able to be connected with high-quality natural landscapes that provide valuable ecosystem services; they were connected by alternative natural and seminatural landscapes with a relatively high level of human influence and low ecosystem support.

The phenomenon of degradation was also found in the total payment for ecological compensation (Fig. S6 and Fig. S7, Table S5). According to the datasets collected in our study area, the regions of disappeared corridors were covered with very high values of ecological compensation (net gain). The relatively low values of compensation in the newly

added corridors suggest the degradation of resources in supporting local society. Even though the ecological connectivity in both groups of corridors is maintained at the same level, the gaps in ecosystem service values to human society and payment to ecological compensation address the challenges in maintaining overall balances in both ecological and social systems.

#### 4.4. Verification

To evaluate the accuracy of modeled landscape connectivity among PAs, a global biodiversity map of amphibians, birds and mammals was used to verify the results in our study area (Jenkins et al., 2013). We categorized all data layers of the species distribution into four grades from low to high (Level 1 to 4, respectively, in Table S6). Although the 20-km effective area with high connectivity accounted for only 1/3 of the study area, it covered 53 % of the high biodiversity area (Level 3 and 4, in Table S7) in the study area. This finding suggests that the contribution of this region to connectivity was twice that of the remaining 2/3. According to monitoring data in Nanling National Protected Area since 2012, slated for inclusion in China's National Park System this year. We found that over 80 monitoring sites are placed within the pixels of connected corridors in our modelling results. The key species in these sites include: *Muntiacus vaginalis*, *Dremomys pyrrhomerus*, *Melogale moschata*, *Macaca thibetana*, *Lophura nycthemera*, *Myophonus caeruleus*, *Tragopan caboti* and *Arborophila gingica*.

In addition, we used GDP data with a 1-km resolution as a counter verification source; these data combine nighttime light and residential density data ([http://www.resdc.cn/DOI/doi.aspx?DOIid%20=%2033&tdsourcetag%20=%20s\\_pcqq\\_aiomsg](http://www.resdc.cn/DOI/doi.aspx?DOIid%20=%2033&tdsourcetag%20=%20s_pcqq_aiomsg)). Our results indicate that only 2.5 % of the high-GDP area was located in the 200-km effective area of high connectivity, which suggests a low level of human-related threats to biodiversity conservation in this area. In general, the comparison of effective areas and other areas reflects the high conservative potential of the modeled connecting areas, and areas with high connectivity can be considered essential conservation corridors adjacent to PAs.

## 5. Conclusions

Biodiversity and habitat protection are global issues that require efforts across multiple scales to maintain metacoupling connectivity and thus ensure the resilience of ecosystem functions, as recommended under the Post-2020 Global Biodiversity Framework. Coastal areas have the lowest coverage of PAs, thus, establishing and connecting PAs in rapid urbanizing areas are among the most challenging and urgent goals. The quantification of the metacoupling network encompassing the well-connected areas in this study highlights the essential role of PAs for adaption to increased human disturbance. The aspect of connectivity from natural level is represented by the connected areas and corridors, and the aspect from human level is shown by the payments for ecosystem services and ecosystem service values. Among the upgraded 89 protected areas in our study area, sites identified with the metacoupling network should be priority conservation areas in China's coastal regions for halting biodiversity loss. Especially, those identified connectivity area for conservation with high value of ecosystem services may contribute to improve efficiency of biodiversity restoration under the global biodiversity framework. The pattern of connectivity under different scenarios represents an efficient improvement in structural connectivity in terms of pericoupling and telecoupling connections. Upgrading PPAs to NPAs yielded effective telecoupling interconnections among NPAs in areas with few connections as well as unconnected areas, such as the national pilot area in Guangdong-Hong Kong-Macao Great Bay Area intend to lead sustainable development of megacities. Our research address the importance of adding new habitats in biodiversity conservation, which try to give an answer to the SLOSS debate in the metacoupled urbanizing areas in China. The areas of increased

connectivity differed from those of decreased connectivity; thus, the offset effect occurred in terms of distant connectivity compensation. This distant restoration of connectivity networks by upgrading PPAs provides a practical approach for improving connectivity and counterbalancing rapid increase of anthropogenic disturbance. To deliver our results at the practical basis, we are collaborating with Wuyishan National Park and Nanling National Protected Area (slated for inclusion in China's National Park System in 2023). We aim to integrate landscape connectivity into the planning of these two sites with local management office.

