Received: 5 July 2022 | Revised: 17 September 2023 | Accepted: 9 October 2023

DOI: 10.1111/cobi.14204

Conservation Biology

CONTRIBUTED PAPER

Prioritizing conservation efforts based on future habitat availability and accessibility under climate change

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Article impact statement: Combining climate velocity and habitat availability with network analysis provides novel insight and informs conservation priorities.

Funding information
National Natural Science Foundation of China, Grant/Award Numbers: 51979101, 51679082; Science and Technology Innovation Program of Hunan Province, Grant/Award Number: 2023RC1041

Abstract

The potential for species to shift their ranges to avoid extinction is contingent on the future availability and accessibility of habitats with analogous climates. To develop conservation strategies, many previous researchers used a single method that considered individual factors; a few combined 2 factors. Primarily, these studies focused on identifying climate refugia or climatically connected and spatially fixed areas, ignoring the range shifting process of animals. We quantified future habitat availability (based on species occurrence, climate data, land cover, and elevation) and accessibility (based on climate velocity) under climate change (4 scenarios) of migratory birds across the Yangtze River basin (YRB). Then, we assessed species' range-shift potential and identified conservation priority areas for migratory birds in the 2050s with a network analysis. Our results suggested that medium (i.e., 5–10 km/year) and high (i.e., ≥ 10 km/year) climate velocity would threaten 18.65% and 8.37% of stable habitat, respectively. Even with low (i.e., 0–5 km/year) climate velocity, 50.15% of climate-velocity-identified destinations were less available than their source habitats. Based on our integration of habitat availability and accessibility, we identified a few areas of critical importance for conservation, mainly in Sichuan and the middle to lower reaches of the YRB. Overall, we identified the differences between habitat availability and accessibility in capturing biological responses to climate change. More importantly, we accounted for the dynamic process of species' range shifts, which must be considered to identify conservation priority areas. Our method informs forecasting of climate-driven distribution shifts and conservation priorities.

KEYWORDS
climate change adaptation, climate velocity, connectivity, habitat suitability, network analysis

Priorizar los esfuerzos de conservación en función de la disponibilidad y accesibilidad futura de hábitats ante el cambio climático

Resumen: El potencial de las especies para desplazar sus rangos y evitar la extinción depende de la disponibilidad y accesibilidad futura de hábitats con climas análogos. Para desarrollar estrategias de conservación, muchos investigadores anteriores utilizaron un solo método que consideraba factores individuales; algunos combinaron 2 factores. Principalmente, estos estudios se centraron en identificar refugios climáticos o áreas climáticamente conectadas y espacialmente fijas, ignorando el proceso de desplazamiento de rangos de los animales. Cuantificamos la disponibilidad futura de hábitats (basada en la presencia de especies, datos climáticos, cobertura terrestre y elevación) y la accesibilidad (basada en la velocidad climática) bajo el cambio climático (4 escenarios) de aves migratorias en la cuenca del río Yangtsé (YRB). Luego, evaluamos el potencial de desplazamiento de rangos

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de las especies e identificamos áreas prioritarias de conservación para las aves migratorias en la década de 2050 mediante un análisis de redes. Nuestros resultados sugieren que una velocidad climática media (es decir, 5–10 km/año) y alta (es decir, ≥ 10 km/año) amenazarían el 18.65% y el 8.37% del hábitat estable, respectivamente. Incluso con una velocidad climática baja (es decir, 0–5 km/año), el 50.15% de los destinos identificados por la velocidad climática eran menos disponibles que sus hábitats de origen. Basándonos en nuestra integración de la disponibilidad y accesibilidad de hábitats, identificamos algunas áreas de importancia crítica para la conservación, principalmente en Sichuan y en las partes media e inferior del YRB. En general, identificamos las diferencias entre la disponibilidad y accesibilidad de hábitats en la captura de respuestas biológicas al cambio climático. Más importante aún, tuvimos en cuenta el proceso dinámico de los desplazamientos de rangos de especies, lo cual debe considerarse para identificar áreas prioritarias de conservación. Nuestro método contribuye a la predicción de cambios en la distribución impulsados por el clima y las prioridades de conservación.

PALABRAS CLAVE
adaptación al cambio climático, velocidad del clima, conectividad, idoneidad del hábitat, análisis de redes

气候变化下基于未来生境可用性和可达性确定保护优先事项

通常而言, 物种转移其分布范围来避免灭绝的潜力, 取决于两个重要因素:未来生境的可用性和可达性。许多研究采用了只考虑单一要素的单一方法来制定保护策略, 很少有研究同时考虑上述两个因素。尽管有部分研究同时考虑了这两个因素, 但大多数侧重于识别气候避难所或气候连通的空间固定区域, 忽略了物种的范围转移过程。本研究量化了长江流域候鸟在4种气候变化情景下未来生境的可用性(基于物种出现、气候数据、土地覆盖和海拔)和可达性(基于气候速度), 然后采用网络分析法评估了物种的范围转移潜力并确定了2050年代的候鸟保护优先区域。结果表明, 中等(5-10 km/year)和高等(≥10 km/year)气候速度将分别威胁18.65%和8.37%的生境稳定区域。即使在低气候速度条件下(0-5 km/year), 也有50.15%的气候变化识别目的地相比其源生境的可用性有所降低。基于对生境可用性和可达性的综合分析, 本研究确定了一些具有重要保护意义的区域, 主要位于四川和长江中下游。总的来说, 我们发现了生境可用性和可达性这两种指标在捕捉生物对气候变化的反应方面存在差异。更重要的是, 本研究考虑到了物种分布范围变化的动态过程, 而这是确定优先保护区域的重要前提。我们的方法为预测气候驱动的分布变化并告知保护优先事项提供了信息。

适应气候变化, 气候速度, 连通性, 生境适宜性, 网络分析

INTRODUCTION

As the impacts of climate change intensify, species will be increasingly forced to relocate to more climatically suitable areas in order to avoid extinction (McGuire et al., 2016; VanDer-Wal et al., 2013). There is mounting evidence that species have shifted their distributions in response to climate change (Chen et al., 2011; VanDerWal et al., 2013), particularly mobile species with complex spatial dynamics (Huang et al., 2017). However, traditional conservation plans are static and generally determined based on species distribution data for a specific period or space (Araujo et al., 2004; Liang et al., 2018b), which may be ineffective to maintain or improve species conservation status over the long-term. Therefore, spatially dynamic threats have sparked a surge in research to investigate the future effects of climate change on species range shifts and to inform conservation priorities under climate change (D'Aloia et al., 2019; Stralberg et al., 2020; Xu et al., 2022; Zhu et al., 2022).

The potential for species to shift their range in response to rapid climate change is contingent on the future availability and accessibility of habitats with analogous climates (Littlefield et al., 2019; Senior et al., 2019), resulting in 2 mainstream approaches to forecasting climate-driven distribution shifts and developing climate-adaptive conservation strategies (Araujo et al., 2004). Suitability-based approaches focus on the future availability of habitats, assuming that species are more likely to persist or establish new populations in habitats with similar environments (Hamann & Aitken, 2013). Species distribution models (SDMs), for example, have been widely used to predict changes in the spatial pattern of biodiversity as a result of climate change. The results of these models are then used to develop conservation strategies (Liang et al., 2018a; Martinez-Lopez et al., 2021; Vaz et al., 2021). However, this approach ignores the fact that unsuitable areas (i.e., movement barriers) may restrict species' movement to areas of future habitat (McGuire et al., 2016).

In contrast, connectivity-based approaches emphasize the accessibility from the species' current distribution to future habitats by considering barriers to species movement under climate change (Carroll et al., 2018; Littlefield et al., 2019; McGuire et al., 2016). Climate velocity (CV), one of the metrics for climate connectivity, estimates the rate at which a species must shift its ranges to retain similar climate conditions over a given time period (Hamann et al., 2015) (Appendix S1; Loarie et al., 2009). This metric has been used to identify the climate refugia (Michalak et al., 2020), assess the climate change exposure of species (Parks et al., 2020), and establish corridors for facilitating climate connectivity (Carroll et al., 2018). Even so, CV is an imperfect metric (Batllori et al., 2017; Dobrowski & Parks, 2016), necessitating the development of composite metrics or multiobjective combined methods.

