

Beyond Site-Specific Criteria: Conservation of Migratory Birds and Their Habitats from a Network Perspective

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Abstract: Many populations of birds depend on networks of sites to survive. Sufficient connectivity that allows movement between the sites throughout the year is a critical requirement. We found that existing international frameworks and policies for identifying sites important for bird conservation focus more at the level of the individual site than on the site network and its connectivity. Only 21% of site criteria acknowledge the importance of movement networks for birds, and such network criteria were mostly (67%) qualitative. We suggest a three-step quantitative approach for informing conservation about the connectivity of bird movements (especially when migrating) from a network perspective, by reviewing current scientific knowledge. The first step is to construct a bird movement network by identifying sites frequently used by birds as ‘nodes’, and then define ‘edges’ from the probability of non-stop flight between each pair of nodes. The second step is to quantify network connectivity, i.e., the extent to which the site network facilitates bird movements. The last step is to assess the importance of each site from its contribution to network connectivity. This approach can serve as a tool for comprehensive and dynamic monitoring of the robustness of site networks during global change.

Keywords: bird movement; migration; site network; conservation; habitat; wetland



Citation: Xu, Y.; Green, A.J.; Mundkur, T.; Hagemeijer, W.; Mossad, H.; Prins, H.H.T.; de Boer, W.F. Beyond Site-Specific Criteria: Conservation of Migratory Birds and Their Habitats from a Network Perspective. *Diversity* **2022**, *14*, 353. <https://doi.org/10.3390/d14050353>

Academic Editor: Miguel Ferrer

Received: 22 March 2022

Accepted: 25 April 2022

Published: 29 April 2022

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1. Introduction

Migratory birds depend on a network of suitable sites/areas (each with one or more types of habitat) to complete their annual life cycle [1]. These sites can serve as places for breeding [2], moulting [3], as stepping-stones during long-distance movements [4], foraging for refuelling and resting [5], and for exchange of social information [6], all essential functions for the survival and reproduction of bird populations that regularly move between, and stop at, multiple locations. Furthermore, they can facilitate pathogen exchange [7], propagule dispersal [8], or transportation of nutrients or contaminants [5].

In an era of rapid global change, disturbance to natural habitats currently poses one of the greatest threats to wildlife [9], and habitat loss or degradation can cause sites to lose their function [10,11]. Such sites may drop out of a site network, potentially causing the connectivity of these networks to decrease or break down rapidly [12,13]. Consequently, decreasing connectivity lowers the robustness of bird populations in terms

of, e.g., migration or breeding success, and lowers resistance and resilience in the face of human disturbance, weather extremes, and long-term environmental change. This can subsequently lead to population declines [10,14,15], change ecological processes, and trigger cascading effects [16]. We elaborate on these different functional consequences of decreasing connectivity in site networks in Supplementary Text S1. Therefore, conserving a network of sites for bird movements not only contributes to the conservation of particular species, but also to the ecological functions provided by these species and their movements [17]. To efficiently maintain or restore the ecological functions of these networks, it is critical to focus conservation efforts on sites that are key in terms of making a crucial contribution to the connectivity of the entire network [17].

The loss of a site from a migration network can have different effects, ranging from no effect to contributing to rapid population decline [10,15,18]. The importance of a site depends not only on its local quality as habitat for a specific bird species, but also on its contribution to the connectivity of that species’ movement network [12,19]. Thus, setting conservation priorities by considering the position of the site within the network may assist informing the conservation of the connectivity of bird movements. Here we review existing major international conservation frameworks and propose a three-step quantitative approach that may facilitate management of migratory birds and their habitats based on site networks. We provide insights for policy makers for site inventories and for maintaining and restoring the connectivity of bird movements, as well as the ecosystem functions they support. Furthermore, the proposed approach can serve as a tool for comprehensive and dynamic monitoring of the robustness of these networks under global change.

2. International Conservation Frameworks for Prioritizing Site Conservation for Birds

To establish the extent to which the concept of network conservation has been included in global conservation policy for birds, we review the existing criteria that major international conservation frameworks and their inventories (acronyms of the reviewed conventions and treaties listed in Tables 1 and S1) for defining a site as important, and hence for setting conservation priorities. We categorize these criteria for site importance into four categories: Diversity, Abundance, Habitat property, and Site network (Table 1; Figure 1). We divide the count of each criterion in the corresponding category by the total number of existing criteria to quantify the contribution of each criterion to policy making in international frameworks.

Table 1. Site selection criteria used in bird conservation frameworks.

