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# Current national nature reserves are insufficient to safeguard the long-term survival of birds and mammals in China

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Enhancing the connectivity of protected areas is a global consensus for conserving biodiversity. Yet, it is unclear whether habitats are sufficiently connected within protected areas to efficiently protect wildlife populations for long-term survival. Here we show that, in general, China's national nature reserves can effectively protect about one-half of the bird and mammal populations within protected areas for long-term survival. However, they can only protect 25% of birds and 13% of terrestrial mammals with high motility. Areas of low conservation effectiveness are highly overlapped with protected areas of small size and high intensity of human activity. Artificial landscapes (arable land and built-up land), which account for less than 2% area of the protected areas, disproportionately cause nearly 40% of the connectivity loss. The results suggest that maintaining high levels of functional connectivity within protected areas is as important as maintaining high connectivity in the national or global protected area networks. Our findings have important implications for improving the management of protected areas in China and beyond.

Protected areas (PAs) are a key tool in the effort to spearhead nature conservation<sup>1,2</sup>. The effectiveness of PAs is impacted through a multi-dimensional approach of design, location, functional connectivity, and management<sup>3</sup>. Assessing their effectiveness in perpetuating the future of biodiversity becomes extraordinarily important, yet challenging<sup>3</sup>. Previous studies on the effectiveness of PAs have often focused on the total extent, representativeness, and governance components of PAs<sup>3,4</sup>. Nevertheless, functional connectivity, an indicator used to evaluate the difficulty of animal movement within habitat networks<sup>5</sup>, has been frequently ignored, although it represents a fundamental dimension that directly regulates ecological effectiveness. Moreover, fewer studies have quantified the impact of PAs on the health and persistence of wildlife populations, particularly at national and regional scales<sup>6,7</sup>. Therefore, the Kunming-Montreal Global biodiversity framework, adopted at the 15th meeting of the Conference of Parties to the UN Convention on Biological Diversity (CBD COP15), reiterates the call to maintain, enhance or restore, and significantly increase functional connectivity of wildlife habitats<sup>8</sup>.

Most analyses of PA effectiveness that focus on conservation tools such as total area, representation, and management have overlooked the impact of habitat quality on wildlife, assuming that the areas designated as PAs provide high-quality, suitable habitats for wildlife populations<sup>9</sup>. In reality,

however, the potential movement of wildlife populations is limited by habitat quality<sup>10</sup>. Natural landscape heterogeneity and changes in landscape patterns due to human activities within PAs may diminish functional connectivity and change habitat circulation patterns for wildlife species<sup>11,12</sup>. Recently, there has been a growing consensus that maintaining well-connected habitats within and among PAs can safeguard wildlife's long-term survival<sup>8,13</sup> and efficiently reduce the risk of population extinction caused by habitat fragmentation<sup>2,7,14</sup>. Hence, functional connectivity is pivotal for many ecological processes at various spatial-temporal scales, for instance, from daily foraging movements to inter-population dispersal<sup>15</sup>. Several studies have explored functional connectivity within PA networks and within individual PAs, emphasizing the necessity to establish and increase new PAs to improve functional connectivity<sup>12,16,17</sup>. However, most studies regarding functional connectivity are often organized and analyzed at a single scale<sup>12</sup>, lacking comprehensive and inter-regional comparability in extension to biological taxa<sup>15,18,19</sup>. Therefore, integrating spatial-temporal scales in evaluating the functional connectivity of PAs is crucial to understanding the effects of specific life cycles on the movements of different species<sup>15</sup>.

Habitat availability and habitat type diversity are the main factors regulating functional connectivity in natural scenarios, whereas human-

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dominated habitat loss and fragmentation are severe challenges to sustaining well connectedness of wildlife habitats<sup>20</sup>. Most PAs are located in human-dominated, fragmented land-use scenarios where wildlife populations are frequently isolated by human-modified landscapes<sup>21</sup>. Several studies have reported that declines in habitat amounts and habitat heterogeneity of natural landscapes can substantially reduce the population flow and gene exchange of wildlife species, further increasing the risk of extinction<sup>10–12</sup>. For example, habitat fragmentation caused by transportation infrastructure has become one of the serious threats to biodiversity<sup>22,23</sup>, especially the impact of roads on intact natural ecosystems such as PAs<sup>24–26</sup>. Hence, there is an urgent need for research that focuses on the key factors that impact the functional connectivity of PAs. National nature reserves (NNRs), which form the key body of PAs and occupy 10% of the country's land surface in China, with the strictest management<sup>27</sup>. However, the NNRs are often established based on province or even county boundaries rather than on gaps in biodiversity conservation. There are significant geographical and regional variations in the amount and/or size distributed. In particular, conservation investments at the national level are disproportionately invested in remote areas that are less likely to be threatened by agriculture or human activities. Because the expansion of NNRs extent in these regions is more easily achieved<sup>28,29</sup>. Therefore, assessing how effective they are in achieving a sustainable biodiversity future is not trivial<sup>9</sup>.

Numerous methods have been developed to model functional connectivity and explore how habitats impact the sustainability of wildlife populations<sup>30,31</sup>. Graph theory is widely used in conservation and landscape planning, which requires less data input to provide reliable visualization of ecological networks<sup>32,33</sup>. The ecological network, a set of habitat patch nodes connected by potential links between populations, is frequently used to model the functional connectivity of wildlife populations<sup>15</sup>. By using these approaches, we conducted a robust evaluation of the impact of PAs on population connectivity at the national scale. Our study is designed to assess how China's NNRs (474 in total number) affect the wildlife populations of 11,424 birds and terrestrial mammals with different habitat preferences within each individual NNR, where populations were defined as virtual species groups characterized by their ecological niches<sup>34–36</sup>. We focused on "landscape species" or "umbrella species" whose viable populations are restricted within a single NNR. The population life histories were combined with a nested scale approach at both intra- and inter-population scales (Fig. S1 in Supporting Information). The effectiveness of NNRs in terms of their ability to sustain bird and mammal populations maintains a minimum threshold of inter-population genetic exchange connectivity for long-term survival. Specifically, we address three questions: First, how do China's NNRs affect the effectiveness of conserving inner populations for long-term survival? Second, what are the natural and anthropogenic factors that regulate the effectiveness of the NNRs? Third, to what degree do the artificial landscapes (e.g., roads) modify the effectiveness of the NNRs?

