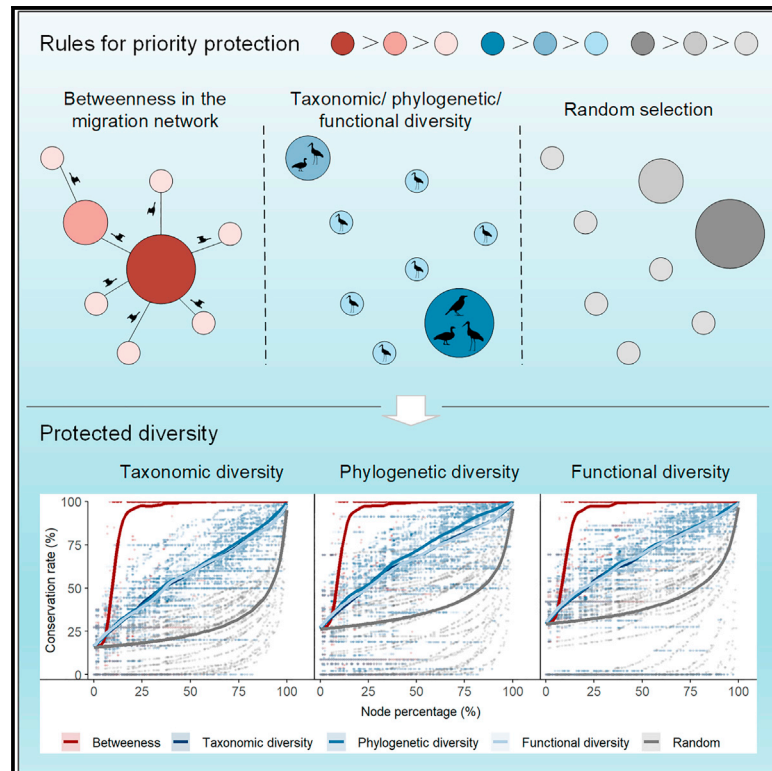


Prioritizing global conservation of migratory birds over their migration network

Graphical abstract



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In brief

One of the most striking features of life on Earth is animal migration. Annual movements along a series of interconnected sites form migration networks. Yet, initiatives for optimal conservation measures have often underestimated the role of network connectivity in maintaining the annual circle of migrations. We showed that insufficient protection of migration networks results in nearly 90% of avian migrants being under threat.

Conservation for migrants should concentrate on maintaining the integrity of migration networks, which calls for international coordination.

Highlights

- Global migration networks of birds are at serious risk
- A small proportion of sites serve as backbone nodes in migration networks
- Prioritizing conservation of backbone nodes can achieve great gains
- Protecting migrants needs intergovernmental partnerships and collaborative actions



Article

Prioritizing global conservation of migratory birds over their migration network

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SCIENCE FOR SOCIETY Conserving a site network for migratory birds is essential for the sustainability of bird populations and ecosystem services provided by their movements. It is effective and efficient to prioritize conservation efforts for sites that have a crucial contribution to the connectivity of the entire network. This specific aspect has not yet been included as a quantitative criterion for designating protected areas in international frameworks of bird conservation. Here, by analyzing migration networks of global birds, we emphasize great conservation gains from protecting a small proportion of sites that have a crucial contribution to migration network connectivity. In the longer term, our work sheds light on solutions for biodiversity conservation with respect to prioritized site conservation actions from a network perspective.

SUMMARY

Halting and reversing biodiversity loss is a grand challenge in the Anthropocene, which suggests an urgent need to effectively protect key areas that support species sustainability. However, large knowledge gaps exist in determining those key areas for migratory species and the extent to which they are protected, albeit with the essential and indispensable functions that migratory species perform in biodiversity conservation. Here, we used over 390 million community-contributed bird observations to derive order-specific, spatially explicit estimates of annual migration networks for 26 bird orders across the world. We found that 35% of the overall 343 important sites that strongly connect the migration network across the annual cycle of global migratory birds are uncovered by protected areas. This leads to nearly 87% of 1,862 migratory bird species being at risk. Migratory species benefit more from considering various levels of site importance to safeguard network integrity, with conservation efforts across countries.

INTRODUCTION

Each year, billions of animals migrate between distant breeding and non-breeding sites connected by a series of stopover sites, forming migration networks.¹ Along these sites, migratory animals accumulate energy, rest, breed, molt, and winter to fulfill their life cycle.² Sites in migration networks (i.e., breeding, non-breeding, and stopover sites) are of various levels of importance.^{3–5} Some sites of the migration network are geographically irreplaceable, given species dispersal distance and habitat availability, while degradation of these key sites (e.g., habitat loss, pollution, and artificial lights) increases the risk of migration

network collapse and, subsequently, biodiversity declines.^{6,7} Site importance (i.e., the differentiated functions of sites in maintaining connectivity of the network) in migration networks allows precise estimates of priorities for conservation efforts and therefore is particularly essential for conservation decision-making of migratory species.⁶

Most protected areas are set up based on biodiversity hotspots, which are defined by *in situ* biodiversity trends or habitat suitability without considering the difference of their functions in migration networks.^{8,9} On the one hand, designation of protected areas for migratory species is different from non-migrants and needs more attention. The mismatch between current



biodiversity hotspots and key sites that are critical for maintaining the network connectivity might threaten migratory species in fulfilling their annual cycle and thus contribute to global migratory species declines.^{10–12} Yet, few studies have capitalized on the information of migration networks to make inferences about the effectiveness of terrestrial protected areas for migratory species conservation. Large knowledge gaps exist in the extent to which the connectivity of global migration networks is protected and how much migratory birds can benefit from prioritizing key network sites for conservation.