Name of Site Inventory (Abbreviation)	Year	Responsible Agencies/Institutions	Governance Framework	Criteria (C)/Articles (A)/Sub-Qualifier for Selection (or Identification) of Sites ¹			
				Diversity	Abundance	Habitat Property	Movement Network
Ramsar Sites (Ramsar)	1971	Ramsar Convention	Global inter-government	C2	C5, C6	C1, C3	C4
Emerald Network of Areas of Special Conservation Interest (ASCI)	1979	Bern Convention, Council of Europe	Regional inter-government	Aa, Ab	-	Ac, Ad	Ae
Natura 2000: Special Protection Areas (SPA)	1979, 1992	European Commission Birds Directive, Europe; Habitats Directive	Regional inter-government	B (Stage1)	-	A (Stage1)	-
Critical Site Network (CSN)	2010	Wetlands International and BirdLife International	Partnership of organisations: African Eurasian Waterbird Agreement, Ramsar, Wetlands International, BirdLife International	C1	C2	-	-
Western/Central Asian Site Network for Siberian Cranes and Other Waterbirds (WCASN)	2007	Convention on Migratory Species (CMS)	Flyway agreement under CMS	C1	Sub-qualifier 2.1	-	Sub-qualifier 2.4

Table 1. Cont.

Name of Site Inventory (Abbreviation)	Year	Responsible Agencies/Institutions	Governance Framework	Criteria (C)/Articles (A)/Sub-Qualifier for Selection (or Identification) of Sites ¹			
				Diversity	Abundance	Habitat Property	Movement Network
Western Hemisphere Shorebird Reserve Network (WHSRN)	1985	WHSRN Committee	Flyway Partnership of governments, international NGOs, and others	-	C2	-	-
East Asian—Australasian Flyway Site Network (EAAFSN)	2006	East Asian—Australasian Flyway Partnership (EAAFP)	Flyway Partnership of governments, conventions, international NGOs, and others	Ca2	Ca5, Ca6	-	Cbi, Cbii, Cc
Global Important Bird Areas (IBA)	1995	BirdLife International	NGO based	A1, A2, A3	A4	-	-

¹ The letters in criteria (C)/articles (A)/sub-qualifiers for selection (or identification) of sites refer to the corresponding terms in the reviewed international frameworks.

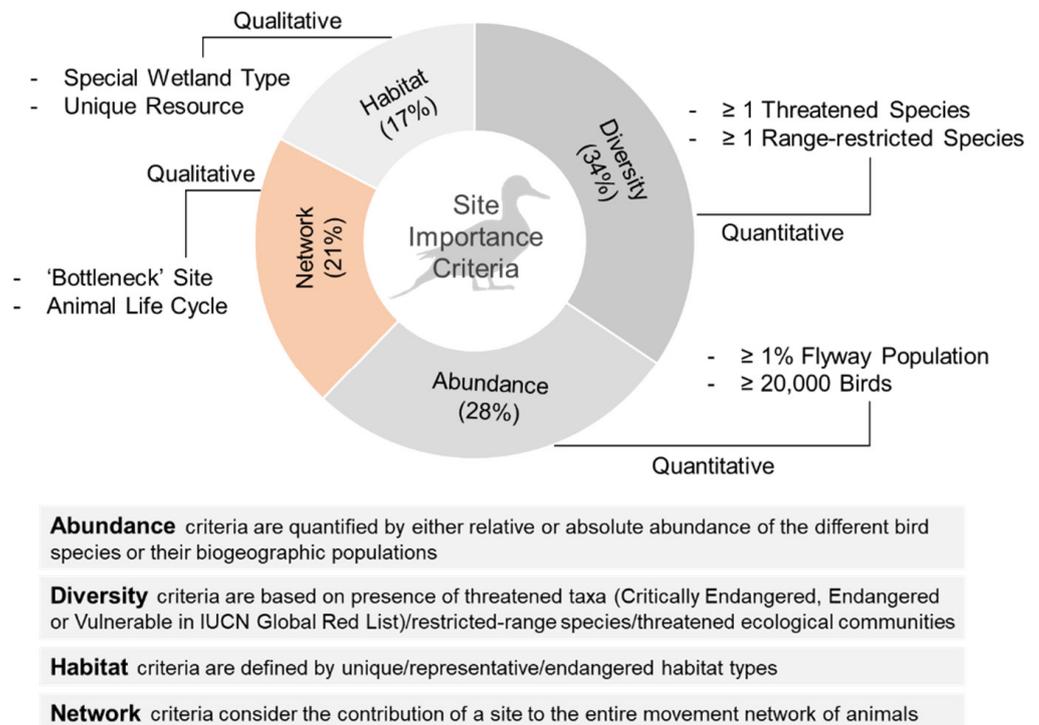


Figure 1. Summary of criteria from international frameworks (those in Table 1) defining the international importance of a site for bird conservation.