Biodiversity conservation is dependent upon protection, and effective connections among PAs are key in biodiversity conservation. Simulations of offset connectivity in response to increased population density and landscape changes indicate a practical way to achieve biodiversity conservation targets from the local to global scales and can be used to compare the impacts of these two key factors in terms of connectivity. Increases in the number of added PAs improved the efficiency of connecting PAs through the cumulative effect of network connectivity. These simulations of offset connectivity can inform the identification of the most ecologically cost-effective corridors to connect PAs in the context of the Convention on Biological Diversity. In recognition of a world where human influence is increasingly pervasive, the significant degradation of ecosystem service values and payment for ecological compensation in offset scenarios address the challenges of maintaining the resilience of coupled human and natural systems. Therefore, it is important to assess both human and natural systems under the global biodiversity framework.

#### CRediT authorship contribution statement

**Yi Li:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Qihao Jin:** Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Conceptualization. **Zhixue Chen:** Writing – review & editing, Visualization, Validation, Software, Methodology, Formal analysis. **Bingchao Yin:** Writing – original draft, Software, Methodology, Formal analysis. **Yangfan Li:** Writing – review & editing, Writing – original draft, Supervision, Resources, Conceptualization. **Jianguo Liu:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization.

#### 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.

#### Data availability

Data will be made available on request.

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#### Appendix A. Supplementary data

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#### References

- Adams, V.M., Iacona, G.D., Possingham, H.P., 2019. Weighing the benefits of expanding protected areas versus managing existing ones. *Nat. Sustain.* 2, 404–411. <https://doi.org/10.1038/s41893-019-0275-5>.
- Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N., Kremen, C., 2022. Functional connectivity of the world's protected areas. *Science* 376, 1101–1104. <https://doi.org/10.1126/science.abl8974>.
- Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M., Levey, D.J., 2009. Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proc. Natl. Acad. Sci. USA* 106, 9328–9332. <https://doi.org/10.1073/pnas.0809658106>.
- Caetano, G.H.D.O., Vardi, R., Jarić, I., Correia, R.A., Roll, U., Verissimo, D., 2023. Evaluating global interest in biodiversity and conservation. *Conserv. Biol.* 14100 <https://doi.org/10.1111/cobi.14100>.
- Chauvenet, A.L.M., Watson, J.E.M., Adams, V.M., Di Marco, M., Venter, O., Davis, K.J., Mappin, B., Klein, C.J., Kuempel, C.D., Possingham, H.P., 2020. To achieve big wins for terrestrial conservation, prioritize protection of ecoregions closest to meeting targets. *One Earth* 2, 479–486. <https://doi.org/10.1016/j.oneear.2020.04.013>.
- Choi, C.-Y., Shi, X., Shi, J., Gan, X., Wen, C., Zhang, J., Jackson, M.V., Fuller, R.A., Gibson, L., 2022. China's Ecological Conservation Redline policy is a new opportunity to meet post-2020 protected area targets. *Conserv. Lett.* 15, e12853 <https://doi.org/10.1111/conl.12853>.
- Cumming, G.S., Allen, C.R., 2017. Protected areas as social-ecological systems: perspectives from resilience and social-ecological systems theory. *Ecol. Appl.* 27, 1709–1717. <https://doi.org/10.1002/eap.1584>.