Several recent studies have combined CV with various metrics to develop climate-informed conservation planning with different conservation goals. Ordonez and Williams (2013) proposed biotic velocity to combine CV metrics with habitat suitability metrics. Carroll et al. (2017) identified refugia with a multiobjective solution based on 6 environmental diversity metrics and climatic velocity. Stralberg et al. (2020) identified priority conservation areas based on microrefugia, macrorefugia, and climate corridors. Michalak et al. (2020) emphasized the importance of incorporating climatic exposure, environmental diversity, and climate tracking data in refugia analyses. However, many previous studies focused on identifying climate refugia or climate connectivity areas in fixed areas based on CV and habitat suitability analyses and ignored the species' range shifts implied by the 2 methods.

According to future habitat availability and accessibility under climate change, what is the likelihood of species successfully shifting ranges in response to rapid climate change? Where are the priority conservation sites and paths (i.e., corridors) for facilitating successful range shifts in such situations? Across the Yangtze River basin (YRB), we applied a mixed approach (Appendices S2 & S3) that combined network analyses with habitat availability and accessibility to determine the critical areas for future habitat availability and accessibility under climate change; the risks and opportunities associated with shifting ranges of migratory birds as the climate warms; the potential for species to successfully shift their ranges in response to future climate change; and the conservation priority sites and corridors that could allow species to successfully shift their ranges under climate change. Finally, we constructed a climate-informed network of priority areas for the conservation of migratory birds across the YRB into the 2050s. We sought to provide decision-makers with a spatially explicit conservation strategy that maximize species persistence under climate change.

METHODS

Study region

The YRB (24°30′N–35°45′N, 90°33′E–122°25′E) is 1.8 million km^2, which is 18.7% of China's total area (Kong et al., 2020). Because of its complex topography and diverse climate, the region provides abundant habitat for a wide range of organisms, making it a biodiversity hotspot in China (Ni et al., 1998). The YRB contains several important wintering areas for migratory birds in the Central Asian and East Asian-Australasian Flyways (Shimazaki et al., 2004; Wang et al., 2017). However, recent environmental changes in this region have altered bird distributions, and this trend is expected to continue (Liang et al., 2021; Wang et al., 2017). Therefore, it is necessary to develop conservation plans for migratory birds to maximize species persistence under environmental change. To reduce the boundary effects of CV caused by artificial truncation of the study area (Senior et al., 2019), we analyzed future habitat availability and accessibility within 100 km of the study area.

Species records

We used species occurrence records from 2001 to 2018 because they were accurate and collected during the period for which climate data were available. Given our emphasis on modeling potential wintering range shifts and identifying protected priority areas, we selected migratory bird occurrences recorded in winter (Thuiller et al., 2019). We used BirdLife data (www.birdlife.org) to identify migratory bird species with wintering ranges within the study area, set November to March as the wintering season, and retained only occurrences recorded during this period (Heim et al., 2020). We downloaded occurrence data for migratory birds from the citizen-science databases eBird (https://science.ebird.org/en/use-ebird-data) and GBIF (https://www.gbif.org/) and excluded occurrences with spatial uncertainty >5 km. These procedures produced a database containing 37,462 winter occurrences (235 species) of migratory birds recorded from 2001 to 2018 (Appendix S4). To reduce sampling bias and spatial autocorrelation related to oversampling, we removed duplicate geographic locations for each species and used R package spThin (Aiello-Lammens et al., 2015) to filter the data set to match the resolution of the climate variable layers used (5×5 km grids); 1 record was kept per grid. Furthermore, we included only those species with at least 25 unique records in the model because this threshold is useful for generating robust distribution models (Hernandez et al., 2006; Pearson et al., 2007; Proosdij et al., 2016; Ureta et al., 2022). Ultimately, 9489 unique occurrence records of migratory birds (n = 104 species) were retained for subsequent analyses (Appendices S3a, S5, & S6).

Environmental variables

Climate data for the current (2001–2018, representing 2010s) and future (2041–2060, representing 2050s) periods were derived from Worldclim 2.1 (https://www.worldclim.org/) at 2.5-min spatial resolution (Hijmans et al., 2005). For the current period, we generated 19 bioclimatic variables based on the average minimum temperature, average maximum temperature, and total precipitation with R package dismo. For the future period, we extracted 19 bioclimatic variables for

4 shared socioeconomic pathways scenarios (SSPs) (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5). Future climate projections were generated using a multimodel ensemble of 22 global circulation models: ACCESS-CM2, ACCESS-ESM1-5, BCC-CSM2-MR, CanESM5, CanESM5-CanOE, CMCC-ESM2, CNRM-CM6-1, CNRM-CM6-1-HR, CNRM-ESM2-1, EC-Earth3-Veg, EC-Earth3-Veg-LR, GISS-E2-1-G, GISS-E2-1-H, INM-CM4-8, INM-CM5-0, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MPI-ESM1-2-HR, MPI-ESM1-2-LR, MRI-ESM2-0, and UKESM1-0-LL. We resampled the original climate data grids at the 5-km spatial grid scale with bilinear interpolation. Given the problems with multicollinearity in climate data, we ran a preliminary screening of the 19 bioclimatic variables to identify the important bioclimatic variables that most affect the occurrence of migratory birds for each species (Appendices S3a & S7).

Nonclimate variables included land cover and elevation (Appendix S3a). The elevation map with a spatial resolution of 2.5 min was obtained from WorldClim 2.1 (Hijmans et al., 2005). Land-cover data at 1-km spatial resolution for 2010 and 2020 were provided by the Data Center for Resources and Environmental Sciences, Chinese Academy of Sciences (RESDC) (http://www.resdc.cn). The land cover for 2010 corresponded to the current period, and the land cover for 2020 corresponded to the future period, based on the assumption that future land use would remain consistent with that of 2020. For future land cover, we did not use simulated land use or cover data due to the low classification accuracy of the available data. Land-cover data included 6 land-cover types: forest, grassland, cultivated land, urban land, water body, and unused land. The classification accuracy of these classes could reach 94.3% (Liu et al., 2014). To be consistent with the climate data, we resampled the elevation and land-cover data to 5-km spatial resolution.

Habitat modeling

We identified the habitat of 104 migratory bird species by fitting SDMs within the ensemble modeling platform SSDM (Schmitt et al., 2017) in R. Climate data, land cover, and elevation were used as environmental predictor variables for the distribution of migratory birds in wintering areas (Appendix S3b). For each species, we fitted models with 9 algorithms: general additive models, generalized linear models (GLM), multivariate adaptive regression splines, classification tree analysis, generalized boosted models, maximum entropy, artificial neural networks, random forests, and support vector machines. Each algorithm was repeated 10 times to yield 90 models.

We adopted the default pseudo-absence selection strategy recommended by Barbet-Massin et al. (2012) for each algorithm (i.e., 10 runs of 1000 randomly selected pseudo-absences are performed for GLM). For each model, 70% of the randomly sampled data were used for training, and the remaining 30% of data were used to evaluate models with the area under curve (AUC) of the receiver operating characteristic curve (Elith et al., 2011). Only models that outperformed a predefined predictive performance threshold were kept (i.e., AUC $\geq$ 0.75). These models were then used to predict habitat occurrence in the current and future periods. To evaluate variable importance, we calculated Pearson's correlation between predictions of the full model and the one without a variable; the higher the value, the greater the influence of the variable on the model. We used the sensitivity-specificity equality to identify the threshold for converting the habitat maps from continuous (0–1) to binary (0, 1) (Martinez-Lopez et al., 2021), where 0 represented no habitat and 1 represented available habitat. The continuous values were divided into 3 categories by the natural breaks (Jenks). Finally, we generated the ensemble SDM (ESDM) for each species by taking the AUC-weighted mean of the outputs of the selected models. The performance of ESDM for each species was examined, and 96 models with an AUC value $\geq$0.8 were retained (Elith et al., 2011) (Appendix S8).

Stacking habitat availability

To generate a community-level property for assessing habitat availability across all modeled migratory bird species within the study area, we stacked the ESDM results (i.e., continuous and binary habitat suitability) for the 96 selected migratory bird species (Appendix S3b). The stacked continuous habitat suitability values were then used to develop the composite indicator range shift potential (RSP), which quantified the potential for species to successfully shift ranges in response to climate change. The stacked binary habitat suitability maps were then used to identify habitats for constructing a potential range shift network. We calculated the mean of continuous habitat suitability maps for the 96 species at each pixel to reflect overall habitat availability for migratory birds in the current and future periods (Naimi et al., 2022). We also stacked and summed the binary maps of potential occurrence for the 96 species. Pixels with values $\geq$1 in the stacked binary habitat suitability maps were considered habitat for these migratory birds. Based on the variable importance obtained from the ESDM of each species, we calculated the overall contribution percentages of each variable in terms of the modeled migratory birds. The standard protocol ODMAP 1.0 (Zurell et al., 2020) of SDM is in Appendix S9.