2.1. Diversity/Species Threat Status Criteria

These types of criteria usually use number of species (of a certain threat status) and presence of species under critical threat status as a measure of diversity, and are included in most of the reviewed frameworks. The scale at which the diversity is considered differs between the frameworks: Ramsar, EAAFSN, CSN, ASCI, IBA, and SPA. Additionally, ASCI lists sites supporting significant numbers of species with a high species richness as areas in need of special conservation actions. WCASN specifically defines as internationally important those sites hosting the Critically Endangered Siberian crane (*Leucogeranus leucogeranus*) or potentially providing habitats for them.

2.2. Abundance Criteria

Another major fraction of the criteria considers the number of birds using the focal site, which are quantified by either relative or absolute abundance of different bird species. For absolute abundance, a site regularly holding $\geq 20,000$ waterbirds/seabirds/shorebirds is included in Ramsar and EAAFSN, WCASN, and WHSRN. Additionally, a site holding ≥ 25 migratory cranes is included in WCASN.

In criteria that use relative abundance, network thinking starts to appear, especially in those that work with populations rather than species. Numbers at the site level are compared with total numbers in the population (i.e., in the site network). Sites regularly holding $\geq 1\%$ of the population of a biogeographic population of a species are included in Ramsar and EAAFSN, WCASN, CSN, and IBA. These relate to the global/flyway/biogeographic/regional population, depending on the type of framework. WHSRN defines sites regularly hosting at least 30% (hemispheric level), 10% (international level), or 1% (regional level) of the biogeographic population of one shorebird species as internationally important. ASCI considers that an area supporting important populations of a species is internationally important for conservation. WCASN combines criteria of relative and absolute abundance, which defines a site as internationally important when $\geq 0.25\%$ of a migratory waterbird population or ≥ 5000 waterbirds are recorded during a single count.

2.3. Habitat Property Criteria

There are two criteria concerning habitat properties in Ramsar, two in ASCI, and one in SPA, but all of them are qualitative criteria. A site is defined as internationally important when it contains a special, representative, or endangered habitat type, or includes plant or animal species important for maintaining a particular ecosystem function. The sites holding range-restricted species may provide unique habitats for these species, thus, the corresponding criteria are also relevant to this category.

2.4. Network Criteria

Ramsar and WCASN define a site as internationally important when it holds migratory species at any critical stage of their life cycles, for example, an important stepping-stone site during bird migration, as well as including sites used mainly during severe weather conditions such as prolonged drought and extreme cold [20]. The EAAFSN recognises sites if they support migratory waterbirds at a stage of their life cycle important to the maintenance of flyway populations. Additionally, the EAAFSN has two categories for staging sites considered internationally important. The first is when the site regularly supports 0.25% of individuals in a biogeographic population of a species or subspecies of waterbirds on migration. The second is when the site regularly supports 5000 or more waterbirds at one time during migration. ASCI defines important areas for migratory species as special targets for conservation.

In summary, 23 (79%) out of the 29 reviewed criteria focus on site-specific characteristics of areas. Eight criteria (28%) considered the number of birds that regularly use the focal site, while ten of the criteria (34%) were from a diversity perspective. Therefore, although the majority of the criteria (20/29, 69%) are quantitative, most of them focus on bird abundance and species occurring at a given site. There are six criteria (21%) relevant to site networks, but four of them are merely qualitative.

2.5. Current Emphasis on Network Conservation

Recent efforts have been made to include bird movement aspects for setting priorities for bird conservation, especially for migratory birds. Globally, the Convention on the Conservation of Migratory Species of Wild Animals (CMS; unep.org) has strongly emphasized the importance of connectivity of movement networks for conservation of migratory animals in CMS Resolution 12.7 (Rev.COP13) and CMS Resolution 12.26 (Rev.COP13). The Aichi Biodiversity Targets from the Convention on Biological Diversity (CBD) included maintaining well-connected systems of protected areas for terrestrial and marine animals

in Target 11 for Strategic Goal C (cbd.int/sp/targets/). At a flyway level, the EAAFSN, WHSRN, CSN and WCASN all promote conservation of migratory birds from a network perspective. Thus, a quantitative methodological framework would facilitate the further strengthening and implementation of these networks to restore and maintain connectivity for bird populations.