- Di Marco, M., Venter, O., Possingham, H.P., Watson, J.E.M., 2018. Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* 9, 4621. <https://doi.org/10.1038/s41467-018-07049-5>.
- Gill, D., Mascia, M., Ahmadi, G., Glew, L., Lester, S., Barnes, M., Craigie, I., Darling, E., Free, C., Geldmann, J., Holst, S., Jensen, O., White, A., Basurto, X., Coad, L., Gates, R., Guannel, G., Mumby, P., Thomas, H., Fox, H., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543, 665–669. <https://doi.org/10.1038/nature21708>.
- Golden Kroner, R.E., Qin, S., Cook, C.N., Krithivasan, R., Pack, S.M., Bonilla, O.D., Cort-Kansinall, K.A., Coutinho, B., Feng, M., Martínez García, M.I., He, Y., Kennedy, C.J., Lebreton, C., Ledezma, J.C., Lovejoy, T.E., Luther, D.A., Parmanand, Y., Ruiz-Agudelo, C.A., Yereña, E., Morón Zambrano, V., Mascia, M.B., 2019. The uncertain future of protected lands and waters. *Science* 364, 881–886. <https://doi.org/10.1126/science.aau5525>.
- Hilty, J., Worboys, G., Keeley, A., Woodley, S., Lausche, B., Locke, H., Carr, M., Pulsford, I., Pittock, J., White, J.W., Theobald, D., Levine, J., Reuling, M., Watson, J., Ament, R., Tabor, G., 2020. Guidelines for Conserving Connectivity through Ecological Networks and Corridors. IUCN, International Union for Conservation of Nature. <https://doi.org/10.2305/IUCN.CH.2020.PAG.30>.
- IUCN, 2021. IUCN's Key Messages First Draft of the Post-2020 Global Biodiversity Framework. IUCN, Gland, Switzerland.
- Jenkins, C.N., Pimm, S.L., Joppa, L.N., 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci. USA* 110, E2602–E2610. <https://doi.org/10.1073/pnas.1302251110>.
- Kühl, H.S., Boesch, C., Kulik, L., et al., 2019. Human impact erodes chimpanzee behavioral diversity. *Science* 363, 1453–1455. <https://doi.org/10.1126/science.aau4532>.
- Li, Y., Yin, B., Li, Y.F., 2019. Early warning signals for landscape connectivity and resilient conservation solutions. *Land Degrad. Dev.* 30, 73–83. <https://doi.org/10.1002/ldr.3206>.
- Liu, J., 2017. Integration across a metacoupled world. *Ecol. Soc.* 22, 29. <https://doi.org/10.5751/ES-09830-220429>.
- Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., Ostrom, E., Ouyang, Z., Provencher, W., Redman, C.L., Schneider, S.H., Taylor, W.W., 2007. Complexity of coupled human and natural systems. *Science* 317, 1513–1516. <https://doi.org/10.1126/science.1144004>.
- Lü, Y., Zhang, L., Zeng, Y., Fu, B., Whitham, C., Liu, S., Wu, B., 2017. Representation of critical natural capital in China. *Conserv. Biol.* 31, 894–902. <https://doi.org/10.1111/cobi.12897>.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, New Jersey.
- McGuire, J.L., Lawler, J.J., McRae, B.H., Nuñez, T.A., Theobald, D.M., 2016. Achieving climate connectivity in a fragmented landscape. *Proc. Natl. Acad. Sci. USA* 113, 7195–7200. <https://doi.org/10.1073/pnas.1602817113>.
- McRae, B.H., Shirk, A.J., Platt, J.T., 2013. *Gnarly Landscape Utilities: Resistance and Habitat Calculator User Guide*.
- MEE (Ministry of Ecology and Environment the People's Republic of China), 2017. *Report on the State of the Environment in China 2017*. Ministry of Ecology and Environment the People's Republic of China (in Chinese).
- Moore, J.W., Schindler, D.E., 2022. Getting ahead of climate change for ecological adaptation and resilience. *Science* 376, 1421–1426. <https://doi.org/10.1126/science.abo3608>.
- Mozelewski, T.G., Robbins, Z.J., Scheller, R.M., 2022. Forecasting the influence of conservation strategies on landscape connectivity. *Conserv. Biol.* 36, e13904 <https://doi.org/10.1111/cobi.13904>.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Boerger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhussaini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.