On the other hand, there is an increasing recognition that maintaining ecological connectivity is fundamental to species persistence.^{13–15} This is because a network of connected habitats allows individuals to seek out food and habitat resources, avoid predation or anthropogenic threats, and promote gene flow,^{14,16} especially considering the accelerating rate of habitat loss and climate change and their negative impacts on animal movement.¹⁷ Maintaining the integrity of habitat networks, therefore, helps to sustain populations through time and to accommodate species undergoing climate- or land-use-driven range shifts.^{18,19} However, current connectivity models that either measured structural (i.e., landscape configuration) or functional (i.e., patches weighted differently for different species considering dynamic flows of matter and energy) connectivity construct the network based on landscape patches.²⁰ They do not necessarily depend on information of actual animal movement but are based on other sorts of knowledge, such as species habitat preferences and movement behaviors from expert knowledge and literature reviews.²¹ This is in fact modeling the “potential connectivity,” which might introduce bias in the identification of key sites of migration networks and mislead the design and implementation of functionally connected protected area networks, especially for multiple species.¹³ Considering data that measure connectivity are costly to acquire, and the lack of appropriate metrics to use to assess connectivity retention or improvement,²² it is essential to develop spatially explicit connectivity models to utilize ongoing animal observation data to incorporate information on animal movement for protected area prioritization of migratory species.

Here, to explore effective and efficient conservation tools for migratory species, we construct global migration networks at a multispecies level and evaluate the conservation status of the key sites in network. Therefore, we define the multispecies migration network as a series of interconnected sites utilized by migratory birds, and the connectivity of this network represents the extent to which these sites facilitate migratory movements of the studied species group (i.e., an avian diversity flow; see [experimental procedures](#) for full details). The key sites in these networks that crucially support multispecies migration through the available habitats, thus, are of great importance for maintaining migratory bird diversity. Prioritization based on the network importance of areas to maintain diversity, as opposed to the design of conservation areas based on endangered species, is a proactive approach to safeguard migratory species against future threats. We focus on different facets of migratory bird diversity at the order (taxonomic rank) level, rather than on populations or individuals, in efforts to provide the conservation status of migratory birds of each order pertaining to the integrity of migration networks. Furthermore, we estimate the risk of migratory

species due to inadequate protection of their key sites in migration networks and simulate conservation gains for migratory species under different conservation prioritization scenarios.

Based on Global Biodiversity Information Facility (GBIF) data and a migratory bird list from Birdlife International,²³ we first explore how protected area coverage of sites in avian migration networks varies across 26 bird orders of 1,862 species and among different regions. Using a network (mathematical structures composed of nodes that are connected by edges) approach,²⁴ we then construct global avian migration networks on the basis of species occurrences and movement probability across pixels of a 0.5° resolution. We use standard range maps to restrict analyses to grid cells within their breeding and non-breeding range,²⁵ which allows us to investigate sites of the entire migration cycle, comprising breeding, wintering, and stopover sites. We identify the relative importance of nodes (i.e., pixels utilized by the studied birds) for maintaining migration network connectivity by their betweenness (i.e., the number of shortest paths passing through individual nodes).²⁶ The betweenness value of a given node, therefore, represents the extent to which this node contributes to the overall connectivity of the network. We define nodes with a betweenness value of more than 0.01 (i.e., the nodes of top importance that are connected to $\geq 1\%$ of all the shortest paths in the migration network) as “key nodes” in the migration network⁶ because betweenness is one of the most relevant metrics describing the stepping stones in migration networks.¹¹ A network consisting of pure key nodes performs as the backbone network, and the nodes are backbone nodes, which provide fundamental functions for species to fulfill their migration cycle. We assess the conservation status of migration networks by calculating spatial mismatch between the distribution of existing protected areas and the nodes of migration networks.

When all backbone nodes throughout the migration network are protected, migratory birds are more likely to fulfill their migration, and their diversity can be well protected. Therefore, to assess the ability of a migration network to represent gains while protecting taxonomic, functional, and phylogenetic diversities, we define a conservation capability as the diversity of all species throughout a given network. The conservation capability is realized under the condition that all its backbone sites are covered by protected areas. We then estimate whether a typical migratory species is protected across five levels: 100%, 75%, 50%, 25%, and one of its backbone nodes covered by protected areas. We next simulate and compare scenarios to achieve network-based conservation targets while prioritizing unprotected areas for conservation by decreasing importance (i.e., betweenness) in migration networks against prioritizing unprotected areas by decreasing diversity (taxonomic, functional, and phylogenetic) or at random ([Figure 1](#)). Specifically, we simulate five prioritization scenarios where prioritizing conservation of unprotected nodes is in order of the highest to lowest (1) betweenness, (2) local taxonomic diversity, (3) functional diversity, and (4) phylogenetic diversity and (5) at random. We compare conservation gains of these scenarios by calculating changes in taxonomic, functional, and phylogenetic diversities when simulating increases in the protected area coverage. We found that 35% of the overall 343 important sites that play an important role in connecting the migration network across the