## Results

### Patterns of functional connectivity and effectiveness of NNRs

NNRs are widely distributed across the geographic and climatic gradients in China (Fig. S2 in Supporting Information). The functional connectivity of wildlife populations (including birds and terrestrial mammals) in NNRs was highly diverse between habitat types within each biome and among different biomes (Fig. 1 and Fig. S4). For forest habitats, the functional connectivity, on average, was the highest in temperate coniferous forests and temperate broadleaf and mixed forests in China's NNRs. For grassland habitats, the functional connectivity was the highest in temperate grasslands, savannas, and shrublands. For wetland habitats, flooded grasslands and savannas exhibited the highest functional connectivity in China's NNRs (Fig. 1 and Fig. S5).

China's NNRs effectively protected 57% of bird populations and 42% of terrestrial mammal populations for long-term survival, and a total of 50% for both birds and mammals (Table S3 in Supporting Information). However, for birds and mammals with high motility, the proportions of effectively protected populations were less than 25% and 13%, respectively.

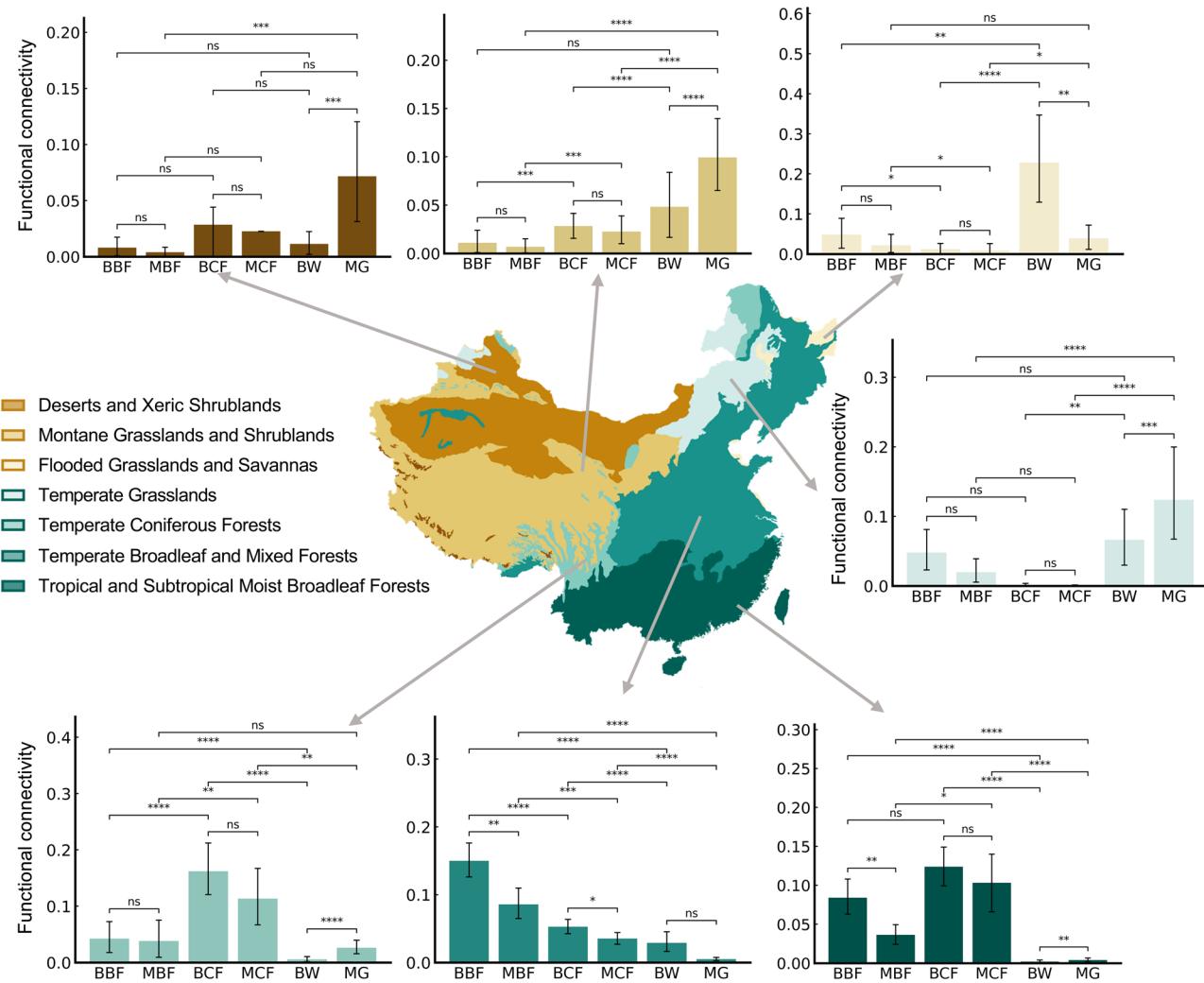
Further, we mapped the distribution extent and effectiveness patterns of birds and mammals using the distribution extent of real species matched to our virtual species (Fig. S9). The results showed that PAs in eastern China provide poor protection for high-mobility birds and terrestrial mammals (Table S5). The habitat area of effective NNRs is, on average, 5.6 times larger for birds and 13.5 times larger for mammals than that of ineffective NNRs for high movement ability species. Our results also showed that about 48% of NNRs exhibited a sufficiently large (>50%) proportion of habitat area (HA), yet NNRs area is too small to effectively protect potentially viable populations (Fig. 2f). Similarly, high overlap occurred between small PAs, high human pressure, and low conservation effectiveness areas (Fig. 2). Specifically, the two biomes, temperate coniferous forests and temperate broadleaf and mixed forests, exhibited the lowest NNR effectiveness (10.8% and 15.9%, respectively) for high motility species (Table S3). In addition, the two biomes showed less than 3% of the NNRs coverage (the global average is 10% and 16%, respectively) (Fig. 2e), and the average area of individual NNRs was less than 4% of the national average PA size (Table S4). More importantly, the two biomes have the second and fifth-highest global average conversion rates of natural vegetation to other land uses (Fig. 2e) and the most densely populated and economically developed regions in China<sup>37</sup>.