CV analyses

To assess habitat accessibility, we calculated CV, defined climate analogs, and delineated potential range shift paths with methods developed by Dobrowski and Parks (2016) and Carroll et al. (2018) (Appendix S3b). Before conducting this analysis, we retained the variable with a percent contribution >1% and identified the 7 most important bioclimatic variables that best predicted the occurrence of all modeled migratory birds (Appendices S3a & S10). In this way, the ecological assumption that tracks analogous habitats, instead of just climate analogs, is realized. Following the methods of Carroll (2018 et al. (2018), we conducted a principal components analysis on the 7 bioclimatic variables to reduce the dimensionality and collapse the original multiple variables into 2 new variables, which incorporated the major information (88.66%) of climatic variability. This procedure yielded the scores of 2 principal components (PC1 and PC2) for the current period climate and the loadings of each climatic variable (Appendix S11). The loadings were then used to generate gridded PC1 and PC2 scores for the future period climate. The subsequent analysis of CV was based on the gridded PC1 and PC2 scores for the current (2001–2018) and future (2041–2060) periods.

We applied the least-cost algorithm (van Etten, 2017) (from R package gdistance) detailed in Dobrowski and Parks (2016) and Carroll et al. (2018) to define climate analogs between the current and future periods. The calculation of distance-based CV is computationally intensive, and its feasibility and computational efficiency rely on the use of the least-cost algorithm. In addition, the least-cost algorithm can help identify the least-cost paths of landscape linkages that may be the most potential range shift trajectories. The identification of these spatially explicit paths facilitates abstracting the spatiotemporal dynamic process of species range shifting and constructing the potential range shift network. For each current period pixel (i.e., source pixel), we determined the individual analog (i.e., destination pixel) that minimized exposure to dissimilar climates based on the minimum-resistance surfaces approach. Then, we delineated the least-cost paths between the source pixels and their corresponding destination pixels. CV (kilometers per year) was calculated by dividing the length of the least-cost paths by the interval between the current and future periods. Finally, we classified the CV values into 3 groups: 0–5 km/year, 5–10 km/year, and ≥10 km/year, defining them as low, medium, and high CV, respectively.

Potential range shift network construction

We used RSP to construct the potential range shift network for the selected 96 migratory bird species (Appendices S3c & S12). We used a graph-theoretic method under the assumption of unrestricted species dispersal. CV and habitat analyses assessed future habitat accessibility and availability under climate change, taking into account different range shift processes for species in response to climate change. The former revealed climate analogs, potential range shift paths, and CV, indicating the extent to which species could reach analogous future climate habitats from their current distribution under climate change. The latter was used to evaluate future habitat availability, reflecting the degree to which analogous future climate habitats would be suitable for species survival in the future. Therefore, RSP was calculated as follows:

$$\mathrm{RSP}_{s(c-f)} = \mathrm{CV}^{-1}{}_{s(c-f)} \times \mathrm{HS}_{d(f)}, \tag{1}$$

where s is the source from which a species migrates, c is the current period, f is the future period, d is the destination of the migrating species, $\mathrm{CV}^{-1}{}_{s(c\text{-}f)}$ is the reciprocal CV value of s from c to f, and $\mathrm{HS}_{d(f)}$ is the stacked continuous habitat suitability value (range 0–1) of the corresponding destination d in f.

Given the possibility of range shift, we constructed the potential network in areas where the future destinations contained habitat (Figure 1d & Appendices S3c, S13a, & S13b). We extracted climate analogs and potential range shift paths as nodes and edges, respectively. The start nodes were the sources in the current period, and the target nodes were the corresponding destinations in the future period. The edges were the least-cost paths between each source and each destination, weighted by the RSP value. Therefore, we constructed a weighted and directed potential range shift network for migratory birds across the YRB (Appendix S3c).

Conservation priority areas identification

We used network analysis to measure site importance by calculating local nodal metrics and analyzing global network robustness with a node-removal process (Appendix S3d). These analyses were carried out with Gephi 0.8.2 (Bastian et al., 2009) and the R igraph package (Csardi & Nepusz, 2006). We assumed that the removal of a node was equivalent to the degradation of a site in the potential range shift network. As a result, network robustness was defined here as the ability of the potential range shift network to continue to function when a habitat lost accessibility and availability due to disruption.

We used 4 nodal metrics related to node centrality: weighted degree (WD), weighted in-degree (Win-D), betweenness centrality (BC), and eigenvector centrality (EC). Each metric measures the importance of sites from a slightly different perspective (Appendices S14 & S15). To simulate the effects of disruption and identify key sites, we analyzed network robustness in an iterative node-removal process in which removal order was determined by the 4 local nodal metrics. First, we calculated 4 nodal metrics for each site in the initial network. Then, we removed nodes sequentially, starting with 1 and progressing by 1 node per iteration until the network crashed. The order of node removal per iteration included 4 scenarios: descending WD, descending Win-D, descending BC, and descending EC. After each iteration, we calculated 3 network metrics (i.e., connectivity robustness, global efficiency, and average path length [Appendix S15]) to evaluate the overall characteristics of the new temporary network (Iyer et al., 2013). The sharp drop in the 3 network metrics indicated that the removed sites had a significant impact on network connectivity and resilience (Luo et al., 2020; Xu et al., 2020). According to this, we identified key sites that, if destroyed, could cause the range shift network to collapse due to the effects of climate change. Important sites were identified by observing a 50% decrease in the network metrics value when nodes were removed according to the order of the sensitivity nodal metric (i.e., the fastest declining metric). The corresponding edges of these important site sites were identified as important paths, which were reclassified based on CV values. For each network metric, we constructed a protected priority areas subnetwork based on the key sites and paths. Then, we combined the 3 subnetworks mentioned above to construct a climate-informed protected areas network for migratory birds (Appendix S3d). Finally, we compared the identified

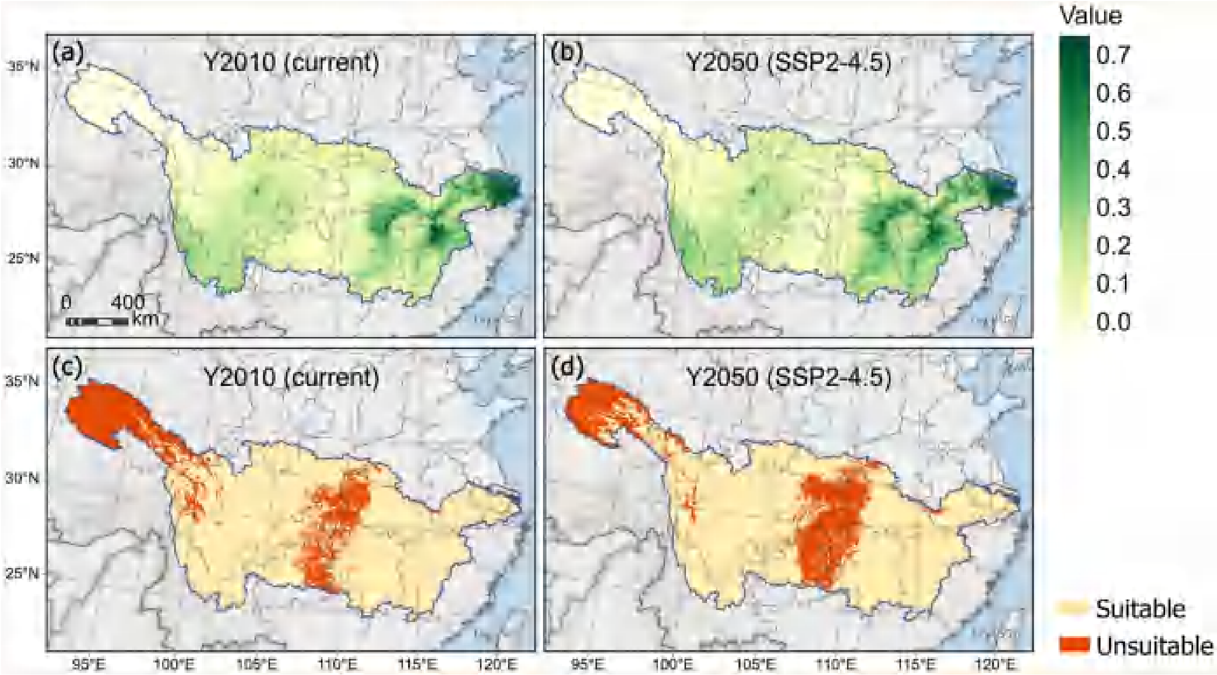

FIGURE 1 For 96 migratory bird species across the study area, distribution of (a, b) stacked continuous habitat suitability and (c, d) stacked binary habitat suitability across the Yangtze River basin (YRB) (a, c) currently and (d, b) under the SSP2-4.5 future climatic scenario.