- P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G. M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. <https://doi.org/10.1038/nature14324>.
- Núñez, T.A., Lawler, J.J., Mcrae, B.H., Pierce, D.J., Krosby, M.B., Kavanagh, D.M., Singleton, P.H., Tewksbury, J.J., 2013. Connectivity planning to address climate change. *Conserv. Biol.* 27, 407–416. <https://doi.org/10.1111/cobi.12014>.
- Pan, W., Wang, J., Li, Y., Chen, S., Lu, Z., 2023. Spatial pattern of urban-rural integration in China and the impact of geography. *Geogr. Sustain.* 4, 404–413. <https://doi.org/10.1016/j.geosus.2023.08.001>.
- Parks, S.A., Carroll, C., Dobrowski, S.Z., Allred, B.W., 2020. Human land uses reduce climate connectivity across North America. *Glob. Change Biol.* 26, 2944–2955. <http://doi.org/10.1111/gcb.15009>.
- Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Fergler, S.W., Frederiksen, S.B., Gebert, F., Gerschlaue, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Kühnel, A., Mayr, A.V., Mwangomo, E., Ngeresa, C., Njovu, H.K., Otte, I., Pabst, H., Renner, M., Röder, J., Rutten, G., Schellenberger Costa, D., Sierra-Cornejo, N., Vollstädt, M.G.R., Dulle, H. I., Eardley, C.D., Howell, K.M., Keller, A., Peters, R.S., Ssymank, A., Kakengi, V., Zhang, J., Bogner, C., Böhning-Gaese, K., Brandl, R., Hertel, D., Huwe, B., Kiese, R., Kleyer, M., Kuzyakov, Y., Nauss, T., Schleuning, M., Tschapka, M., Fischer, M., Steffan-Dewenter, I., 2019. Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature* 568, 88–92. <https://doi.org/10.1038/s41586-019-1048-z>.
- Ren, Y., Deng, L., Zuo, S., Luo, Y., Shao, G., Wei, X., Hua, L., Yang, Y., 2014. Geographical modeling of spatial interaction between human activity and forest connectivity in an urban landscape of southeast China. *Landsc. Ecol.* 29, 1741–1758. <https://doi.org/10.1007/s10980-014-0094-z>.
- Saura, S., 2021. The Habitat Amount Hypothesis implies negative effects of habitat fragmentation on species richness. *J. Biogeogr.* 48, 11–22. <https://doi.org/10.1111/jbi.13958>.
- Saura, S., Bertzky, B., Bastin, L., Battistella, L., Mandrici, A., Dubois, G., 2019. Global trends in protected area connectivity from 2010 to 2018. *Biol. Conserv.* 238, 108183. <https://doi.org/10.1016/j.biocon.2019.07.028>.
- Tesfaw, A.T., Pfaff, A., Golden Kroner, R.E., Qin, S., Medeiros, R., Mascia, M.B., 2018. Land-use and land-cover change shape the sustainability and impacts of protected areas. *Proc. Natl. Acad. Sci.* 115, 2084–2089. <https://doi.org/10.1073/pnas.1716462115>.
- Theobald, D.M., 2010. Estimating natural landscape changes from 1992 to 2030 in the conterminous US. *Landsc. Ecol.* 25, 999–1011. <https://doi.org/10.1007/s10980-010-9484-z>.
- Tromboni, F., Liu, J., Ziaco, E., Breshears, D.D., Thompson, K.L., Dodds, W.K., Dahlin, K. M., LaRue, E.A., Thorp, J.H., Viña, A., Laguë, M.M., Maasri, A., Yang, H., Chandra, S., Fei, S., 2021. Macrosystems as metacoupled human and natural systems. *Front. Ecol. Environ.* 19, 20–29. <https://doi.org/10.1002/fee.2289>.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., et al., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359, 466–469. <https://doi.org/10.1126/science.aam9712>.
- UNEP, 2016. WCMC (United Nations Environment Program-Environment World Conservation Monitoring Centre). IUCN (International Union for Conservation of Nature). *Protected Planet Report 2016*.
- United Nations (UN), 2015. Transforming our World: The 2030 Agenda for Sustainable Development. United Nations. <https://sdgs.un.org/2030agenda>.
- Ward, M., Saura, S., Williams, B., Ramirez-Delgado, J.P., Arafeh-Dalmau, N., Allan, J.R., Venter, O., Dubois, G., Watson, J.E.M., 2020. Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nat. Commun.* 11, 4563. <https://doi.org/10.1038/s41467-020-18457-x>.
- Woolmer, G., Trombulak, S.C., Ray, J.C., Doran, P.J., Anderson, M.G., Baldwin, R.F., Morgan, A., Sanderson, E.W., 2008. Rescaling the Human Footprint: a tool for conservation planning at an ecoregional scale. *Landsc. Urban Plann.* 87, 42–53. <https://doi.org/10.1016/j.landurbplan.2008.04.005>.
- Xu, W., Xiao, Yi, Zhang, J., Yang, W., Zhang, L., Hull, V., Wang, Z., Zheng, H., Liu, J., Polasky, S., Jiang, L., Xiao, Yang, Shi, X., Rao, E., Lu, F., Wang, X., Daily, G.C., Ouyang, Z., 2017. Strengthening protected areas for biodiversity and ecosystem services in China. *Proc. Natl. Acad. Sci. USA* 114, 1601–1606. <https://doi.org/10.1073/pnas.1620503114>.
- Yang, W., Liu, W., Viña, A., Luo, J., He, G., Ouyang, Z., Zhang, H., Liu, J., 2013. Performance and prospects of payments for ecosystem services programs: evidence from China. *J. Environ. Manag.* 127, 86–95. <https://doi.org/10.1016/j.jenvman.2013.04.019>.
- Yoon, H.S., Vijay, V., Armsworth, P.R., 2022. Accounting for spatial heterogeneity in the added conservation value of land protection when prioritizing protected areas. *Conserv. Biol.* 36, e13960. <https://doi.org/10.1111/cobi.13960>.