3. A Quantitative Approach Regarding Bird Movements

Millions of birds are being watched, tracked, or ringed each year, providing a large number of occurrence and movement data (Supplementary Text S3). Meanwhile, a growing body of models and algorithms have been introduced to measure the structure of bird migration networks and site contributions to their connectivity [12,19,21–23]. Combining the abundant observations for bird movements with these scientific approaches may be harnessed to quantitatively identify keystone sites in a site network for bird migration. We thus suggest a quantitative assessment of site importance in a bird movement network. This approach can be useful for prioritizing conservation efforts for a group of sites based on their greater contribution to network connectivity compared to other sites. However, the feasibility of this approach should be evaluated with scientific understanding of spatiotemporal bird distributions. For example, it may not be suitable for species that skip stopovers, using a “jump migration” strategy [24]. In addition, we suggest dynamically measuring the networks because loss or degradation of certain sites in the network could affect the distribution of keystone sites. This suggested approach goes through the following steps, where we specify the potential approaches from existing scientific studies for each step (Figure 2).

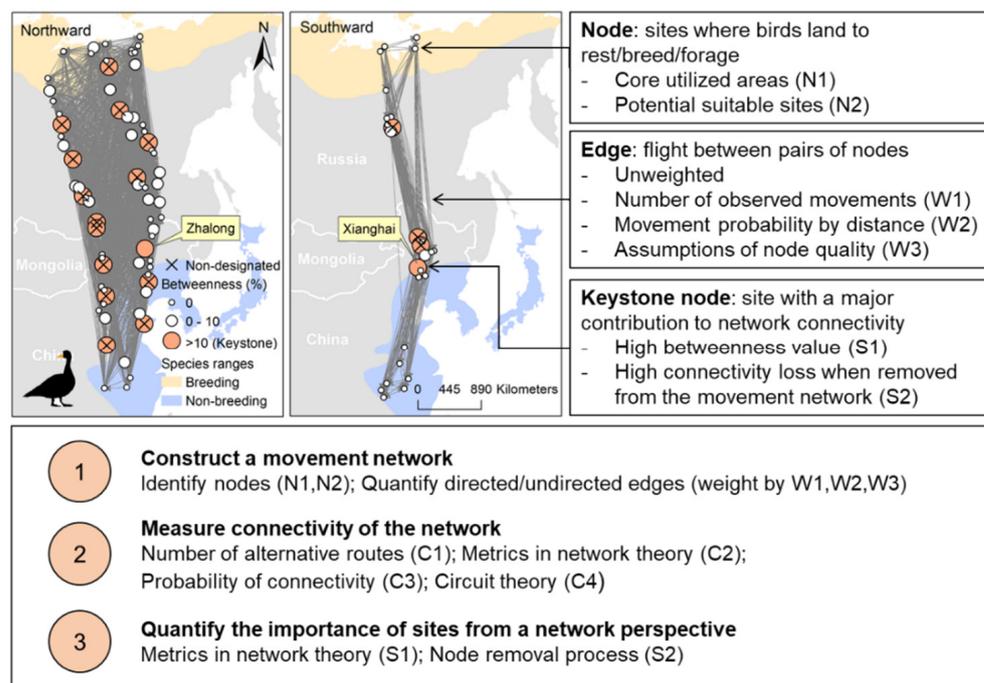


Figure 2. Main components and steps for the suggested approach for movement network conservation. The example shown is a northward and southward migration network of *Anser albifrons* in East Asia, which was constructed on the basis of utilized core areas (N1) and movement probability (W2) with satellite tracking data (see [13] for details). The only protected keystone nodes are Zhalong and Xianghai National Nature Reserves.