### Impact of habitat characteristics on functional connectivity

The random forest importance analysis for natural and anthropogenic factors influencing the functional connectivity of NNRs showed that the proportion of HA contributed more than other factors in determining the variation of functional connectivity of NNRs (Fig. 3). For NNRs located in the eastern part of the Hu-line, the dividing line between population development and the social economic pattern in China<sup>38</sup>, functional connectivity was more likely to be regulated by artificial landscape intensity (ALI). For NNRs near the Hu-line, functional connectivity was more easily constrained by NNRs area (AREA), whereas it was more vulnerable to ecosystem diversity (ED) for NNRs located in the western part of the Hu-line (Fig. 3). The best-fitting generalized additive model (GAM) analysis showed that functional connectivity was influenced by the interactions of HA, ALI, AREA, and ED. Functional connectivity increased with an increasing proportion of HA. However, functional connectivity decreased with increasing ALI (Fig. S13a) and exhibited a significant quadratic relationship with ED, peaking at the medium levels of ED (Fig. S13b). In addition, functional connectivity decreased with increasing protected area for small PAs and increased with increasing protected area for large PAs. The effect of the protected area on functional connectivity increased with an increasing proportion of HA and ED (Fig. S13c, d).

### Impact of human activities on functional connectivity and NNR effectiveness

Artificial landscapes, which account for less than 2% of the total NNR areas, disproportionately reduced nearly 40% of the functional connectivity for highly mobile terrestrial mammals (Fig. 4a and Table S6). Terrestrial mammals with stronger median daily and dispersal movement capacity were generally more vulnerable to the impacts of human activities. However, birds with weaker median daily and dispersal movement capacity were more sensitive to the impacts of artificial landscapes (Fig. S6). The effectiveness of NNRs decreased with increasing intensity of human activities (Fig. S11). In addition, non-human dominated NNRs ( $HF > 4$  is often used as a threshold to measure whether dominated by humans; see Table S7) provided great effectiveness for wildlife populations. For high-mobility birds and terrestrial mammals, the proportion of effectively protected populations in NNRs with  $HF < 4$  increased up to 50%; whereas the proportion of effectively protected populations decreased to less than 30% with increasing intensity of human activities (Fig. 4b). In the scenario of removing artificial landscapes, we found that barrier effect-induced decreases in functional connectivity reduced the conservation effectiveness of the population. However, this does not make a complete reversal of whether the population can be effectively conserved.



**Fig. 1 | Map of the functional connectivity.** The gradation of colors from green to yellow represents seven different biomes. The horizontal axis labels of the histogram represent the following: BBF, birds living in broadleaf forest habitats; MBF, terrestrial mammals living in broadleaf forest habitats; BCF, birds living in coniferous forest habitats; MCF, terrestrial mammals living in coniferous forest habitats; BW, birds living in wetland habitats; MG, terrestrial mammals in grassland habitats. The vertical lines denote the 95% confidence interval. Significance levels are as follows: \* $< p \leq 0.05$ ; \*\* $, 0.001 < p \leq 0.01$ ; \*\*\* $, 0.0001 < p \leq 0.001$ ; \*\*\*\* $, p \leq 0.0001$ . Statistical methods using the Mann-Whitney  $U$  non-parametric test.

birds living in wetland habitats; MG, terrestrial mammals in grassland habitats. The vertical lines denote the 95% confidence interval. Significance levels are as follows: \* $< p \leq 0.05$ ; \*\* $, 0.001 < p \leq 0.01$ ; \*\*\* $, 0.0001 < p \leq 0.001$ ; \*\*\*\* $, p \leq 0.0001$ . Statistical methods using the Mann-Whitney  $U$  non-parametric test.