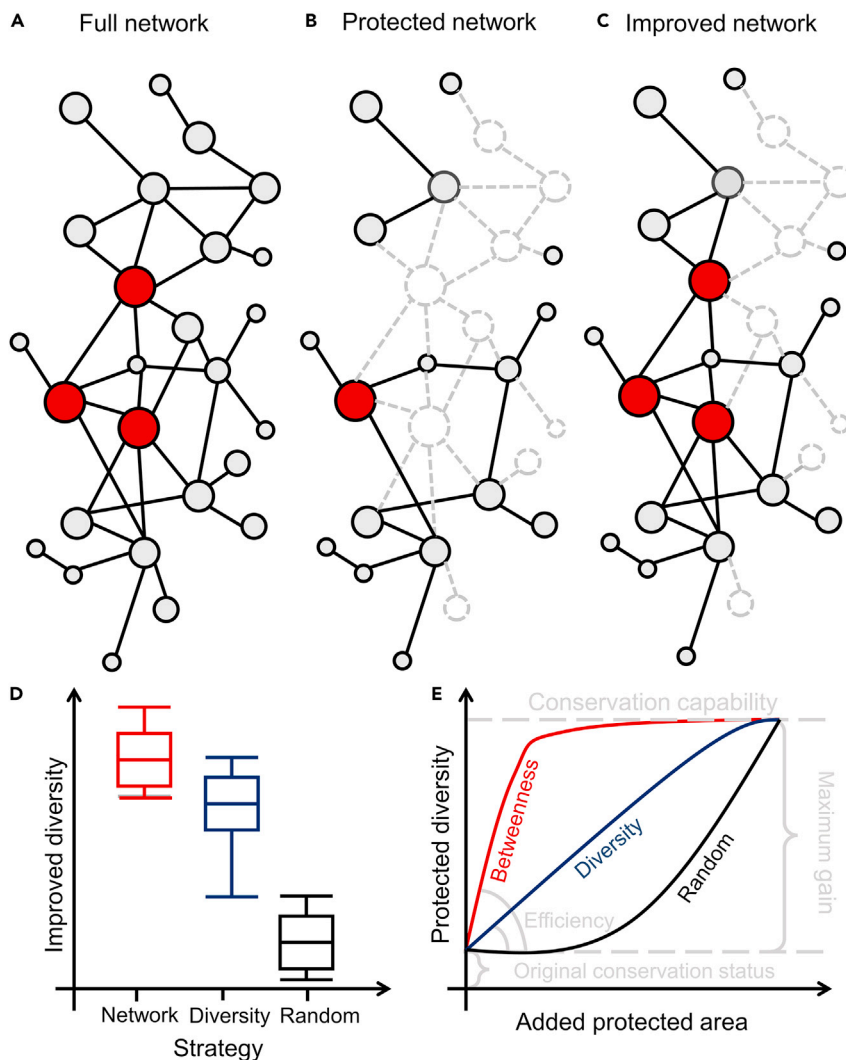


Figure 1. Schematic illustration showing how protecting migration network benefits migratory bird conservation

(A) A full migration network consists of multiple sites, serving various levels of importance. Sites that are important for maintaining connectivity of a migration network are key nodes (red nodes).

(B) Migratory species have great risk in fulfilling the migration cycle due to inadequate protected area coverage of nodes (gray dashed nodes) and the potential of losing corresponding connections (gray dashed line).

(C) By protecting key network nodes, migratory species can maintain their network despite spatial mismatch existing in coverage between network nodes and protected areas.

(D) Compared improved diversity (taxonomic, functional, and phylogenetic diversities) for increasing the same number of protected nodes across three conservation designations; prioritizing unprotected nodes for conservation by betweenness (red) is expected to rise up higher than by local diversity (blue), followed by at random (gray). Betweenness is quantified by the number of shortest paths passing through individual nodes and represents the extent to which a given site acts as a stepping stone in a migration network.

(E) Difference in conservation effectiveness between network prioritized scenario (red line) and diversity prioritized scenario (blue line) and random scenario (gray line) is measured by cumulatively increased protected diversity after adding an unprotected node to protected networks.

annual cycle of global migratory birds are not covered by protected areas. This can result in nearly 87% of 1,862 migratory bird species being at risk. Prioritizing the conservation of migration birds by importance in connecting migration networks can increase more diversity than by local diversity metrics or by randomizing their importance. We urge that migratory bird conservation should carefully consider maintaining the integrity of global migration networks and call for intergovernmental partnerships and collaborative actions.

RESULTS

Protected migration network

The protected nodes in bird migration networks have a significantly lower betweenness compared with unprotected ones (Wilcoxon signed-rank test, $W = 70,375,457$, $p < 0.01$, $n = 28,658$; Figure 2). Moreover, over 35% of backbone nodes are uncovered by protected areas, while 26% of other migration nodes have inadequate protected area coverage (Figures 2 and S1). Only 12.3% of 1,862 migrant species obtain effective protection under the assumption that a species is

protected only if all its backbone nodes are protected (Table S1). We found that a typical backbone migration network relies on two or three key nodes for migrants to fulfill their annual cycle, whereas few biodiversity hotspots are determined covering all major regions throughout a species' migration network.