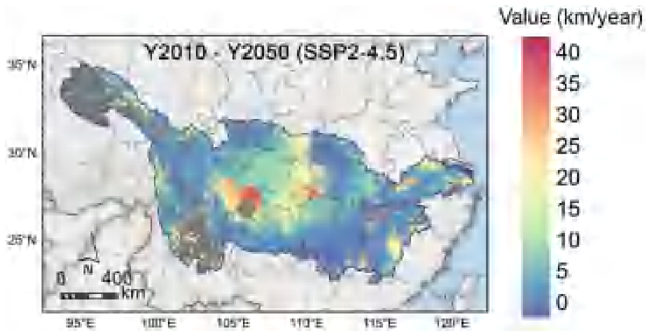

FIGURE 2 Distribution of climate velocity across the Yangtze River basin (YRB) under the future climatic scenario of SSP2-4.5 for migratory birds (dark gray, areas of disappearing climates).

conservation priority areas network with the current protected areas (UNEP-WCMC & IUCN, 2023).

RESULTS

Future habitat availability and accessibility under climate change

Our primary focus in the analysis was the SSP2-4.5 scenario. Results for the other 3 scenarios are in Appendices S16–S25. Habitat availability and accessibility presented distinct geographic distribution patterns across the YRB (Figures 1 & 2). The stacked habitat suitability maps revealed stable habitat availability across the YRB as the climate changes (Figure 1). Details on changes in the proportion of habitat area for each species are in Appendix S19. Currently, about 79.85% of the study area contained habitat. This proportion was predicted to be 74.62% by the 2050s under the SSP2-4.5 scenario (67.08% maintained area [stable areas] and 7.54% new area [area gain]) (Figure 3b). Some species were predcited to shift their ranges from current habitats to future destination habitats (i.e., stable areas). However, when climate change velocity was accounted for, species living in 18.65% of these areas experienced medium CV (i.e., 5–10 km/year), whereas 8.37% experienced higher CV (i.e., ≥10 km/year) (Figure 3b).

Other species were predicted to shift their ranges from areas that did not currently contain habitat to areas that in the future would contain habitat (i.e., habitat gain). Those regions contained higher percentages of the areas threatened by medium and high CV, up to 31.43% and 25.20% (Figure 3b). For 4.71% of current habitats, there was an accompanying transformation of areas into nonhabitat (i.e., habitat loss) even under low climatic velocity (i.e., 0–5 km/year). Species living in 9.10% of current habitats would be unable to reach their destinations due to disappearing climates by the 2050s (Figure 3b). Such trends were observed in all climatic scenarios but were more pronounced in scenarios with higher emissions (see Appendices S20–S22 for the other 3 scenarios).

In terms of CV, the mean velocity was 4.64 km/year under the SSP2-4.5 scenario; maximum values reached 39.23 km/year across the study area (Figure 2) (see Appendices S23–S25 for the other 3 scenarios). However, 50.15% of destinations had less habitat availability than their source habitats, despite being exposed to low CV (i.e., 0–5 km/year) (Appendix S27). The 53.49% of sources predicted to face high CV (i.e., ≥10 km/year)

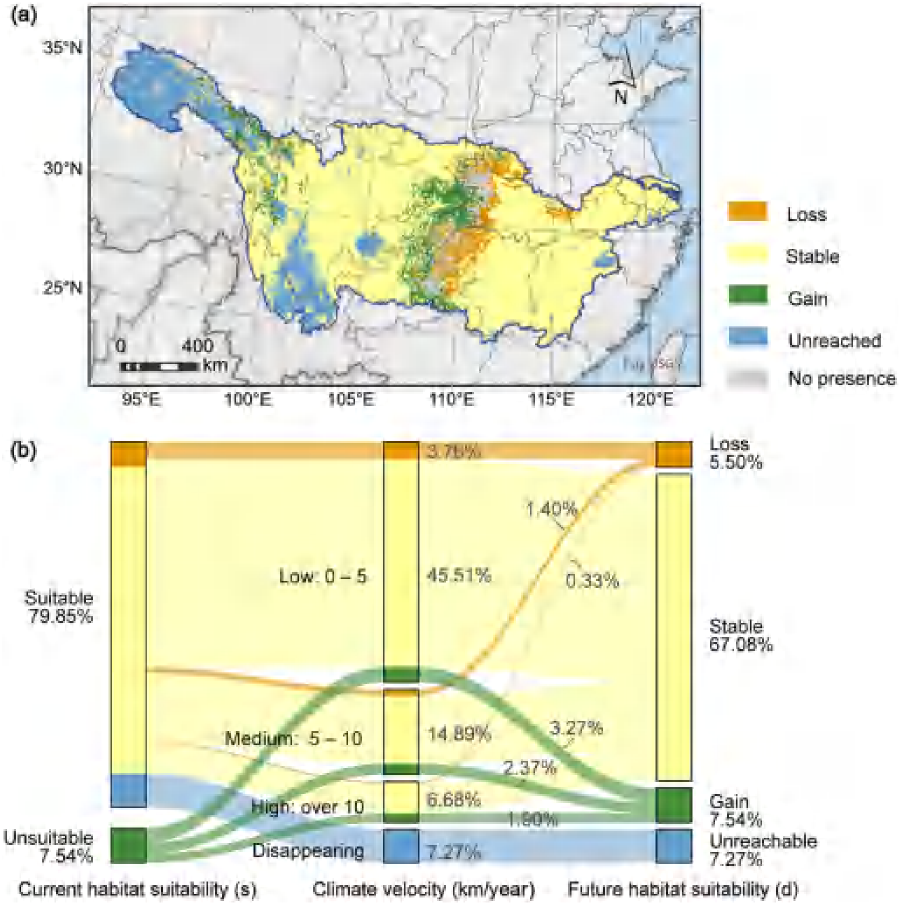

FIGURE 3 Projection of habitat conversion and climate velocity from habitat source pixels to habitat destination pixels under the future climatic scenario of SSP2-4.5 for migratory birds: (a) loss, stable, gain, unreachable, and no-presence habitat conversion types in the destination-pixel locations of current habitats under climate change and (b) percentage of habitat types (suitable or unsuitable) in source-pixel locations (left bar), fraction of habitat conversion types (loss, stable, gain, or unreachable) in the destination-pixel locations (right bar), and climate velocity levels species may experience as they migrate from source pixels to destination pixels (middle bar) (percentages, percentage of conversion type in the study area).

would also experience a decline in habitat availability (Appendix S27, see Appendices S26, S28, & S29 for other scenarios). Furthermore, the comprehensive assessment, measured by current habitat availability and accessibility under the SSP2-4.5 scenario, showed that 10.82% of the study area predicted to have medium-high habitat availability (i.e., habitat suitability) and low-medium habitat accessibility (i.e., $\geq$5 km/year CV) overlapped in Sichuan and the eastern YRB (Figure 4a). Some areas of high habitat availability were subject to climate change at rates exceeding 10 km/year. The areas with disappearing climates were mostly located in southern Sichuan, northeast Yunnan, eastern Qinghai, and eastern Jiangxi (Figure 4a). About one-half of them were in the species' current potential distribution regions (Appendix S27). Again, trends are qualitatively consistent across emissions scenarios (Appendices S30a, S31a, & S32a).

Consideration of the future habitat availability of destination pixels revealed an increase in the proportion of habitat in each CV range (Appendix S27). In particular, for areas predicated to face low habitat accessibility (i.e., $\geq$10 km/year CV), 75.03% of them were in current potential distribution regions, whereas 91.84% of their destination pixels were in future potential distribution regions under the climatic scenario SSP2-4.5 (Appendix S27). In comparison with the current habitat availability and accessibility assessment, the assessment of future habitat availability and accessibility suggested that overlapping areas of medium-high habitat availability and low-medium habitat accessibility would increase by 1.84% (Figure 4b). This increase in overlapping areas was mostly in eastern Sichuan and Chongqing (Figure 4b). Furthermore, the assessment of future habitat and CV revealed a 2.32% decrease in high-potential range shift areas with high future habitat availability and high habitat accessibility (Figure 4b). Such trends were found in other climatic scenarios (Appendices S30b, S31b, & S32b).