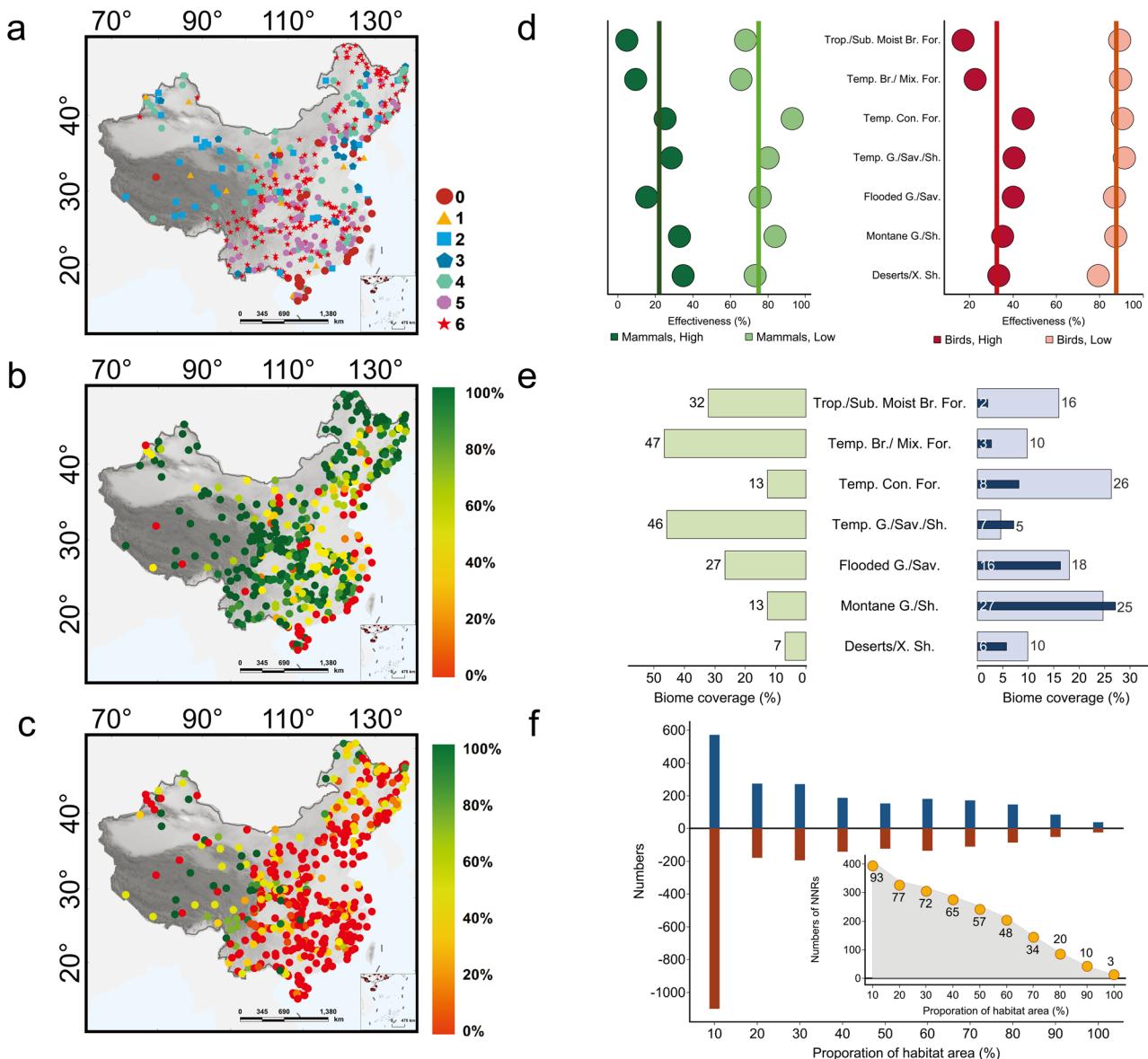
## Discussion

**Small-sized NNRs limit the effectiveness of safeguarding wildlife**  
 Our results demonstrate that nearly one-half of NNRs in China face risks of being too small for the long-term survival of bird and mammal populations. These findings highlight the importance of PAs size for safeguarding biodiversity, especially for sustaining the long-term survival of high-motility and large-body-size species<sup>2</sup>. Our findings suggest that the smaller size of PAs in eastern China limits their effectiveness in safeguarding wildlife, although most species with high movement ability are mainly distributed in western China. However, a considerable portion of threatened species were historically widespread in eastern China through our analysis of the list of Chinese terrestrial wildlife important habitats. Inadequate PA sizes result in higher exposure to human activities for these threatened species and, thus, higher risk of extinction. Moreover, from the lens of functional connectivity, we found a high degree of overlap between PAs of small size and high human activity intensity and areas of low conservation effectiveness. Global anthropogenic pressure assessment also shows that small PAs have higher anthropogenic intensity and undermine conservation effectiveness<sup>39</sup>. Our study adds new considerations to the debate on “single large or several small PAs”. Previous studies have shown that several small PAs generally support higher species richness than single larger ones but that larger PAs

are critical for the long-term survival of larger species<sup>6,40,41</sup>. The functional connectivity lens in this study differs from those of biodiversity and endangered species in conservation studies. First, biodiversity-focused studies are often based on the potential range of species, while ignoring the viable populations. Our study shows that sufficiently large PAs are critical for the long-term survival of populations. Second, we combined population life-history traits to define long-term survival using the concept of “meta-patches” that were nested at different scales such as population foraging and dispersal. Although the species we defined are virtual species constructed based on ecological niches, they can represent the vast majority of scenarios and provide inter-regionally comparable analyses.

## Multiple natural and anthropogenic factors regulate the functional connectivity of NNRs

Numerous studies have shown that human activities<sup>16,42–47</sup> and natural landscapes (e.g., habitat area size<sup>48</sup> and ecosystem type diversity)<sup>49</sup> have different degrees of impact on functional connectivity<sup>42,45</sup>. Yet, few studies have investigated the complex influences of these natural and anthropogenic factors on functional connectivity and how these influences vary across regions. Our abundant modeling data provide strong evidence for the complexity of factors influencing functional connectivity. First, habitat loss



**Fig. 2 | Proportion of effectively protected by National Nature Reserves (NNRs).** **a** The number of potentially resident species categories in NNRs. **b** and **c** The effectiveness of NNRs under low and high motility, respectively (for detailed information, refer to Fig. S7). **d** The effectiveness patterns of species within NNRs in various biomes. The green and red dots represent low and high-motility species, respectively. The colored lines parallel to the column axis represent the average proportion of effectiveness protected for various movement ability species, respectively (for detailed information, refer to Table S3). **e** Habitat conversion and protection in the world's 14 terrestrial biomes (following Watson et al. 2016). The light blue bars in the habitat protection proportions represent the global scale, whereas the

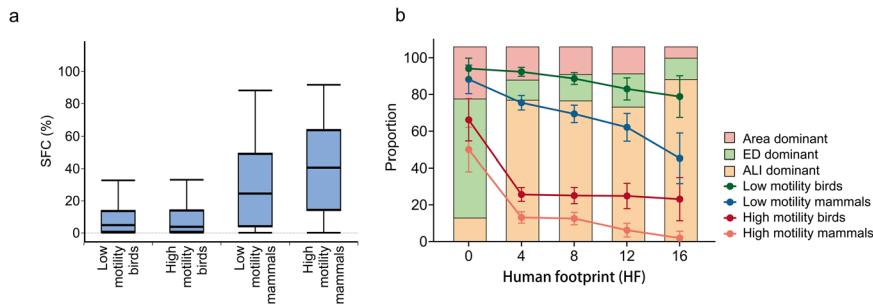
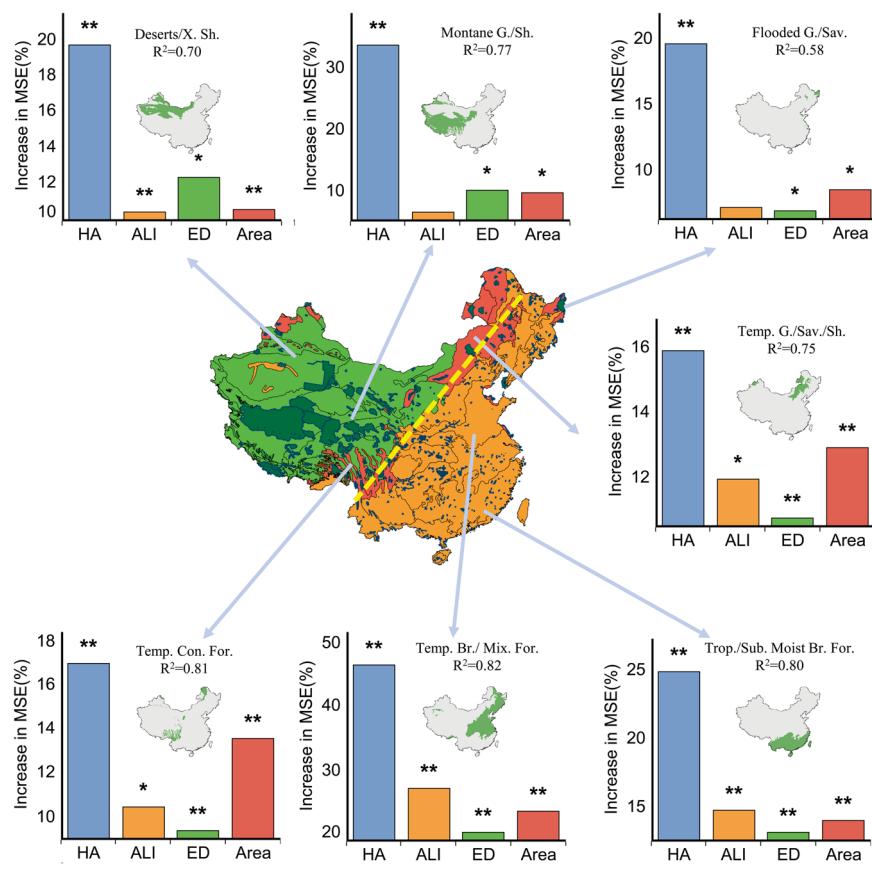
dark blue bars represent the China scale. **f** The relationship between the proportion of habitat area (HA) and effectiveness. The horizontal axis of the bar graph represents HA, and the vertical axis represents the number of populations that can/cannot be effectively conserved. Blue and positive values represent effective conservation, and red and negative values represent cannot be effectively conserved. The horizontal coordinate of the scatter plot represents HA, and the vertical coordinate represents the number of NNRs in which populations cannot be effectively conserved. The numbers near the dots represent the proportion of NNRs that cannot be effectively protected among all NNRs.