Different prioritizing scenarios

Migratory birds benefit more from prioritizing conservation efforts for unprotected areas with a higher contribution to the connectivity of migration networks than by diversity indices or at random (Figures 3 and S3). Despite varied levels for determining a species as a protected species, prioritizing conservation efforts for unprotected nodes by their betweenness values could reach the conservation capability six times faster than doing so by diversity indices or at random (Figures 3 and S6). Limiting the available conservation input to the number of unprotected backbone nodes, at a 100% level, the increased taxonomic, functional, and phylogenetic diversities by protecting the backbone network are significantly higher than those by protecting nodes with a relatively high diversity value and those at random (Table S2; Figure 4). For example, the number of protected species jumped from 229 to 1,644 under the network prioritizing scenario, which is almost five times more than by the diversity scenario and is fifty times quicker than by the random scenario.

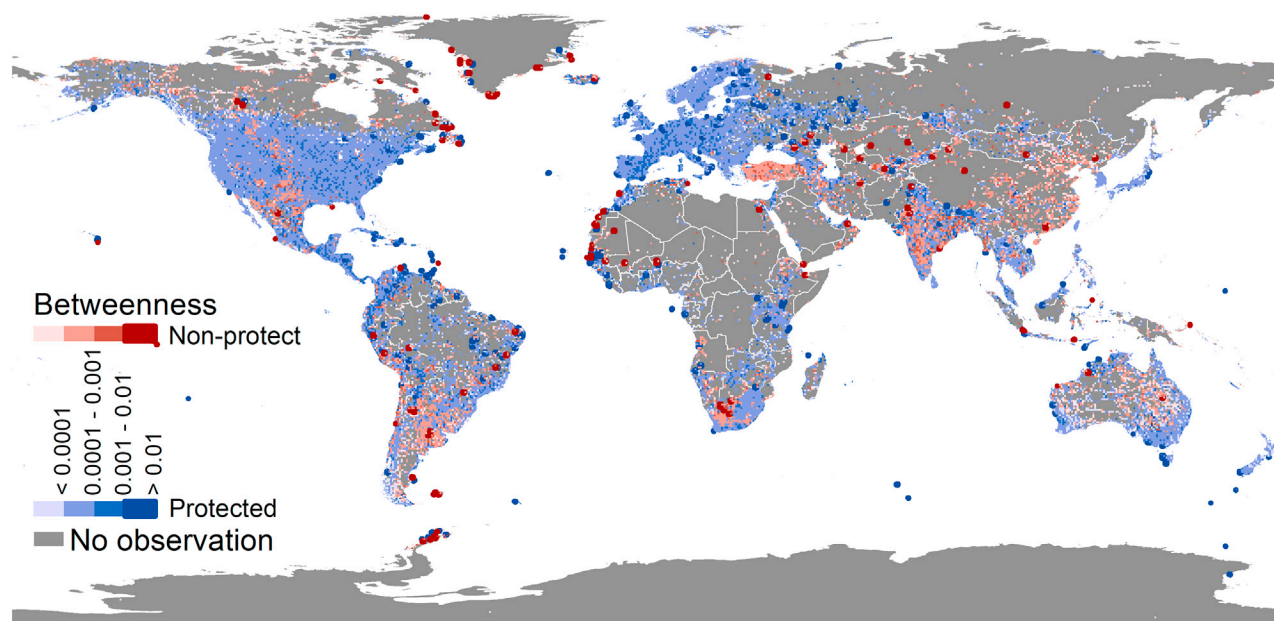


Figure 2. Global distribution of migration network and protected area coverage

Assemblages of migratory birds across the globe are facing risks of losing key sites to support migration networks. Shading represents protected (blue) and non-protected (red) migration network nodes; numbers in the inset denote the average betweenness value of migration network nodes calculated from 26 bird orders. Nodes with betweenness values higher than 0.01 serve as backbone nodes. See also [Figure S2](#) and [Table S1](#).

When all backbone nodes are protected, taxonomic, functional, and phylogenetic diversities increase by 433.3%, 271.7%, and 182.7%, respectively, whereas increased diversity by protecting the same number of nodes in order of diversity values are all no more than 100% ([Figures 4](#) and [S5](#)). We found no significant difference between the increased diversity by protecting nodes with a higher taxonomic, functional, or phylogenetic diversity value ([Figure 4](#)).

DISCUSSION

Ongoing efforts in biodiversity conservation have attracted great attention, and there is an increasing recognition that ceasing biodiversity loss is not an unachievable goal.²⁷ However, conservation of migratory species is different from non-migrants. Previous studies suggested that protected area placement does not cover the full annual cycle of migratory species which may contribute to the world's migratory bird population decline (e.g., Runge et al.²⁸). We demonstrate that not only areas of protected area coverage but also the migration network structure is important for conservation of migratory species. To optimize conservation efforts for migratory species, conservation decision-makers should consider designating protected areas in regions that are not only with high local biodiversity or rapid population declines but also backbone nodes of migration networks.