Conservation priority sites and paths

In terms of the important sites for range shifts, the 4 local nodal metrics exhibited slightly different distribution patterns under scenario SSP2-4.5 (Figure 5) (see Appendices S33–S35 for the other scenarios). Weighted degree and Win-

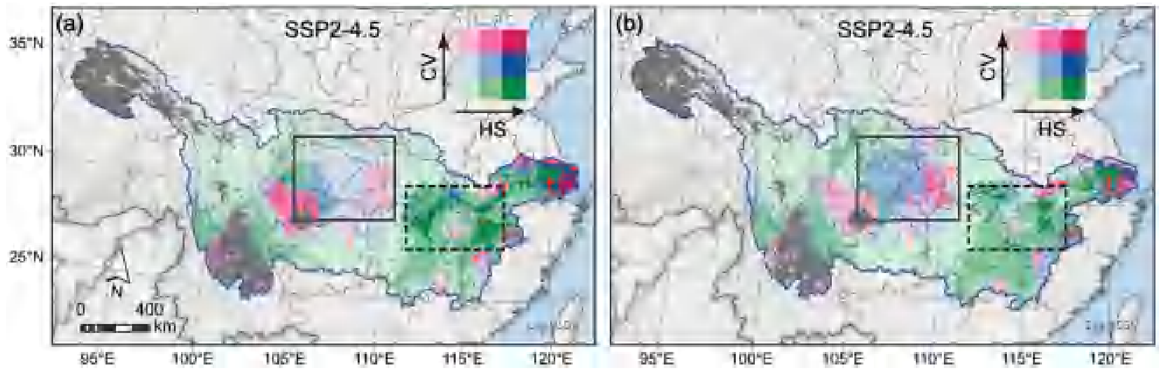

FIGURE 4 (a) Overlap of current stacked continuous habitat suitability and (b) future stacked continuous habitat suitability with climate velocity under the future climatic scenario SSP2-4.5. Habitat availability (i.e., habitat suitability) and accessibility (i.e., climate velocity) were split into 3 classes to define categories of different risk for migratory birds' dispersal (current, source habitat pixels under the current period; future, habitat destination pixels in the future; solid rectangles, areas of increased risk with medium-high habitat availability and low-medium habitat accessibility in the future; dashed rectangles, decreased amount of potential areas with high habitat availability and high habitat accessibility in the future; dark gray, areas of disappearing climates).

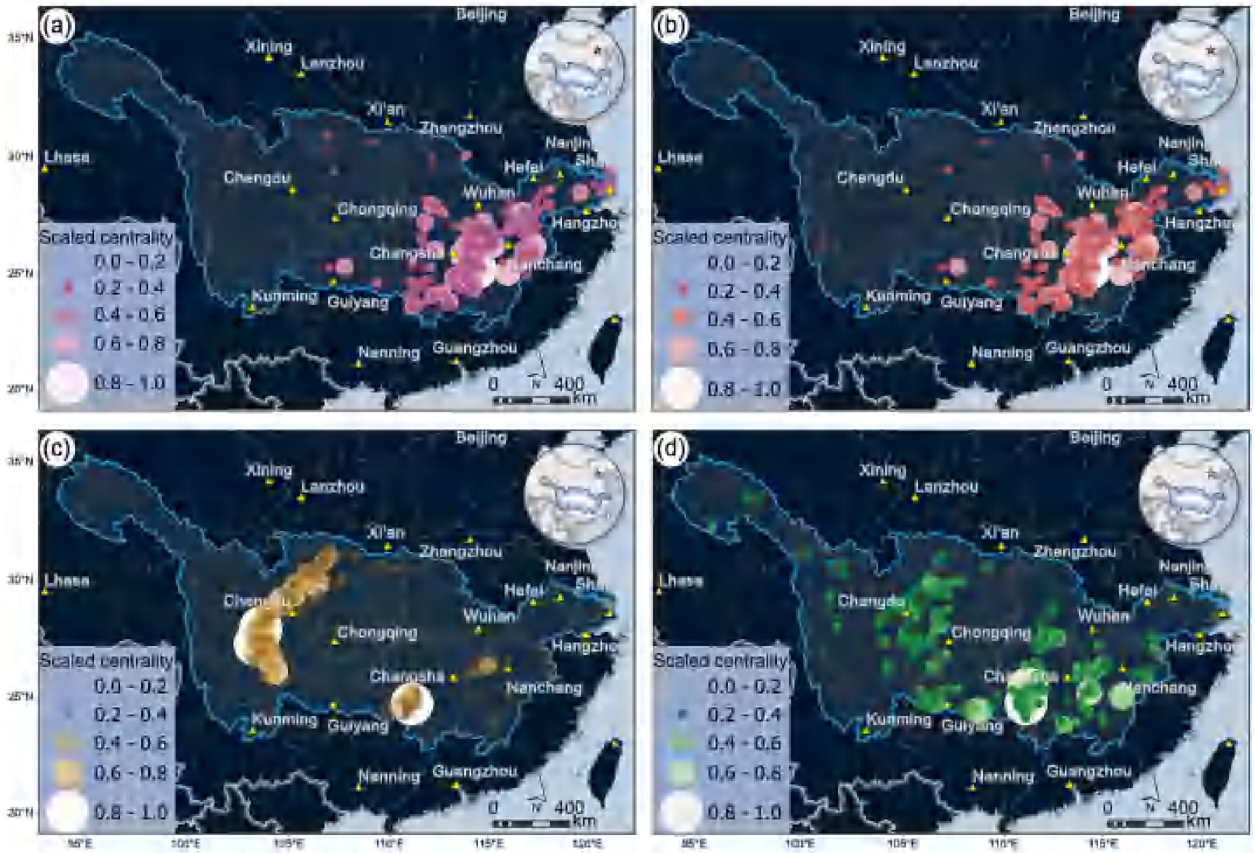

FIGURE 5 Spatial patterns of important sites for conservation of migratory birds in Yangtze River basin (YRB) evaluated based on 4 nodal metrics under the future climatic scenario of SSP2-4.5: (a) weighted degree (high values, important sites as potential outgoing or incoming sites for migratory birds' dispersal), (b) weighted in-degree (high values, important sites as potential incoming sites for migratory bird dispersal), (c) betweenness centrality (high values, important intermediary sites to facilitate dispersal), and (d) eigenvector centrality (high values, sites important for efficient ecological networks).

D showed high centrality in the middle to lower reaches of the YRB (Figure 5a,b), revealing significant potential outgoing or incoming sites for migratory birds' dispersal. High betweenness centrality and EC values were concentrated in Sichuan and the middle reaches of the YRB (Figure 5c,d). These areas were not only crucial intermediary sites for migratory birds' dispersal, but also well-connected to other important sites.

In general, the 3 network metrics used to evaluate the network characteristics changed in 3 phases during the robustness analysis: rapid decline, slow decline, and leveling off. Connectivity robustness, global efficiency, and average path length were all reduced by nearly half when nodes were removed by 0.45%, 0.4%, and 0.6%, respectively, under the SSP2-4.5 scenario (Appendices S37a, S37c, & S37e). Global efficiency was the first of the 3 network metrics to fall by half from its original value. It declined fastest when nodes were removed in descending order of their importance as measured by EC (Appendix S37d). However, connectivity robustness and average path length of the range shift network declined fastest when nodes were removed in descending order of their importance as measured by BC (Appendices S37b & S37f). This trend was largely consistent across all climate scenarios (see Appendices S36, S38, & S39 for the other scenarios), with the exception of SSP1-2.6, under which connectivity robustness decreased the fastest when nodes were removed in the descending order of their importance as measured by EC (Appendix S36b).

The identified priority areas subnetworks for protection showed that the networks built based on connectivity robustness and average path length were similarly concentrated in Sichuan and the middle and lower reaches of the YRB under the SSP2-4.5 scenario (Appendices S41a & S41c, see Appendices S40, S42, & S43 for the other scenarios). The network built based on global efficiency was primarily concentrated in Sichuan, Chongqing, Guizhou, and the middle and lower reaches of the YRB (Appendix S41b). Important sites linked by high CV paths indicated high-risk areas where exposure to climate change could limit species range shift to future habitats, whereas important sites linked by low CV paths revealed areas with high potential for species range shifts. Under the SSP2-4.5 scenario, the priority protected-areas network contained 335 important sites and 8876 important paths (Figure 6a). Seventeen of these sites were in currently protected areas, and 16 had a high potential to be areas to which species could move. In scenarios with higher emissions, more critical sites and paths were identified, resulting in a more complex network of protected priority area than under the SSP1-2.6 scenario (Appendices S44–S46).