should be considered in all regions as the most coherent and critical threat to the functional connectivity and effectiveness of biodiversity conservation. Second, the impacts of NNR area, ecosystem diversity, and artificial landscape intensity on functional connectivity vary across different geographic areas. Hence, it is necessary to distinguish the degree of potential threats to functional connectivity and effectiveness of NNRs in different regions. We propose a framework of common but differentiated management strategies to enhance the role of NNRs in different geographic regions of China for safeguarding the long-term survival of bird and mammal populations. Moreover, decisions should be made with reference to the setting of relevant priority management strategies, maximizing functional connectivity benefits<sup>12</sup>.

### Infrastructure offsets conservation gains

Our study suggests that the construction of artificial hard-surface landscapes, such as roads and settlements, can substantially reduce functional connectivity and change the flow patterns of species in NNRs. Reducing the proportion of artificial landscapes in NNRs with high human footprints can improve functional connectivity more than increasing the proportion of habitat. Such findings support the current calls that merely expanding the size of existing NNRs probably did not improve conservation effectiveness to the high level expected<sup>29,50</sup>. Our study distinguished two important biota taxa, i.e., birds and terrestrial mammals, in the absence of current research on the conservation effectiveness of birds<sup>6,44,51–53</sup>. For terrestrial mammals, we found that the greater the movement capacity, the greater the loss of

**Fig. 3 | Potential drivers of functional connectivity in various biomes.** Random forest (RF) mean predictor importance (percentage of increase of mean square error) of proportion of habitat area (HA), artificial landscape intensity (ALI), ecosystem diversity (ED), and NNRs area (AREA) as drivers for functional connectivity. The accuracy importance measure was computed for each tree and averaged over the forest (500 trees). Percentage increases in the MSE (mean squared error) of variables were used to estimate the importance of these predictors, and higher MSE% values imply more important predictors. Significance levels are as follows: \* $P < 0.05$  and \*\* $P < 0.01$ . MSE, mean squared error.



**Fig. 4 | Effects of artificial landscape intensity (ALI) and human footprint (HF) on functional connectivity.** **a** Relative gain (sensitivity) of functional connectivity with different mobility in modeled scenarios without artificial landscapes. Error bars indicate the 95% credible intervals. **b** The impact of the human footprint on the

effectiveness of NNRs. Colored dots represent the mean effectiveness ratios of birds or terrestrial mammals with various motility abilities. Error bars indicate the 95% credible intervals. Colored blocks represent the proportion of effectiveness of NNRs in various driver-dominated biomes.

functional connectivity caused by human activities, which is corroborated by findings from a previous study<sup>34</sup>. For birds, however, we show that the weaker the movement ability, the higher the vulnerability of functional connectivity to the impact of infrastructure. Because highly mobile birds tend to rely more on flight than surface movement, linear infrastructure such as roads tend to have less impact on their movements. Migratory birds, for example, usually suffer from the risk of population extinction due to the loss of stepping-stone habitat<sup>54</sup>. Nonetheless, non-flying birds, such as the white-tailed ground chough, *Podoces biddulphi*<sup>35</sup>, and the Chinese rousie, *Tetrastes sewerzowi*<sup>36,37</sup>, are often threatened by habitat fragmentation due to human activities.

Importantly, we show that the conservation effectiveness of birds is less vulnerable to landscape fragmentation than terrestrial mammals with the same dispersal ability. This might be explained by the fact that birds of the same dispersal ability are generally less sensitive to roads than terrestrial

mammals when only road isolation effects are considered<sup>58</sup>. Agricultural fields within PAs may also provide a potential source of food and habitat for them<sup>59</sup>. It is worth noting that it does not imply that birds have a lower risk of extinction than terrestrial mammals - in fact, just the opposite<sup>52,60,61</sup>. Our study compares the difference of conservation effectiveness between birds and terrestrial mammals at the same dispersal distance. Their body size differs by tens or even hundreds of folds. The requirements for habitat patch size and food quantity are much lower than the needs of terrestrial mammals with the same movement abilities. Therefore, appropriate agricultural activities in non-core zones of PAs might be beneficial for some birds. However, the accompanying transportation infrastructure construction and other human activities such as noise from roads, vehicle crashes, and even the increase in tourism and poaching activities caused by road accessibility will undoubtedly undermine the overall conservation effectiveness<sup>62,63</sup>. Future conservation efforts should continue to focus on protecting the

agricultural field biodiversity out of NNRs to supplement the lack of conservation for vulnerable birds by NNRs alone<sup>64</sup>.

### Implications for management of PAs

Our study has important implications for improving the management of PAs in China and beyond. First, previous studies regarding the establishment and management of PAs are often discussed at the global or national scale, yet some important social and environmental issues need to be considered at a much more detailed scale due to intra-country and intra-regional heterogeneities. We propose a common but differentiated management framework to facilitate sub-regional priority implementation. Strategies of increasing the number/area of PAs and reducing the intensity of human activities in PAs combine to maximize benefits<sup>12</sup>. However, different conservation strategies should be prioritized in geographical areas with different socioeconomic conditions. Our findings suggest that increasing habitat diversity will be beneficial for improving the functional connectivity of NNRs because low ecosystem diversity limits the availability of suitable habitats for mammals and birds, such as water sources and wetlands. Second, we demonstrate that reducing human activity within PAs may improve functional connectivity and, thus, the degree of effective conservation. Nearly half of the PAs might suffer from being too small for viable populations for long-term survival. Merely restricting human activities in these PAs cannot effectively safeguard viable populations. We suggest that conservation investments that priority in size should be made for PAs that are too small to be effectively protected. Optimize and integrate previously established PAs based on administrative boundaries such as provinces and counties to create larger and more separated ownership and responsibility for PAs. For example, the establishment of large national parks as prioritized conservation investments<sup>65</sup>. Finally, given that most PAs are small in China, expanding PAs to the extent necessary to provide sufficient conservation for species may be politically, economically, and socially difficult due to its large population<sup>66</sup>. Therefore, it is critical to improve functional connectivity among PAs and link the PA nodes into national networks for maintaining and conserving high levels of biodiversity. Under the impact of climate change or increased human activity, viable populations may become less resilient, increasing the long-term extinction risk<sup>2</sup>. The establishment of cross-border PA networks, ecological corridors, and inter-regional cooperative efforts all enhance the migration of wildlife species and the connectedness of PAs.