While information about the relative importance of different network nodes is rarely considered to contribute to conservation decision-making,^{29,30} we found that a significant number of key sites of avian migration networks are not protected, particularly the backbone sites. The inadequate protected area coverage of backbone networks indicates that despite widespread recognition of the need for an internationally coordinated strategy for

conservation of ecological connectivity,^{20,31} the conservation strategy is not yet systematically designed across the migration network of species. For example, key biodiversity areas (KBAs) have been arguably used by many non-governmental organizations as a standard means to identify “sites of importance for the global persistence of biodiversity,”^{32,33} but only 15% of priority KBAs are set to protect migratory species if just considering the winter and spring ranges rather than migration networks.³⁴ Therefore, prioritizing biodiversity network and target selection systematically is highly urged by the scientific community to mitigate these biases.³⁵

Conservation decision-making needs to consider the complex ecological contexts across different spatial scales,³⁶ especially when determining where to allocate resources across heterogeneous landscapes.³⁷ Migratory birds tend to follow multiple spatial processes to select their habitat during migration. They may consider migratory corridors and breeding and nonbreeding areas based on landscapes and environments at a coarse scale (first-level habitat selection) and then local environments at finer scales (second-level habitat selection).^{38–40} This suggests that estimates of migration networks may also need implications from a multiple-spatial-scale perspective. Here, we used a relatively coarse resolution for our analyses, aiming to provide insights for more abstract conservation planning at larger regional and continental scales. However, more detailed information about local movements of birds and their conservation implications can be incorporated on the basis of our study in future. For example, recent advances in wildlife-tracking techniques have revolutionized our capacity to gather highly detailed information on the spatial and temporal movements of various species.^{41,42} This will allow exploration of the detection and attribution of variation among species, populations, and even

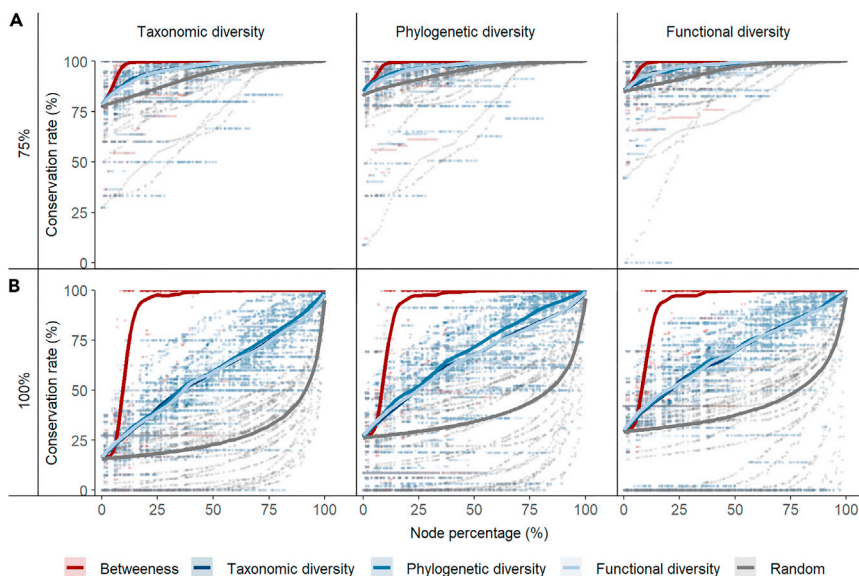


Figure 3. Changes of conservation rate under different conservation scenarios

The overall increasing rate of conservation rate for prioritizing unprotected areas conservation by betweenness (red line) is greater than by taxonomic (dark blue line), functional (light blue line), and phylogenetic diversities (blue line) and at random (gray line). A species is considered adequately protected when 75% (A) or 100% (B) of its backbone network nodes are covered by protected areas. Conservation rate depicts the ratio between taxonomic, functional, or phylogenetic diversity of current protected species and conservation capability (diversity of all species within given networks). The relationship between conservation rate and added node percentage over 26 orders is fitted by generalized additive models with a 95% confidence interval. To facilitate the visualization, 100 values are selected randomly and are shown for each individual order (dots). See also Figures S3 and S6.

individuals, in terms of the covariation patterns between the local movements and environmental contexts, as well as their physiological state, behavioral traits (e.g., personality), or cognitive skills (e.g., spatial memory).⁴² It is also beneficial for directing conservation practice by measuring the effects of potential barriers that hinder local movements of species within coarse-scale backbone nodes determined using our approach.

Given that data that directly measure animal movements are costly to obtain, and the lack of appropriate metrics to assess connectivity retention or improvement, our results highlight an urgent need to develop proper approaches to modeling connectivity for animal movement networks. Different from models that measure habitat connectivity based on landscape patches, current models of migration networks are based on graph theory and construct a network of species using their actual utilized sites (i.e., nodes).^{15,43} Those models require animal-tracking data and provide precise information on species' movement networks. They can help to identify key sites that are geographically irreplaceable (e.g., measured by betweenness centrality) to maintain the integrity of the network. However, those approaches, similar to social network analyses that construct spatially implicit networks at a node-by-node level, rely on population trends or distance-based dispersal probability to weight for the connectivity (i.e., edges in a network analysis).⁶ As nodes are estimated by topology relationship (connected or not), those approaches are less likely to provide information at a pixel-by-pixel level, which has hampered efforts of proper conservation prioritizations as a result. We identified backbone sites of migration networks based on avian diversity flow between each pixel and provided the potential to construct spatially explicit migration networks for multiple species with movement information incorporated. This also provides guidelines for further studies that can include information such as stakeholders' interests²¹ and ecosystem resilience⁴⁴ into weighting the edges of connectivity for prioritization of protected areas based on the framework of our approach.