3.1. Step 1: Constructing a Bird Movement Network

3.1.1. Identifying Nodes

1. Nodes can be defined as areas that birds regularly or frequently visit (Approach N1), which can be identified from existing diversity, abundance or habitat criteria (Table 1), through count, marking, or capture data (e.g., bird banding and recovery sites), or by applying home range estimators to bird tracking data [25]. This approach assumes the sites where birds were observed, marked, or captured to be staging areas for birds, and are widely defined as nodes in a species' movement network [26–28]. Potential sampling biases may be taken into account, e.g., poor visualization at night reduces the observation rate for nocturnal feeding, or roosting sites that are intensively used by some species (e.g., dabbling ducks [29]). Such potential biases may be tackled by home range estimators to bird tracking data, which identify areas with intensive animal movements based on spatio-temporal point patterns [25]. Main home range estimators include Maximum Convex Polygons Methods (MCP), Kernel Density Estimators (KDE), and Brownian Bridge Movement Models (BBMM), among which dynamic BBMM and movement-based KDE were shown to be the most accurate estimators for home ranges [25]. An equally good alternative is the Guéguen method [30,31], using a Bayesian division algorithm to classify animal behaviour according to turning angles and step lengths.
2. Nodes can also be identified by classification of all sites that are potentially suitable for a species of conservation interest for resting, breeding, moulting, or foraging, based on relevant environmental factors (Approach N2). A straightforward way is to identify areas classified as a suitable land cover class for the focal species, e.g., wetland patches for waterbirds [19], and forest patches for woodpeckers [32]. Some studies define protected areas as nodes within a movement network to measure the efficiency of current conservation efforts for conserving the movements of animals [33,34]. We suggest adding other crucial variables that shape the distribution of species such as, for instance, fish densities for fish-eating birds, and climatic conditions for migratory birds. Species distribution models can incorporate a variety of relevant environmental factors to identify potential suitable sites by, e.g., Generalized Linear Models, Maximum Entropy, Random Forests, or ensemble models [35–37]. Taking advantage of abundant bird occurrence data and remote sensing data for environmental monitoring, these models can take most crucial factors shaping distribution of a species into account [38]. Furthermore, nodes identified by these models could also be compared to the nodes identified by bird counting because they are often protected areas that are already known to harbour concentrations or combinations of species.

Approach N1 more accurately defines the nodes used by birds, but different datasets could be combined to cover a representative proportion of a focal population over an extensive period to capture heterogeneous patterns. The nodes defined by tracked individuals do not include other sites used by the unmarked ones. There are also sites currently not used by birds but may be used later when their movement network changes. For example, temporary wetlands in Mediterranean and arid climates may only flood in a small number of years, which may not fall within the surveillance period of the tracked birds. Thus, approach N1 may underestimate the dynamics of bird movement networks. Approach N2 accounts for this uncertainty by detecting more potential nodes based on long-term and fine-temporal-resolution remote sensing data. However, the flexibility of bird species to environmental changes may be overestimated [39], partly because the ability of birds to explore novel sites remains uncertain. We suggest combining N1 and N2 when investigating the dynamics of networks, and to use long time windows (covering the average generation time of focal species and/or the critical period for environmental changes) to quantify these dynamics. Specifically, nodes of current movement networks can be identified as sites known to be visited, while the other potential sites may be included when modelling the changes in networks. The distances from the visited sites to the other potential sites can serve as proxies for the probability of the potential sites to become used.

3.1.2. Quantifying Edges

A directed network accounts for the direction of movement between a pair of nodes (edges) [23], which is useful for describing movement patterns of migrating birds that often move seasonally in one direction. A network can also be undirected [40], in which the edges do not have directions. Meanwhile, edges can be weighted or unweighted. For the unweighted ones, if movements occur between two nodes, an edge forms between them [14]. Weighted networks weigh the edges by estimations of the probability of bird movements between nodes.

1. The most straightforward quantification for the weight is the count of movements between two nodes from tracked or marked individuals (Approach W1; [26]). The more representative the covered individuals are to the focal population, the closer the distribution of this count is to that of the movement probability distribution. This approach is suitable for ringing/banding recapture datasets. This approach also works for high-resolution datasets of local bird movements, e.g., the Wytham tit study in which the majority of wild birds in the population were tracked [41].
2. Another empirical approach is weighting the edges in terms of the distribution of bird flight distances (e.g., from tracking data) and the geodesic distances between nodes (Approach W2; Figure S1). A decreasing exponential function of distances [42], assuming that greater node-to-node distance is associated with increased cost of movements between nodes, resulting subsequently in a decreased between-nodes dispersal probability (Figure S1), is widely used for weighting edges in movement networks [4,19,34]. In addition, for migration, or immigration, angles that the bird take to move from one node to another can be added to edge weighting [23], based on, e.g., the angle distribution of bird flights and the angles between nodes. Approach W2 is suitable for bird tracking data, which cover a limited number of individuals but provide precise distances and angle distributions of their movements.
3. When empirical bird movement data are not available, assumptions regarding, e.g., predation risk, forage abundance, costs of searching and settling in target nodes (sites that birds move to) can be used to weigh the edges (Approach W3). As an example, the migration flow quantified by differences between node attractiveness of start and target nodes [43] can be an index for weighting the edges. Predation risk or disturbance, forage abundance and/or quality, costs of searching and settling in target nodes [44] can also be included as components to weight edges. We suggest considering other environmental factors en route, such as prevailing winds and landscape barriers (i.e., oceans, high mountains, and deserts), that may play an important role in avian movements [45,46].