### Methods

We modeled functional connectivity using Graphab, a software application for modeling ecological networks<sup>67</sup>, which is widely used in ecology, conservation, and landscape planning<sup>32</sup> that based on a graph theoretic method for simplified representation of visualizing ecological networks (Fig. S1 in Supporting Information). The nodes of ecological networks are habitat patches and the links represent the potential flow between them to simulate habitat connectivity of wildlife populations<sup>33</sup>. This approach is based on the theory of least-cost path (LCP) analysis, which designates a landscape resistance surface based on the hypothetical “cost” imposed by landscape components on species movement and identifies pathways that minimize the cumulative cost between locations<sup>68</sup>. Two inputs are required for this analysis: landscape resistance surface and the potential movement ability of wildlife.

**Landscape resistance surface.** The resistance of each landscape unit is calculated to reflect the “high” or “low” suitability of different landscape factors (e.g., land cover, topography, and human activities) and is intended to represent the sum of the assumed energy expenditures, mortality risks, or facilitative (or hindering) effects of landscape elements on wildlife movement. The resistance values for each factor were weighted according to their relative importance and combined to produce a movement resistance surface. The path cost between habitat patches for species is the resistance distance weighted by the cumulative resistance value of all crossed cells<sup>32</sup>. LCP analysis identifies paths that minimize the cumulative cost between

habitat patches and that minimize the cumulative resistance of movement<sup>68</sup>. We defined resistance values for each ecosystem type and artificial landscape (land cover/use type) based on various species taxa and their habitat preferences (Table S1 in Supporting Information). In particular, we set the resistance values for terrestrial mammals crossing the artificial hard-surface landscape as high as possible, especially for main roads, highways, and railroads. These linear infrastructures would often be separated on both sides by iron fences and barbed wire. Despite the design of corridors or culverts, these linear infrastructures still severely impede the movement of most terrestrial mammals<sup>69–72</sup>. We also set a high resistance value for birds to cross the artificial hard-surface landscape. The study has found that roads are not only a physical barrier to birds but include other impacts such as traffic accidents, chemical pollution, noise disturbance, poaching, etc<sup>22</sup>. To ensure the accurate evaluation of the long-term survival of bird populations, the impact of roads on birds is estimated to be large enough to avoid underestimation. Furthermore, it is important to note that the distribution of roads may be underestimated due to limited data accessibility, and the fences enclosing the roads are usually much wider than the vector data<sup>34</sup>. Therefore, it may be reasonable to consider the greater impact of roads on mammals and birds. We further revised the value of the resistance surface weighted by slope in terms of reflecting the cost of resistance to movement in steep topography (see subsequent DEM for calculation details).

**Potential movement ability of wildlife.** A distance needs to be defined when exploring the graph theory modeling of functional connectivity based on a resistance model approach to characterize the mobility of each species. Concurrently, the research target is oriented to the species, which could either refer to one or more realistic and specific biotic species<sup>73</sup>, as well as based on virtual species characterized by an ecological niche in a broader spatial and temporal scale and more widespread scenarios<sup>34,36</sup>. For the purpose of comparison among national nature reserves (NNRs) of different geographical regions and ecosystem types across China, we used a virtual species approach to provide a standardized and comparable protocol for all species<sup>34,74</sup>. We constructed six virtual species groups (birds for coniferous, broadleaf, and wetland habitat types; terrestrial mammals corresponding to coniferous, broadleaf, and grassland habitat types; abbreviated respectively as BCF, BBF, BW, MCF, MBF, and MG) based on two biological taxa and four habitat preferences. Since the dispersal process is a key factor in population viability<sup>35</sup>, each virtual species group is characterized by its dispersal distance. To fit the scale of movement within a single NNR, we used the 25th and 75th percentiles of the minimum enclosing circle diameter of NNRs vector boundary as the median dispersal distance for low and high motility virtual species groups, the distance is 10 km and 50 km respectively. To ensure a realistic match, we verified the reasonableness of the virtual species dispersal distance set by collecting the real species dispersal distance in literature and documents. We also examined other models with different dispersal distances and confirmed the high correlation between all models (see Reasonableness and sensitivity analysis for details). Moreover, we obtained three ecological variables, including median daily movement distance within populations, key patch area for meta-populations, and species geographic range area of isolated populations, based on the allometric relationships that allowed these ecological traits to be derived from dispersal distance among populations and diet (see The definition of NNR effectiveness for details). Given the lack of references on average daily movement distances for birds and terrestrial mammals, we adopted an allometric relationship model that calculates the home range of species<sup>75,76</sup>. The radius of a circle with the same home range area is used to approximately represent the average daily movement distance. In this study, we used herbivorous allotropic relationships to model the ecological traits of low movement ability species and carnivorous allotropic relationships to model the ecological traits of high movement ability species (Table S2). Our research focuses on these short-distance, long-timescale movements as they are more representative of the scale of movement occurring within each PAs and thus represent movements that promote gene flow, rescue effects, or climate adaptation<sup>12</sup>.

**Nature reserve data.** We used the robust polygon data collected from multiple data sources revised and integrated for the boundaries of NNRs in China. Up to 2024, there are 474 NNRs in China. Due to differences in data availability and management systems, Taiwan Province, Hong Kong, and Macau Special Administrative Regions are excluded. These NNRs account for 10.4% of China's total territorial surface area and 58% of the total area of various nature reserves in China. The distribution of the NNRs on the climatic gradient and NNRs' basic information are detailed in Figs. S2 and S3. For some watershed NNRs that are too small in size and have linear boundaries, we extended a buffer zone of 10 km outward from the known boundaries as the study area. For NNRs with marine ecosystems and marine creatures as conservation targets, the conservation effectiveness is only shown in Fig. 2a–c for the proportion of single NNR effectively protected. These NNRs are not included in the subsequent calculation of the proportion of effectively protected biomes and national scales.