This first global attempt to assess the performance of existing protected areas in conserving avian migration networks reveals

stark shortfalls, but our findings must be interpreted cautiously. First, we only modeled the migration network for species identified as “full migrant,” whereas “partial migrants,” of which a proportion of a population migrates and other individuals remain residents, can have very different migration networks. Migration networks of unmodeled species may be influenced by morphological,⁴⁵ physiological,⁴⁶ and behavioral traits,⁴⁷ controlled by phenotypic plasticity⁴⁸ and the underlying genetic complex.⁴⁹ Prioritizing protected areas for those species needs systematic considerations on both backbone networks and hotspots for residents.

Second, our study focused on constructing migration networks and prioritizing protected areas on terrestrial lands, and yet marine protected areas can also play an important role in maintaining migration networks, especially for waterbirds. This needs future work that accounts for the role of marine stopovers and effectiveness of marine protected areas for migratory waterbirds.^{50,51}

Third, there are potential sampling biases underlying bird occurrences. Differences in betweenness values between protected and unprotected areas were more marked in continents with larger sample coverage (e.g., Europe and North America) and were more equitable in continents with lower coverage (e.g., Africa and South America; Figure S4). This plausibly implies that developed continents are more likely to attain backbone networks than other continents by protecting a few more backbone nodes. However, it would be beneficial for future works to explore the extent to which such effects are attributed to spatial sample coverage. In addition, there are taxonomic biases in citizen science data in relation to societal preference.⁵² In this case, bird species in some orders might be poorly monitored, and our results should be viewed as conservative with a possible bias against orders with a certain percentage of poorly monitored species.

Fourth, integrating movement behaviors into conservation decision-making is one of the major challenges in current ecological sciences.⁵³ Although we investigated networks of migratory birds based on basic movement traits (i.e., location, direction, distance, and community similarity), our approach has

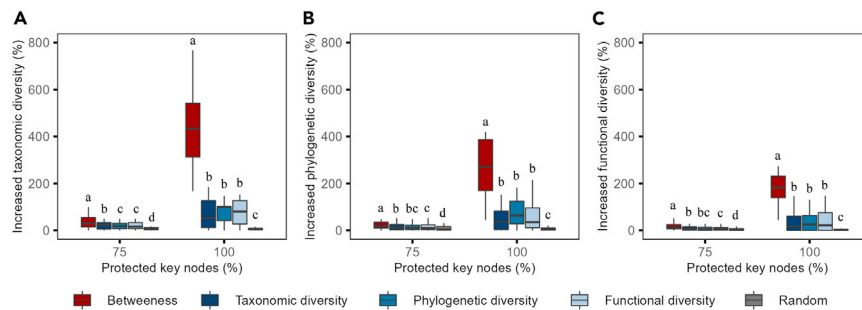


Figure 4. Comparisons of increased diversity under different conservation scenarios

Prioritizing conservation for unprotected areas by betweenness (red) increased more diversity (taxonomic, functional, and phylogenetic diversities) than by taxonomic diversity (dark blue), functional diversity (light blue), phylogenetic diversity (blue), and at random (gray) in taxonomic (A), functional (B), and phylogenetic (C) diversities when limiting available conservation input to the number of unprotected backbone nodes. A species is considered adequately protected when 75% or 100% of its backbone network nodes are

covered by protected areas. The increased diversity of all 26 orders under five conservation scenarios is compared by a Wilcoxon signed-rank test. A bar graph showing the median values and inter-quartile range of increased diversity for 26 avian orders is shown. Different letters indicate significant differences ($p < 0.05$). See also Figure S5.

limitations in inferring effects of other migratory behaviors (e.g., seasonal difference, energy strategy,⁵⁴ discrimination between short- and long-distance migration). For example, future studies can benefit from carefully incorporating the difference between longitudinal and latitudinal migration across different geographic regions into migration network algorithms. It is also beneficial to quantify different functions of the migration nodes as to breeding, wintering, staging, molting, and refueling into weighting the edges of migration network.

Since our analyses focus principally on patterns and conservation of global migration networks, elucidating the mechanism underlying observed migration patterns remains a vital research frontier. In particular, understanding migration network shifts and how they respond to environmental change remains a pressing challenge. Many of the regions are seasonally occupied by migrants,⁵⁵ and broad patterns of some species shift geographically during spring and autumn migrations.^{10,56} Therefore, allocation of conservation resources should balance the site importance in migration networks and the difference between seasonal migration and local population dynamics. Another major gap is evaluating the combinations of abiotic and biotic gradients that are responsible for shaping the robustness of migration networks and how they might respond to future environmental changes. Conservation strategy design should also consider vulnerability of migration nodes. It is also possible that nodes of migration networks of some taxa are of similar betweenness values (Figure S2), which may generate no significant difference by different conservation scenarios (Figure S3). This is particularly important for conservation plans that are constrained to certain taxa because these taxa would be effectively protected only by full coverage of their migration sites.

Global biodiversity is experiencing a serious decline, especially for migratory species,^{3,57,58} despite the increasing size and representation of the global protected areas.⁵⁹ Our analyses highlight a potential failure of adequate consideration for the varied levels of importance in linkages between protected areas. Particularly, in light of the urgent need to address broader ecological challenges such as climate change, we raise concerns regarding the effectiveness of protected areas in supporting avian migration networks across continents. Financial burdens and conflicts stemming from demands for human resources complicated conservation efforts to link different continents and integrate the needs of both wildlife and people.^{27,60} Designating protected areas for migratory species based on

their migration network, therefore, has the great potential to aid in bending the curve of biodiversity loss; fully realizing that potential will require collaborative international partnerships and concerted intergovernmental coordination and action.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Wenyan Zhang (wzhang.ecoevo@gmail.com).