Dhanjal-Adams et al. [23] used a combined approach (W1 and W2), which provides a good example for weighting edges (W_{ij}) using empirical data:

$$W_{ij} = N_j \times D_{ij} \times A_{ij}$$

where N_j is the proportion of tracked birds using the target node j (Approach W1), and D_{ij} is the probability of flight from node i to j . This probability is quantified by the distance between them and the distribution of non-stop flight distances of tracked birds (Approach W2), e.g., via a decreasing exponential function of distances (Figure S1). A_{ij} is the probability of flight according to the angles between the nodes, and this parameter may be excluded when studying local movements of birds.

In summary, these approaches for quantifying edge weights require the assumptions for upper limits of non-stop flights for focal species, energetic costs, migratory/immigration directions, or energetic efficiency of flying and settling in the target nodes, which are all dependent on the available sample sizes and the variables that have been measured. We suggest empirically estimating the probability of travelling different distances by the distribution of travelling distances or the count of movements between two nodes. When using Approach W1 and W2, biases caused by uneven sampling methods should be taken into account, e.g., by including sampling effort as part of the weight.

3.2. Step 2: Measuring the Connectivity of the Movement Network

The connectivity of a site network expresses the degree to which the landscape facilitates the movements of populations of birds, which quantitatively indicates the strength of edges connecting different nodes over the whole network. Quantifying changes in the connectivity of site networks can provide early warning signals for (complete or partial) network collapse, e.g., a network is closer to collapse when the connectivity it provides for bird movements is rapidly decreasing.

1. For unweighted networks, the number of alternative routes between two representative nodes (e.g., breeding and non-breeding sites) [13] can measure the connectivity (Approach C1). The number of alternative routes is an index for how flexible birds can be when moving in the network, and the degree to which birds can cope with network changes due to, e.g., environmental disturbances such as extreme drought events.
2. For weighted networks, the Probability of Connectivity index (Approach C2) [4] is widely used to quantify functional connectivity in animal movement networks [19,34]. This approach uses a graph-based algorithm that quantifies functional connectivity by both the area/suitability of habitat in each node and the probability of movements between nodes; thus, both local habitat availability and between-site connectivity are measured. This approach requires data on the landscape configuration, e.g., the node-specific area of different habitat classes, which can be measured by analyzing land cover maps derived from remote sensing images.
3. Classic global metrics in network theory can also be usefully deployed for quantifying the connectivity of site networks (Approach C3, Box 1), although they were originally designed for other fields, e.g., social science. As an example, the modularity [47] of a network, based on classified community memberships [48], can be used to measure the degree to which the movement network is divided into sub-networks (i.e., modules) located in smaller separate spatial regions [26,49]. This is important for identifying spatial units for different functional activities of birds, e.g., day roosting and nocturnal feeding of dabbling ducks [29,50], night roosting and daytime feeding of gulls [51], or high tide roosting of shorebirds [52], which is important for targeted conservation efforts. The generalized clustering coefficient algorithm for weighted directed networks [53] measures the strength of nodes clustering together, which is an alternative to measuring the connectivity of local movements of birds [27]. Degree counts the number of edges pointing to (in-degree) or from (out-degree) the focal node, which is useful for defining hubs and sources of avian movements. Specifically, in a directed network, in-degree and out-degree define hubs (i.e., where birds fly to) and sources (where birds fly from) of the nutrients, contaminants, seeds, or diseases transported by avian movements.

Box 1. Definitions for a network in graph theory, and their applications in bird movement networks.