DISCUSSION

There is a profound interest in the development of climate-informed conservation strategies. Many previous studies used habitat suitability and CV analyses to identify climate refugia or climate connectivity areas in fixed areas. Here, we combined habitat availability and accessibility with network analyses to quantify future habitat under climate change, thereby assessing RSP and identifying conservation priority areas.

We found spatial heterogeneity of habitat availability and accessibility in areas critical for the conservation of migratory birds. The stabilization of habitats suggests that it will persist for species under climate change, but most of it will be in areas of high CV, resulting in low accessibility (Figure 3 & Appendices S20–S22). The implicit assumption of SDMs is that the realized niches of species remain constant or change slowly (Parmesan, 2006). This means that, if climate change occurs, species may be forced to shift their ranges to find habitat (Martinez-Meyer et al., 2004). However, due to limited dispersal capacity, the maximum speed species could achieve when tracking their habitats is likely to be slower than the velocity of climate change. In fact, CV above 10 km/year has already exceeded the range shifting abilities of most species (Batllori et al., 2017; Santini et al., 2016). Thus, existing research focusing solely on habitat presence may overestimate the odds of successful range shifts.

Our findings showed that many climate-velocity-identified destinations will lose habitat over time. CV is a coarse-filter approach that lacks species-specific information in general (Batllori et al., 2017; Dobrowski & Parks, 2016). In our study, the destinations tracked by this method were climate analogs instead of analogous habitats. It is unknown whether the climate analogs will be suitable for species survival in the future. We cannot rule out the possibility that assessing CV alone might overestimate species' long-term survival. Hence, focusing solely on habitat suitability or CV would underestimate shift risks. The use of habitat suitability and CV should take into account their differences in capturing complex biological responses to climate change.

Some studies show differences in climate exposure patterns revealed by habitat suitability and CV (Brito-Morales et al., 2020; Carroll et al., 2017; Stralberg et al., 2020). They mostly concentrated on current habitat suitability and CV (Brito-Morales et al., 2020). We further investigated the relationship between future habitat and CV. Our findings revealed more overlapping areas with medium-high habitat availability and low-medium accessibility and fewer overlapping areas with high habitat availability and high habitat accessibility.

Although there were differences between habitat availability and accessibility, integrating them could reflect different risks and opportunities for species shifting in response to climate change (Appendix S13). High habitat availability and low habitat accessibility combined revealed potential risk areas where high climate-change exposure might limit species movement to future habitats if they exist (Appendices S13a & S13b). High habitat availability and high habitat accessibility combined revealed areas with high potential for species range shifts (Appendices S13a & S13b). Low habitat availability and high habitat accessibility combined revealed potential areas for species extinction due to a lack of habitat, even with low exposure to climate change (Appendix S13c). These assessments would provide critical information on habitat availability and accessibility to quantify RSP and inform conservation priorities (Carroll et al., 2017; Dobrowski & Parks, 2016).

The successful species distribution shift process is influenced by 2 critical factors: future habitat availability and accessibility of habitats along pathways. Habitat changes and dispersal limitations have been considered in graph-theoretic prioritization of areas for conservation (Phillips et al., 2008). Here, we used network theory to develop the RSP indicator and identify conservation priorities. Compared with graph theory, network theory treats dynamic range shift as an entire network containing information about movement behavior (Kenett et al., 2015), so it offers a foundation for studying the effects of

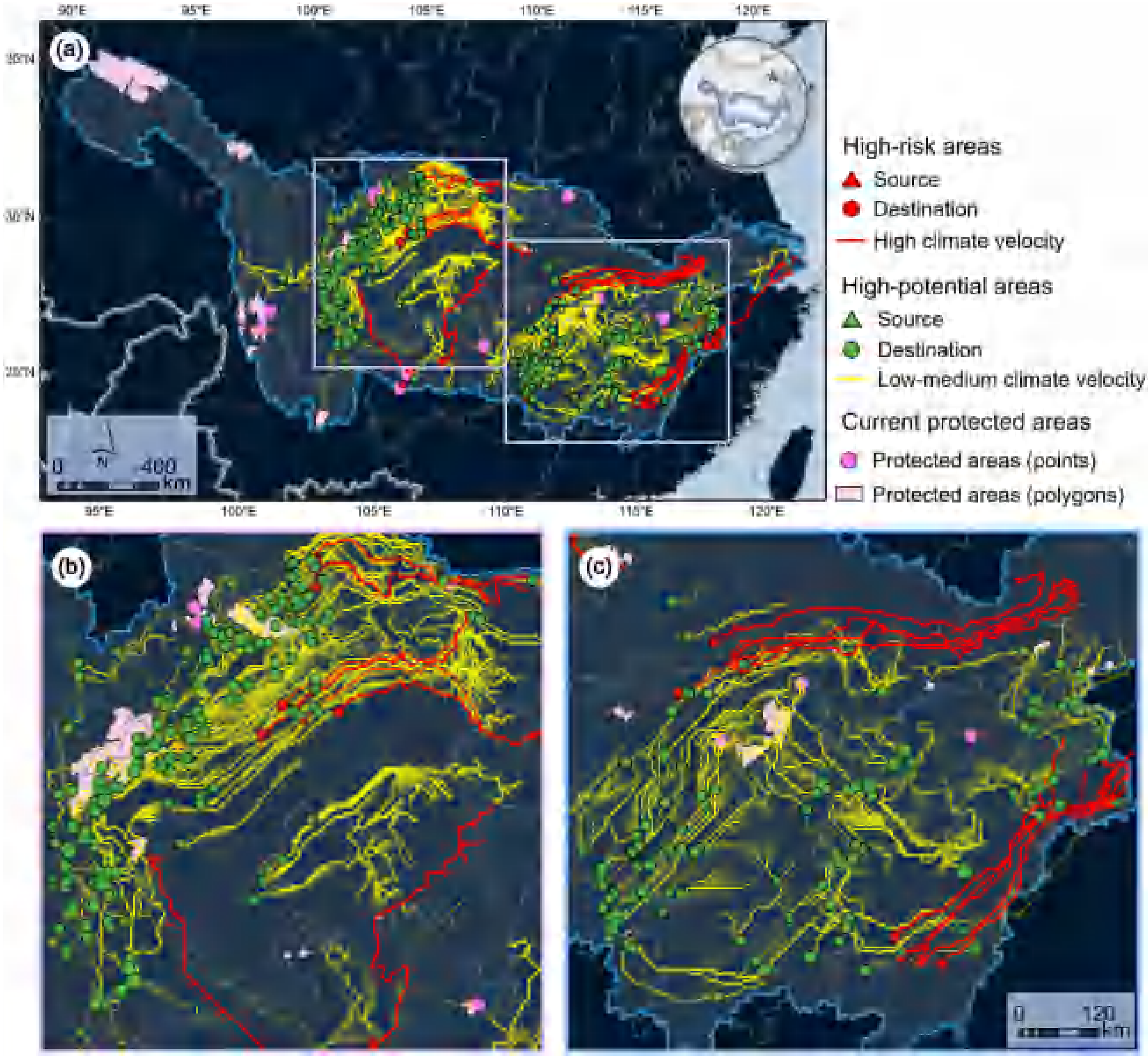

FIGURE 6 Priority areas for migratory bird conservation across the Yangtze River basin (YRB) under the future climatic scenario of SSP2-4.5: (a) combined protected priority areas network built based on 3 subnetworks (Appendix S41) and (b, c) close-ups of the regional networks in Sichuan and the middle and lower reaches of the YRB (source, source from which a species migrates under the current period; destination, destination of the migrating species under the future period; lines, potential range shift paths in the current and future periods). Important sites linked by high climate velocity paths indicate high-risk areas where climate exposure could limit species shift to future habitats, whereas important sites linked by low climate velocity paths indicate high potential areas for species' range shifts.

habitat change on the dispersal network (Rayfield et al., 2011). Additionally, network theory is particularly useful for extracting information from complex networks, such as the potential range shift network we considered. Simulating the impact of site removal on the network can quickly identify key areas. The RSP indicator does not account for species dispersal capacity, so our findings revealed the upper bounds of possibility associated with species successfully shifting their ranges in response to climate change. More species may be unable to reach habitat in the future due to their limited dispersal capacity (Thuiller et al., 2019).