Materials availability

This study did not generate new unique materials.

Data and code availability

Data are publicly available from GBIF (<https://doi.org/10.15468/dl.vkpzfb>), and codes are available from GitHub (https://github.com/plmyann/migration_network).

Avian data

We used a list of migratory birds identified as “full migrant” from Birdlife International,²⁵ comprising a total of 1,958 species from 27 orders. We obtained the occurrence data of migratory birds from the GBIF.⁶¹ GBIF is the largest online repository of biodiversity information in the world, principally storing species occurrence data, which include the geographical coordinates where a given species was observed. We downloaded the point occurrence data on April 26, 2020,⁶² including 391 million records between 2015 and 2019 for all birds.

We applied the following cutoffs for a point occurrence to be included in subsequent analyses. We first removed records where the scientific names were not included in the migratory bird list. For birds that may have multiple scientific names, we obtained their scientific names and matched them with the names in the migratory bird list using the R package “taxize.” We then eliminated all records without georeferenced latitude and longitude points and records that have either their latitude or longitude equal to 0, indicating a missing value. To aggregate data within equal-sized areas large enough to allow robust estimates of phenology, we used a uniform grid of 50 km (Mollweide projection). We also excluded all observations where the margin of error was larger than 50 km (our selected pixel size). The margin of error is calculated as “the horizontal distance (in meters) from the given decimalLatitude and decimalLongitude describing the smallest circle containing the whole of the Location.”⁶³ We restricted observations to the period from 2015 to 2019 to represent the current distribution of migratory birds. We did not include the *Bucerotiformes* order in the subsequent analyses because the available records of this order belong to one single migratory species, which does not support the subsequent network analysis. For each species, we used standard range maps to restrict analyses to grid cells within their breeding and non-breeding ranges.²⁵

Protected areas

To map the boundaries of areas under conservation, we obtained polygons of global protected areas from the World Database on Protected Areas⁶⁴ in May 2020. There were 227,548 protected areas with polygons and 21,168 with

points. We excluded protected areas with unknown boundaries and geographical areas (7,260 sites). Protected areas submitted as points were converted to circular buffers under the Mollweide projection. We assumed these points as the centroids and assigned the reported geographical areas in the World Database on Protected Areas as their areas (13,908 sites).

Network analyses

The network analysis approach was derived from graph theory, which provided important insights into animal social structure,^{65,66} epidemiology,⁶⁷ and community ecology.²⁰ Based on different definitions of nodes and edges, network modeling usually presents the contribution of the node in the connectivity of the whole network. This can be measured by betweenness centrality, which measures the centrality of the shortest paths going through the focal node. The connection of two nodes can be measured by weighting the edges (e.g., cost) as well as a binary measurement of connecting or not. A node with higher betweenness centrality will have more control over the network because more information will pass through that node. Therefore, nodes with higher betweenness values are more important in maintaining the connectivity of migration networks.⁶

To quantify the importance of nodes for connecting migratory diversity and identifying backbone sites for bird migration, we calculated a weighted network where betweenness of each node indicates the extent to which a site acts as a stepping stone in a migration network. Specifically, we calculated the betweenness value quantified by a second-generation weighted betweenness measure,²⁶ which counted the number of least-cost weighted paths going through the focal node.^{68,69}

Typical migration theory considered migration connectivity as the extent to which individuals from the same breeding area migrate to the same non-breeding area, and vice versa.⁷⁰ Since we aim to study the migration network at a multispecies level, we extend the definition of migration connectivity as the extent to which sites facilitate migratory movements of the studied species group. Therefore, a bird migration network consists of sites used by the birds (i.e., nodes) and connections between each pair of these sites (not only neighboring sites) that are used as weights for betweenness calculation and indicate the probability of migration movements between the nodes (i.e., edges).⁶ Given varied life history strategies for different bird orders, we carried out our analyses at the order level in an effort to provide the conservation status of migratory birds of each order considering the integrity of migration networks and estimated their network performance both individually and overall using their average network indices.

A network analysis based on graph theory tends to only consider the graph structure of nodes (e.g., whether they are connected or not) rather than their explicit locations. We used the network analysis in a spatially explicit way by weighting the connection of pixelated nodes over bird movement traits. The nodes of these networks are spatial pixels with a size of $0.5^\circ \times 0.5^\circ$. Firstly, we assigned each obtained GBIF record to the pixel that contains the geographic location of the record. Pixels where species in a given order were sighted or marked were then taken as nodes in a migration network. Secondly, we overlapped the pixels with protected areas and added “protection status” as an attribute to each pixel. We defined a pixel as protected when it fully or partly overlapped (more than half of) the protected areas; otherwise, it was unprotected.