**Resistance surface.** The landscape data used for the resistance surface is based on the ChinaCover 2010 (30 × 30 m resolution) land cover dataset<sup>77</sup>, and the 2020 land cover changes are monitored by visual interpretation of 2010 and 2020 Landsat satellite images and further overlayed with the OpenStreetMap dataset to refine the information on roads, waters, farm-lands, and settlements to obtain the 30 m resolution 2020 land cover dataset specifically built for the study of NNRs. Finally, the digital elevation model (DEM) is used to deduce the slope, which is overlaid with the land cover map to define the resistance surface.

**ChinaCover.** ChinaCover 2010 is based on remote sensing data as the main data source, supplemented by the vegetation map of the People's Republic of China (1:1,000,000), land use maps of 2000 and 2005, and slope and slope direction data, etc., produced by ASTERDEM, and adopts object-oriented technology to realize the interpretation. The primary classes of the classification system are consistent with the IPCC for 6 categories, and the secondary classes adopt 38 types with global unified code generated by FAO's LCCS. At present, the accuracy of ChinaCover2010 is 91% for primary classes and about 82% for secondary classes.

**Open Street Map.** Based on the updated ChinaCover for 2020 land cover, we overlaid the land cover categories that need to be focused on, especially the linear artificial landscape. We mainly used the Open Street Map (OSM) data (OpenStreetMap contributors, <https://www.openstreetmap.org>) to update the line features data for roads and paths, railways, and waterways, as well as the polygon features data for bodies of water and some buildings. A more detailed process is to divide the roads into major roads and minor roads. For linear road data, a width of 90 m is set for major roads, and a width of 30 m is set for minor roads. The rivers are divided into major rivers and minor rivers (stream, canal, and drain), and widths of 90 m and 30 m are set for these linear water bodies, respectively. However, in OSM, larger waters, rivers, and reservoirs are often used as polygonal geometries. The line geometries will then run through the middle of the polygon geometries in the direction of the water flow. We superimpose linear and polygonal geometric data during data processing related to water. In addition, we also overlaid the built-up and related land (residential, industrial, quarry, and farmland) layer data. Given the pace of road construction and data limitations, our results underestimate the intensity of artificial landscapes and the magnitude of human impacts.

**DEM.** We use a digital elevation model (DEM) to calculate the slope that is used together with the land cover map to define the resistance surface and to calculate the cost distance<sup>18</sup>. The DEM dataset was used with ASTER GDEM v2 (30 m), which was obtained from the Geospatial Data Cloud (<http://www.gscloud.cn>), and slope layers in percent were extracted using ArcGIS 10.2. Resistance values previously defined can be weighted by slope with the parameter coef ( $c$ ), which can adjust the importance of the slope ( $p$ ) weighting. For a given pixel, the resulting resistance value ( $r_{\text{final}}$ ) is calculated with the following formula:

$$r_{\text{final}} = r * (1 + c.p) \quad (1)$$

$p = 0$  if the slope is flat,  $p = 1$  for a slope of 100%.

We defined  $c = 10$ , which means the resistance value is doubled for a slope of 10%<sup>18</sup>.

**Functional connectivity and sensitivity of functional connectivity (SFC).** In this study, we used functional connectivity to quantify the conservation effectiveness of their viable populations. The analysis of functional connectivity is based on The Probability of Connectivity (PC) index<sup>5</sup>. This index provides the probability that two points randomly placed in the study area are connected. It is the most widely used index to quantify the functional connectivity efficiency of ecological networks. Functional connectivity has different distribution patterns among vegetation types and biomes (see Figs. S4 and S5). The PC index is given by the following expression:

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

where  $a_i$  and  $a_j$  are the areas of the habitat patches  $i$  and  $j$ , and  $A_L$  is the total studied area (both habitat and non-habitat patches).  $p_{ij}^*$  is defined as the maximum product probability of all possible paths between patches  $i$  and  $j$ <sup>67</sup>.

$p_{ij}$  is determined with an exponential function such that:

$$p_{ij} = e^{-\alpha d_{ij}} \quad (3)$$

where  $d_{ij}$  is the least-cost distance between patches  $i$  and  $j$ , and  $\alpha$  expresses the intensity of decreasing the dispersal probability  $p$  resulting from the exponential function<sup>67</sup>.

Different movement ability species have different sensitivity of functional connectivity after infrastructure (artificial landscape intensity) removal (see Fig. S6 and Table S6). The connectivity gain due to the removal of infrastructure ( $D$ ) is evaluated using the following expression to represent the sensitivity of functional connectivity (SFC):

$$\text{SFC} = \frac{(\text{PC}_D - \text{PC}) \times 100}{\text{PC}} \quad (4)$$

**Nested spatial and temporal scales of ecological processes.** We used the concept of metapatches, a concept that considers a nested scale from the interactions of individuals within populations to the interactions between separate populations<sup>15,34,73</sup>. Individuals within populations living and interacting on small spatial and temporal scales. Daily or seasonal movements connected a continuous habitat patch or several discontinuous habitat patches into a metapatch. This metapatch may include several home ranges of overlapping or non-overlapping individuals, and these collections of individuals are defined as a (local) population. The spatial and temporal scales of inter-population interactions are much larger, and usually exist several dispersal or genetic pathways linking several (local) populations to form a meta-population (Fig. S1).

**The definition of NNR effectiveness.** We measure the effectiveness of NNRs in terms of their ability to sustain wildlife populations over the long term. Populations must be large enough to maintain long-term survival in NNRs, or to maintain periodic genetic exchange by keeping well-connected with nearby populations. We used a trait-based criterion of survival, using the relationship between life history traits and movement ability to estimate the minimum meta-population size that could maintain NNR effectiveness. We refer the criteria of related literature and combine with the allometric relationship<sup>2,52,78–81</sup>, it is estimated that the minimum meta-population size is about 60 individuals for herbivorous mammals with interpopulation dispersal movement ability less than 10 km, and about 20 individuals for carnivorous mammals with interpopulation dispersal close to 50 km. For birds, both herbivorous birds with an interpopulation dispersal distance of about 10 km and carnivorous birds with an interpopulation dispersal distance close to 50 km have a minimum meta-population size of about 400 individuals. Particular emphasis must be placed on the fact that this is the least strict standard, preferring PAs as refugees rather than as solutions to biodiversity loss. We obtained the minimum key patch area for meta-

populations ( $\text{MinA}_k$ ) to maintain the above meta-population size based on allometric relationships similarly. The NNR effectiveness is defined by evaluating whether  $\text{MinA}_k$  in NNRs is sufficient to support the minimum meta-population size.