- a. **Main components** **Nodes** are points in networks, which can represent e.g. individuals, locations, or communication endpoints. In a bird movement network, we define nodes as the sites that birds use for foraging, resting, moulting, or breeding. **Edges** are connections between nodes, which represent bird movements between the sites in a bird migration network. **Modules** are groups of nodes which are intensively connected with each other, but sparsely connected to other nodes from a different module in the network [47]. **Shortest paths** are the least-cost path from one node to the other, in which other nodes in the network may be included as stepping stones [54]. Here a path is a potential route for moving from one node to the other, which includes one or more edges. **Keystone nodes** are nodes with a major contribution to the network connectivity.
- b. **Global metrics** (the structural characteristics of an entire network) **Network size** is the number of nodes, which e.g., represent the number of sites used by birds from a given species during regular movements. **Number of edges** represent the number of direct connections between sites in a network. **Average path length** is the mean length of all shortest paths, which measures the average cost of moving from one site to the other in a network. **Graph path length** is the maximum length of all shortest paths (including the shortest paths between each combination of nodes in the network), which measures the maximum cost of moving from one site to another in a network. **Transitivity** is a generalized clustering coefficient [53], which measures the strength of sites clustering together. **Modularity** measures the strength of dividing a network into smaller modules based on classified module memberships [47,48]. **Effective resistance** uses ecological circuit theory [8] to quantify the flexibility of bird movements within a site network.
- c. **Ego metrics** (the degree to which a site contributes to the connectivity of the network) **Degree** is the number or summed weight of edges connected to a focal node [54], which measures to what extent a site is directly connected to other sites in a network. **Closeness** is the inverse sum of the (weighted) shortest distances to all other nodes [54], which measures the extent to which a site is closely connected to other sites in a network. **Betweenness** is the number of shortest paths going through a node [55,56], which measures to what extent a site acts as a stepping stone in a network. **Bridging centrality** is the local bridging centrality value [57], which measures to what extent a site connects different modules in a network.

4. Electrical circuit theory for ecological processes [58] is another promising pathway for measuring the connectivity (Approach C4), which introduces effective resistance as a measure for the difficulty of movements in a site network (e.g., a higher effective resistance when there are fewer alternative edges for movements). Other algorithms based on resistance surfaces for quantifying connectivity and identifying least-cost paths [59] are comparable to this approach. We suggest using Approach C4 when data allows, because it directly measures the degree to which the site network or landscape facilitates/impedes bird movements.

3.3. Step 3: Determining the Importance of Nodes by Their Contribution to the Connectivity of the Movement Network

The last step is to quantify the importance of a node from its contribution to the connectivity within the movement network. The aim is to identify keystone nodes, which are the most important sites to conserve network connectivity. Removal of one or more keystone nodes will significantly reduce the overall connectivity and may threaten the survival of a migratory species.

1. Classic ego metrics in network theory (Box 1) express the contribution of a node to the connectivity of its network (centrality), which is useful for quantifying node importance in a site network (Approach S1) [26,49]. There are three main measures of node centrality: betweenness, closeness, and degree [12] (Box 1). Among these metrics, ‘betweenness’ better captures keystone nodes, because nodes with high betweenness values are important stepping-stones, which, when lost, can result in rapid decreases in network connectivity [12]. In addition, other node-level metrics may be used,

depending on specific objectives. For instance, bridging centrality [57] is important when measuring crossroads between different flyways or movement modules.

2. Another approach uses a node removal process (Approach S2), which enables quantifying the changes in connectivity of the site network (measurements from Step 2) when removing nodes in different orders [12]. There are three main methods for node removal: single removal, group removal, and cumulative removal. Single removal removes one node at a time from a site network and quantifies node importance by the difference in network connectivity before and after removing it [60]. Group removal removes a group of nodes with certain attributes (e.g., unprotected nodes or nodes in the same geographical zone) [13]. Cumulative removal removes nodes one by one in a certain order without replacements, until the network collapses (e.g., in order of high to low degree of habitat loss [12]).

Xu et al. [12] combined approaches S1 and S2 by comparing the effect of different removal orders in terms of values of different node-level network metrics for cumulative removal, and found that for bird migration, the betweenness value best captured node importance from a network perspective. For other movements (e.g., emigration and local dispersal), we suggest using these combined methods to first explore which is the most suitable network metric explaining the node importance as identified by a node removal process, and then use this selected metric to define importance of a node in the entire network.

The consequence of site loss may be overestimated in the existing modelling studies where the resilience of the bird movement network was not taken into account [12,13,26]. A relevant example of the influence of resilience comes from studies for social networks of wild birds. Firth et al. [61] experimentally showed that new social ties formed among the remaining individuals immediately after removing an individual from a bird social network. These new social ties maintained the connectivity of the social network, indicating the strong resilience of the network. This can also be the case in a bird movement network, because birds may establish new movement pathways or make use of novel sites to compensate when a favored site is disturbed, or when new sites are added to the network [62,63]. Spatially explicit individual-based models [64,65] and other theoretical modelling frameworks for migratory populations regarding migration flows [15,21,22,66,67] can improve understanding of a species' resilience and its decision rules for habitat selection. These theoretical approaches can be used to quantify the importance of site groups by their contribution to set a conservation target, accounting for focal changes in all the sites in a network [68,69], and may ultimately improve the accuracy of simulations for dynamics in movement networks [70].