The edges of the networks represent the probability of avian diversity flow, which were defined with distance (D_{ij}), angle (A_{ij}), and community similarity (CS_{ij}) between each pair of nodes. The weight of the edges was quantified with the following algorithm:

$$W_{ij} = A_{ij} \times CS_{ij} / D_{ij},$$

where W_{ij} is the weight of the edge between node i and node j . D_{ij} was measured by the geodesic distance between centroids of nodes i and j . In this way, we quantify the opportunities for community movements between nodes based on a “resistance surface,” where a shorter distance represents less cost for the community to move between the nodes and predicts a lower probability of bird movements. However, given different movement patterns of migratory birds, e.g., Theunis Piersma’s⁷¹ hop-skip-jump model and potential implications of their energy strategy,⁵⁴ our methods might be limited in estimating the effects of movement patterns. We assumed that most migratory

birds tend to migrate in southward and northward directions, and therefore the angle (radian) for the weight was quantified by the arctangent of the ratio between the absolute value of latitude and longitude distances:

$$A_{ij} = \arctan(|Lat_i - Lat_j| / |Lon_i - Lon_j|),$$

where Lat is the centroid latitude and Lon is the centroid longitude of the corresponding node. We defined a higher weight for the edge connecting two nodes holding similar species compositions, which means that two nodes with higher community similarity will have higher probability to be utilized as connected nodes in migration by the objective order of species; thus, we measured community similarity by a Jaccard similarity index⁷²:

$$CS_{ij} = (Spec_i \cap Spec_j) / (Spec_i \cup Spec_j),$$

where $Spec$ are the species observed in the corresponding node. Note that two nodes with higher community similarity, shorter distance, and more south-northward directions could have a higher probability to be connected, but they might still have low betweenness values in the migration network, as the calculation of betweenness considers the connection between the focal node and all other nodes.

Avian diversity

To evaluate the extent to which migratory diversity is protected under the protected network and conservation effectiveness by improving the migration network protection, we calculated taxonomic, functional, and phylogenetic diversities. We used species richness (the sum of all species of a network for each order) for taxonomic diversity. For the calculation of functional diversity, we used 16 traits from Elton Traits 1.0.⁷³ These traits included body mass, diet (i.e., proportional use of invertebrates, vertebrates, carrion, fresh fruits, nectar and pollen, seeds, and other plant materials in a species’ diet), foraging niche (i.e., prevalence of foraging below water surfaces, on water surfaces, on terrestrial ground level, in understory, in mid-canopy, in upper canopy, and aerial), and broad habitat types (i.e., pelagic or not). We gave equal weights to each trait category, which resulted in 1 weight for body mass and broad habitat type and 1/7 for each diet and foraging niche variable. The functional distance was calculated using a multivariate trait dissimilarity under Gower’s distance⁷⁴ for each pairwise species, followed by unweighted pair group method with arithmetic mean (UPGMA) clustering. Phylogenetic diversity was calculated using 100 dendrograms sampled from a full pseudo-posterior distribution of phylogenetic trees (<http://birdtree.org>). The mean phylogenetic diversity across these 100 dendrograms was calculated. For each network, functional diversity was calculated as the total lengths of the functional dendrograms of the subtree joining the observed species on a network,⁷⁵ and phylogenetic diversity was calculated by summing up the total branch length of a subphylogenetic tree joining the observed species on a network via root.⁷⁶

Analysis

We defined the nodes with a betweenness value of ≥ 0.01 as key nodes in the corresponding migration network. We mapped the distribution of key nodes by averaging the betweenness value of each studied node over the 26 studied orders. We compared the difference in betweenness values between protected and unprotected nodes by a Wilcoxon signed-rank test.

To compare the effectiveness of conservation designations by network, diversity, and random approaches, we added the unprotected nodes to the migration networks with five different scenarios, i.e., from the node with the highest betweenness value to the lowest, from the node with the highest taxonomic diversity, from the node with the highest phylogenetic diversity, from the node with the highest functional diversity, and with random orders (100 times). To assess conservation gains for different prioritization scenarios, we defined a conservation capability as the taxonomic, functional, and phylogenetic diversities of all species throughout the given migration networks. Conservation capability is realized when all these species obtain effective protection. We measured the conservation rate by $R_i = d_i / D_i$, where R_i is the conservation rate, d_i is the protected diversity, and D_i is the conservation capability under conservation scenario i . We employed a generalized additive model to fit the correlation between conservation rate and percentage of added unprotected nodes over the 26 studied orders. Furthermore, by setting the same number

of unprotected nodes (i.e., the number of key nodes) as protected nodes, we compared the increased diversity (taxonomic, phylogenetic, and functional diversities, respectively) between five different scenarios with a Wilcoxon signed-rank test.

For a given migratory species, we estimated its conservation status across five levels: 100%, 75%, 50%, 25%, and one of its backbone nodes covered by protected areas. Specifically, we first examined whether backbone nodes of a given order are occupied by a focal species. For those occupied nodes, we calculated their conservation coverage, i.e., the proportion of backbone nodes covered by protected areas. We then evaluated whether a focal species is at risk across those five levels. For example, the most extreme level represents that a focal species is safe only under the condition that 100% of its backbones are covered by protected areas.

We used R 4.0.3 for the calculations of taxonomic, functional, and phylogenetic diversity metrics and statistical analyses. We used MATLAB R2020a for the network analysis. All the codes and data are available in the [resource availability](#) section.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.oneear.2023.08.017>.

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AUTHOR CONTRIBUTIONS

W.Z. and Y.X. conceived of the study. W.Z. and J.W. performed the analyses, and Y.X. shaped the study. W.Z. led the paper writing, and J.W. and Y.X. contributed to the writing. All authors contributed critically to the drafts and gave final approval for publication.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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