The network of priority protected areas was mainly distributed in Sichuan and the middle to lower reaches of the YRB. These regions are mainly plains with warm climates and abundant water resources, which are ideal habitats for migratory birds (Liang et al., 2021). However, as agricultural and population centers, these regions have recently experienced rapid environmental change. In such cases, species ranges would shift across the landscape, especially for migratory birds, which are highly mobile species that can respond quickly to environmental changes (Tingley et al., 2009). Several lines of evidence suggest that many migratory birds have relocated due to climate change (Huang et al., 2017; Liang et al., 2021). Previous studies of avian distribution changes focused on range edges or distribution centroid shifts (Saupe et al., 2019; Socolar et al., 2017). In contrast, our research provided clear patterns on which to base predictions of range shifts by delineating potential range shift paths among habitat areas. The climate-informed protected priority areas network showed that current protected areas may not be adequate in assisting species to respond to future climate change. To effectively address the challenge of climate change, we recommend that managers act in advance by increasing the designation of protected areas in the aforementioned critical regions based on network results and practical considerations.

Species with restricted ranges, which are typically considered threatened, had likely limited occurrences and were thus excluded from our modeling process for generating the stacked habitat suitability maps. As a result, the stacked habitat suitability values prioritized generalist species over habitat specialists. Furthermore, we included elevation as a predictor variable, viewing it as a relatively stable factor under climate change. However, the relationships between elevation and climatic variables may evolve in the future (Guisan & Zimmermann, 2000; IUCN, 2022). Consequently, the incorporation of elevation in our models could compromise the accuracy of future predictions and result in an underestimation of the projected effects of impending climate change. By stacking the SDMs, we generated a community-level property to evaluate habitat availability for all modeled migratory bird species in the study area. However, stacking the SDMs could lead to a focus on hotspots, potentially excluding certain communities or species (Ferrier & Guisan, 2006). Community-level models may prove more advantageous in generating more representative predictions for all species and communities (Ferrier & Guisan, 2006; Mateo et al., 2013).

In addition, given the predicted general trend of habitat degradation in the study area (Liang et al., 2021; Zhang et al., 2022), our results might also overestimate future habitat, revealing the upper bounds of successful odds associated with species range shifts in response to climate change. As simulation techniques continue to improve (Ren et al., 2019; Zeferino et al., 2020), the classification accuracy of simulated land-use data is expected to increase significantly, allowing for more accurate predictions of habitat availability. Moreover, land use can also be a crucial barrier to species range shifting. However, the existing least-cost-based CV algorithm primarily relies on climate data as the input variable (Carroll et al., 2017; Dobrowski & Parks, 2016; Dobrowski et al., 2013; Hamann et al., 2015; Loarie et al., 2009; Stralberg et al., 2020). Incorporating land use would significantly increase the complexity of the algorithm, demanding a substantial investment of time and computing resources. Therefore, due to technological, temporal, and equipment constraints, we opted to use only climate data as the input variable, which might result in an overestimation of future habitat accessibility.

In general, we used a conceptually simple, widely available, species-specific, and biologically meaningful method to address the question of protection priority. The comprehensive assessments of habitat availability and accessibility revealed different risks and opportunities for migratory birds to shift ranges under climate change. The climate-informed protected priority areas network considered species dynamics and was useful for informing conservation priorities. For those important sites linked by low CV paths, protecting the paths and their destinations to facilitate successful shifts under climate change is the most efficient strategy. Conversely, for those important sites linked by high CV paths, maintaining the current habitat is urgent because exposure to large climactic changes along such paths is more likely to cause species extinction. Our research is the first step toward developing conservation plans that take into account future habitat availability and accessibility under climate change. Future works can incorporate more factors into the evaluations to predict the effects of climate change on species.

ACKNOWLEDGMENTS

This work was supported by the National Natural Science Foundation of China (51979101 and 51679082) and the Science and Technology Innovation Program of Hunan Province (2023RC1041).

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REFERENCES

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, *38*, 541–545.

Araujo, M. B., Cabeza, M., Thuiller, W., Hannah, L., & Williams, P. H. (2004). Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, *10*, 1618–1626.

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*, 327–338.

Bastian, M., Heymann, S., & Jacomy, M. (2009). Gephi: An open source software for exploring and manipulating networks. Third International AAAI Conference on Weblogs and Social Media. Available from https://doi.org/10.1136/qshc.2004.010033

Batllori, E., Parisien, M.-A., Parks, S. A., Moritz, M. A., & Miller, C. (2017). Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network. *Global Change Biology*, *23*, 3219–3230.

Brito-Morales, I., Schoeman, D. S., Molinos, J. G., Burrows, M. T., Klein, C. J., Arafeh-Dalmau, N., Kaschner, K., Garilao, C., Kesner-Reyes, K., & Richardson, A. J. (2020). Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. *Nature Climate Change*, *10*, 576–581.

Carroll, C., Parks, S. A., Dobrowski, S. Z., & Roberts, D. R. (2018). Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Global Change Biology*, *24*, 5318–5331.

Carroll, C., Roberts, D. R., Michalak, J. L., Lawler, J. J., Nielsen, S. E., Stralberg, D., Hamann, A., Mcrae, B. H., & Wang, T. (2017). Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. *Global Change Biology*, *23*, 4508–4520.

Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *Inter Journal*, *Complex Systems*, *1695*, 1–9. Available from https://igraph.org

D'Aloia, C. C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J. M. R., Darling, E., Guichard, F., Leroux, S. J., Martensen, A. C., Rayfield, B., Sunday, J. M., Xuereb, A., & Fortin, M.-J. (2019). Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. *Frontiers in Ecology and Evolution*, *7*, 27.

Dobrowski, S. Z., Abatzoglou, J., Swanson, A. K., Greenberg, J. A., Mynsberge, A. R., Holden, Z. A., & Schwartz, M. K. (2013). The climate velocity of the contiguous United States during the 20th century. *Global Change Biology*, *19*, 241–251.

Dobrowski, S. Z., & Parks, S. A. (2016). Climate change velocity underestimates climate change exposure in mountainous regions. *Nature Communications*, *7*, 12349.

Elith, J., Phillips, S. J., Hastie, T., Dudik, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists: Statistical explanation of MaxEnt. *Diversity and Distributions*, *17*, 43–57.

Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, *43*, 393–404.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*, 147–186.

Hamann, A., & Aitken, S. N. (2013). Conservation planning under climate change: Accounting for adaptive potential and migration capacity in species distribution models. *Diversity and Distributions*, *19*, 268–280.

Hamann, A., Roberts, D. R., Barber, Q. E., Carroll, C., & Nielsen, S. E. (2015). Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, *21*, 997–1004.

Heim, W., Heim, R. J., Beermann, I., Burkovskiy, O. A., Gerasimov, Y., Ktitorov, P., Ozaki, K., Panov, I., Sander, M. M., Sjöberg, S., Smirenski, S. M., Thomas, A., Tøttrup, A. P., Tiunov, I. M., Willemoes, M., Hölzel, N., Thorup, K., & Kamp, J. (2020). Using geolocator tracking data and ringing archives to validate citizen-science based seasonal predictions of bird distribution in a data-poor region. *Global Ecology and Conservation*, *24*, e01215.

Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, *29*, 773–785.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.

Huang, Q., Sauer, J. R., & Dubayah, R. O. (2017). Multidirectional abundance shifts among North American birds and the relative influence of multifaceted climate factors. *Global Change Biology*, *23*, 3610–3622.

IUCN. (2022). Guidelines for using the IUCN Red List categories and criteria. Version 15.1. Prepared by the Standards and Petitions Committee. Available from https://www.iucnredlist.org/documents/RedListGuidelines.pdf

Iyer, S., Killingback, T., Sundaram, B., & Wang, Z. (2013). Attack robustness and centrality of complex networks. *PLoS ONE*, *8*, e59613.

Kenett, D. Y., Perc, M., & Boccaletti, S. (2015). Networks of networks—An introduction. *Chaos, Solitons & Fractals*, *80*, 1–6.

Kong, R., Zhang, Z., Zhang, F., Tian, J., Chang, J., Jiang, S., Zhu, B., & Chen, X. (2020). Increasing carbon storage in subtropical forests over the Yangtze River basin and its relation to major ecological projects. *Science of the Total Environment*, *709*, 136163.

Liang, J., Gao, X., Zeng, G., Hua, S., Zhong, M., Li, X., & Li, X. (2018a). Coupling Modern Portfolio Theory and Marxan enhances the efficiency of Lesser White-fronted Goose's (*Anser erythropus*) habitat conservation. *Scientific Reports*, *8*, 214.

Liang, J., He, X., Zeng, G., Zhong, M., Gao, X., Li, X., Li, X., Wu, H., Feng, C., Xing, W., Fang, Y., & Mo, D. (2018b). Integrating priority areas and ecological corridors into national network for conservation planning in China. *Science of the Total Environment*, *626*, 22–29.