For species with relatively low movement ability, we define PAs as effective for conservation if the NNR is large enough to contain several populations and the habitat area occupied by the meta-population is up to  $\text{MinA}_k$ . For species with relatively high motility, the outer boundary of wildlife population survival has exceeded the extent of NNR. Single NNRs are unable to sustain any individual (local) populations, so we define them as NNRs that cannot be effectively protected. However, given that the habitats of some wildlife populations occupied a large part of the PA and that the habitats were geographically contiguously distributed, it is not possible to build the above scale-nested connectivity model. We considered species with habitat patches connected by daily distances larger than the species geographic range area of isolated populations ( $A_g$ , also obtained based on the above-mentioned allometric relationship) as effectively protected (Table S2). The minimum isolated population size is about 500 individuals for herbivorous mammals with a median daily movement distance of less than 1 km and about 60 individuals for carnivorous mammals with a median daily distance of 5 km. For birds, both herbivorous birds with a median daily distance of about 0.5 km and carnivorous birds with a median daily movement distance close to 2.4 km have a minimum meta-population size of about 10,000 individuals.

**Proportion of NNR effectively protected.** An individual proportion of NNR effectively protected is the ratio of the number of population types of virtual species that can be effectively protected over the number of potentially viable population types (the existence of ecosystems within NNR that are preferred by several of the six types of populations). For example, there are four types of ecosystems in NNR: coniferous forest, broadleaf forest, grassland, and wetland, but only the populations that live in the coniferous forest and broadleaf forest ecosystems are evaluated as being effectively protected. Then the proportion of effectively protected is 50%.

The proportion of effectively protected at biome or national scales is the sum of the number of population types that can be effectively protected in each NNRs over the total number of potentially viable population types.

**Human footprint.** For the dataset of human footprint intensity within the reserve, we used HumanFootprint, v2 (2009) (<https://wcshumanfootprint.org/v2/>). We analyzed the human footprint intensity within different biomes and the intensity of human footprint in different functional areas of the reserve under different biome gradients (see Tables S4 and S7; and Fig. S10). Furthermore, the relationship between human footprint intensity and conservation effectiveness was analyzed (Fig. S11). To ensure the analysis is robust, we also used Global Human Modification of Terrestrial Systems, v1 (2016)<sup>82</sup>, for comparison to show the consistency pattern of the two datasets (Fig. S10).

**Reasonableness and sensitivity analysis.** To ensure the reasonableness of the virtual species we defined could match with the real species. We used the list of Chinese terrestrial wildlife important habitats for important protected species (<https://www.forestry.gov.cn/search/538542>). In total, 122 important protected species were selected by weight, movement ability, and other allotropic relationships to match with the virtual species. Moreover, we obtained the distribution extent of the 122 species from the IUCN Red List of threatened species (<https://www.iucnredlist.org/>). Their distribution extent was merged to obtain the distribution extent of the virtual species group classified by various gradients of movement ability. It is important to note that the merged distribution extent is only used to analyze the reasonableness of the virtual species group. Matched real species are probably distributed outside the merged ranges since our samples are only parts of the important protected species.

We conducted a series of tests to evaluate (a) the sensitivity of functional connectivity to movement distances of various taxa and (b) the sensitivity of effectiveness of conservation to different ecological characteristics of various taxa, such as dispersal distances and diet. First, to

ensure our results have the consistency to be generalized to more common species with different dispersal abilities, we calculated and compared the functional connectivity values between our main model and the sensitivity test model using the same methodology. We approximated the allometric relationship equation for birds and terrestrial mammals with dispersal distances less than 20 km as low movement ability and used the allometric relationship equation for low movement ability species in Table S2. Birds and terrestrial mammals with dispersal distances of more than 30 km were considered as high movement ability, and the allometric relationship equation for high motility species was used. Functional connectivity values for birds and terrestrial mammals were highly correlated between the models (Pearson's  $R^2 > 0.97$ ; Fig. S12). Second, we examined the relationship between dispersal distance and diet and conservation effectiveness and compared the effectiveness between our main model and the sensitivity test model. Conservation effectiveness was highly correlated between the models (Pearson's  $R^2 > 0.85$ ; Fig. S8).

**Statistical analyses of prediction variables.** We used GAMs with negative binomial distribution to determine complex nonlinear relations of functional connectivity and prediction variables (Fig. S13). We used habitat characteristic variables (i.e., PAs area, proportion of habitat area, ecosystem type diversity, and artificial landscape intensity) as predictors and fitted their interactions to functional connectivity. We implemented GAMs models on R (version 4.2.2) using the “mgcv” package. We used restricted maximum likelihood as the method for estimating the smoothing parameters and applied tensor product smoothing as the smoothing function when fitting the interactions<sup>17</sup>. We restrict the maximum degrees of freedom of the smoother to 2. To determine the most suitable model, we performed a stepwise backward selection using the Akaike Information Criterion (AIC) (see Tables S8 and S9).

We also applied random forest analysis with a tenfold cross-validation approach<sup>83</sup> to estimate the significance of habitat characteristic variables to explain the limiting factors affecting functional connectivity. The “rfPermute” package was used to assess the significance of each predictor on the response variable<sup>84</sup>.

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

All data used in this manuscript is openly available online. The ChinaCover land cover dataset is available from: The land cover atlas of the People's Republic of China (1:1,000,000), Beijing: SinoMaps Press, 2017. Road data are available from: <https://www.openstreetmap.org>. ASTER GDEM v2 (30 m) is available from: <http://www.gscloud.cn>. Dataset of human footprint intensity are available from <https://wcshumanfootprint.org/v2/>, and Global Human Modification of Terrestrial Systems, v1 (2016) available from: <https://sedac.ciesin.columbia.edu/data/set/lulc-human-modification-terrestrial-systems>. The main data analyzed are the connectivity model outputs, for the data used to plot the main graphs used in this study can be accessed at <https://doi.org/10.6084/m9.figshare.25928938.v1>.

## Code availability

All statistical analyses were performed using Graphab (version 2.6), ArcMap (version 10.2), and R (version 4.2.2). We used the following R packages for analyses: mgcv (version 4.2.2), randomForest (version 4.7-1.1), rfPermute (version 2.5.1). The connectivity model building parameters in Graphab refer to the user manual<sup>67</sup>, and there is no code for the operating interface. The data analyses in R software are basic calculations of each package, with no custom code used in this study.

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## Author contributions

Y.B. conceived the study. W.S., Y.Z., W.C., and Y.B. conducted data analysis and drafted the manuscript. All authors contributed to the revision of the paper, and Y.B. edited the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

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