Liang, J., Peng, Y., Zhu, Z., Li, X., Xing, W., Li, X., Yan, M., & Yuan, Y. (2021). Impacts of changing climate on the distribution of migratory birds in China: Habitat change and population centroid shift. *Ecological Indicators*, *127*, 107729.

Littlefield, C. E., Krosby, M., Michalak, J. L., & Lawler, J. J. (2019). Connectivity for species on the move: Supporting climate-driven range shifts. *Frontiers in Ecology and the Environment*, *17*, 270–278.

Liu, J., Kuang, W., Zhang, Z., Xu, X., Qin, Y., Ning, J., Zhou, W., Zhang, S., Li, R., Yan, C., Wu, S., Shi, X., Jiang, N., Yu, D., Pan, X., & Chi, W. (2014). Spatiotemporal characteristics, patterns, and causes of land-use changes in China since the late 1980s. *Journal of Geographical Sciences*, *24*, 195–210.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055.

Luo, Y., Wu, J., Wang, X., Wang, Z., & Zhao, Y. (2020). Can policy maintain habitat connectivity under landscape fragmentation? A case study of Shenzhen, China. *Science of the Total Environment*, *715*, 136829.

Martinez-Lopez, O., Koch, J. B., Martinez-Morales, M. A., Navarrete-Gutierrez, D., Enriquez, E., & Vandame, R. (2021). Reduction in the potential distribution of bumble bees (Apidae: *Bombus*) in Mesoamerica under different climate change scenarios: Conservation implications. *Global Change Biology*, *27*, 1772–1787.

Martinez-Meyer, E., Townsend, P. A., & Hargrove, W. W. (2004). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity: Ecological niches as distributional constraints. *Global Ecology and Biogeography*, *13*, 305–314.

Mateo, R. G., De, L. A., Estrella, M., Felicísimo, Á. M., Muñoz, J., & Guisan, A. (2013). A new spin on a compositionalist predictive modelling framework for conservation planning: A tropical case study in Ecuador. *Biological Conservation*, *160*, 150–161.

McGuire, J. L., Lawler, J. J., McRae, B. H., Nunez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 7195–7200.

Michalak, J. L., Stralberg, D., Cartwright, J. M., & Lawler, J. J. (2020). Combining physical and species-based approaches improves refugia identification. *Frontiers in Ecology and the Environment*, *18*, 254–260.

Naimi, B., Capinha, C., Ribeiro, J., Rahbek, C., Strubbe, D., Reino, L., & Araújo, M. B. (2022). Potential for invasion of traded birds under climate and land-cover change. *Global Change Biology*, *28*, 5654–5666.

Ni, J., Chen, Z. X., Dong, M., Chen, X. D., & Zhang, X. S. (1998). An ecogeographical regionalization for biodiversity in China. *Acta Botanica Sinica*, *40*, 370–382.

Ordonez, A., & Williams, J. W. (2013). Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters*, *16*, 773–781.

Parks, S. A., Carroll, C., Dobrowski, S. Z., & Allred, B. W. (2020). Human land uses reduce climate connectivity across North America. *Global Change Biology*, *26*, 2944–2955.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669.

Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Townsend, P. A. (2007). Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar: Predicting species distributions with low sample sizes. *Journal of Biogeography*, *34*, 102–117.

Phillips, S. J., Williams, P., Midgley, G., & Archer, A. (2008). Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications*, *18*, 1200–1211.

Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, *39*, 542–552.

Rayfield, B., Fortin, M.-J., & Fall, A. (2011). Connectivity for conservation: A framework to classify network measures. *Ecology*, *92*, 847–858.

Ren, Y., Lü, Y., Comber, A., Fu, B., Harris, P., & Wu, L. (2019). Spatially explicit simulation of land use/land cover changes: Current coverage and future prospects. *Earth-Science Reviews*, *190*, 398–415.

Santini, L., Cornulier, T., Bullock, J. M., Palmer, S. C. F., White, S. M., Hodgson, J. A., Bocedi, G., & Travis, J. M. J. (2016). A trait-based approach for predicting species responses to environmental change from sparse data: How well might terrestrial mammals track climate change? *Global Change Biology*, *22*, 2415–2424.

Saupe, E. E., Farnsworth, A., Lunt, D. J., Sagoo, N., Pham, K. V., & Field, D. J. (2019). Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic. *Proceedings of the National Academy of Sciences*, *116*, 12895–12900.

Schmitt, S., Pouteau, R., Justeau, D., Boissieu, F., & Birnbaum, P. (2017). ssdm: An r package to predict distribution of species richness and composition based on stacked species distribution models. *Methods in Ecology and Evolution*, *8*, 1795–1803.

Senior, R. A., Hill, J. K., & Edwards, D. P. (2019). Global loss of climate connectivity in tropical forests. *Nature Climate Change*, *9*, 623–626.

Shimazaki, H., Tamura, M., Darman, Y., Andronov, V., Parilov, M. P., Nagendran, M., & Higuchi, H. (2004). Network analysis of potential migration routes for Oriental White Storks (*Ciconia boyciana*). *Ecological Research*, *19*, 683–698.

Socolar, J. B., Epanchin, P. N., Beissinger, S. R., & Tingley, M. W. (2017). Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences*, *114*, 12976–12981.

Stralberg, D., Carroll, C., & Nielsen, S. E. (2020). Toward a climate-informed North American protected areas network: Incorporating climate-change refugia and corridors in conservation planning. *Conservation Letters*, *13*, e12712.

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, *10*, 1446.

Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences*, *106*, 19637–19643.

UNEP-WCMC, IUCN. (2023). *Protected planet: The world database on protected areas (WDPA) and world database on other effective area-based conservation measures (WD-OECM)*. UNEP-WCMC and IUCN. Available from http://www.protectedplanet.net

Ureta, C., Ramírez-Barrón, M., Sánchez-García, E. A., Cuervo-Robayo, A. P., Munguía-Carrara, M., Mendoza-Ponce, A., Gay, C., & Sánchez-Cordero, V. (2022). Species, taxonomic, and functional group diversities of terrestrial mammals at risk under climate change and land-use/cover change scenarios in Mexico. *Global Change Biology*, *28*, 6992–7008.

VanDerWal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B. L., Perry, J. J., & Reside, A. E. (2013). Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, *3*, 239–243.

van Etten, J. (2017). R package gdistance: Distances and routes on geographical grids. *Journal of Statistical Software*, *76*, 1–21.

Vaz, L., Sousa, M. C., Gomez-Gesteira, M., & Dias, J. M. (2021). A habitat suitability model for aquaculture site selection: Ria de Aveiro and Rias Baixas. *Science of the Total Environment*, *801*, 149687.

Wang, W., Fraser, J. D., & Chen, J. (2017). Wintering waterbirds in the middle and lower Yangtze River floodplain: Changes in abundance and distribution. *Bird Conservation International*, *27*, 167–186.

Xu, X., Huang, A., Belle, E., De Frenne, P., & Jia, G. (2022). Protected areas provide thermal buffer against climate change. *Science Advances*, *8*, eabo0119.

Xu, Y., Si, Y., Takekawa, J., Liu, Q., Prins, H. H. T., Yin, S., Prosser, D. J., Gong, P., & Boer, W. F. (2020). A network approach to prioritize conservation efforts for migratory birds. *Conservation Biology*, *34*, 416–426.

Zeferino, L. B., Souza, L., Amaral, C. H. D., Filho EI, F., & Oliveira, T. S. D. (2020). Does environmental data increase the accuracy of land use and land cover classification? *International Journal of Applied Earth Observation and Geoinformation*, *91*, 102128.

Zhang, S., Yang, P., Xia, J., Wang, W., Cai, W., Chen, N., Hu, S., Luo, X., Li, J., & Zhan, C. (2022). Land use/land cover prediction and analysis of the middle reaches of the Yangtze River under different scenarios. *Science of the Total Environment*, *833*, 155238.

Zhu, Z., Wang, K., Lei, M., Li, X., Li, X., Jiang, L., Gao, X., Li, S., & Liang, J. (2022). Identification of priority areas for water ecosystem services by a techno-economic, social and climate change modeling framework. *Water Research*, *221*, 118766.

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., …, & Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*, 1261–1277.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Liang, J., Wang, W., Cai, Q., Li, X., Zhu, Z., Zhai, Y., Li, X., Gao, X., & Yi, Y. (2024). Prioritizing conservation efforts based on future habitat availability and accessibility under climate change. *Conservation Biology*, e14204. https://doi.org/10.1111/cobi.14204