3.4. Summary and Example of the Three-Step Approach

When available movement data (Supplementary Text S3) can sufficiently describe bird movement patterns, we suggest Approach N1 for node identification in step 1; a combined approach of W1 and W2 as used by Dhanjal-Adams et al. [23] for edge quantification in step 1; Approach C4 for measuring network connectivity (step 2), and a combined approach of S1 and S2 as used by Xu et al. [12] for defining site importance (step 3). However, in many cases, the resolution or quantity of movement data is not sufficient for these approaches. Other modelling approaches, taking advantage of finer-resolution information of environmental conditions, may assist (e.g., Approach N2).

As an example of applying this three-step approach, we here summarize a study of *Anser albifrons* migration in East Asia following these steps [12]. In step 1, both northward and southward migration networks were constructed by analyzing the satellite-tracking data (Figure 2). Specifically, the nodes were identified on the basis of utilized core areas (Approach N1) and the edges were weighted by estimating movement probability between each pair of the nodes by Approach W2. In step 2, the network connectivity was measured dynamically with electrical circuit theory (Approach C4) when the nodes were removed from the constructed networks. In step 3, 19 keystone nodes were identified via between-

ness values (Approach S1), only two (Zhalong and Xianghai National Nature Reserves) of which are currently designated as Ramsar and/or EAAF Flyway Network Sites (Figure 2).

4. Prospects

At a time when an increasing number of migratory bird species are declining worldwide [10,71], improved approaches to conserve these species are urgently required. A quantitative approach for identification of site importance from a network perspective should provide timely support to strengthen existing policymaking aimed at prioritizing flyway network sites so that they can be managed to meet the specific needs of migratory birds. Furthermore, given ongoing human driven habitat and climate driven changes, networks are unlikely to be stable over time. Applying the quantitative measures for connectivity advocated in the suggested approach facilitates comprehensive monitoring of the dynamics in site networks. Periodic reviews of these networks should identify sites where conservation action should be prioritized through incorporation of new research on migration movements and habitat use information.

This quantitative approach takes advantage of a detailed understanding of the regular patterns of species' movements (potential datasets listed in Supplementary Text S3). It may also be used for identifying a network of sites of importance for "resident" bird species undertaking long-distance dispersal or range expansion/contraction due to environmental changes [4]. However, this approach is less useful for some terrestrial birds or waders that do not regularly use stopover sites during migration [24]. Although many of the international conservation frameworks are specially formulated for waterbirds (Table 1) and a large proportion of the reviewed studies are for waterbirds, this approach also fits other taxa that use similar migration strategies. Besides birds, this approach may also be appropriate for setting conservation priorities for some terrestrial or marine species [34], which regularly move between fragments in the landscape or rely on fragmented foraging habitat. Furthermore, understanding of other ecological processes based on animal movements [8,72] can also benefit from following this approach. The applicability of this approach relies on the availability of animal movement data. While national and local research projects contribute by collecting movement data on species, central archiving of such data (e.g., through Movebank) can provide large datasets of tracking points for a range of taxa, which are optimal datasets for network constructions.

Different species display different movements and select different habitats [73], even in the case of congeneric species [74], so we recommend applying this approach or other relevant scientific tools for each species separately based on available knowledge about their movement strategies. Although new technologies allow smaller sized species to be marked, the feasibility of applying the suggested approach is species-size-limited because transmitter tags should be $\leq 2\text{--}4\%$ of the body weight of a species [75]. In addition, movements and habitat selection within the same species may vary considerably between different regions. For example, wild geese in Europe and North America intensively use agriculture lands [76], while geese in East Asia avoid farmland and intensively use natural lakes and riverine wetlands [39]. Thus, the availability of information for birds in different flyways or regions also affects the applicability of this approach.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14050353/s1>, Supplementary Text S1: Functional aspects of the consequences of decreasing connectivity in bird movement networks; Table S1: Sources of the reviewed criteria; Figure S1: Quantifying the probability of dispersal by a decreasing exponential function of distances; Supplementary Text S2: Examples of the practices for keystone sites defined by the proposed approach; Supplementary Text S3: Examples of data sources for constructing bird movement networks; Supplementary Text S4: References for the contents in Supporting Information [77–127].

Author Contributions: Y.X. and A.J.G. designed the study and Y.X., A.J.G., T.M., W.H., H.M., H.H.T.P., W.F.d.B. conceived the ideas. Y.X., H.M. and T.M. reviewed the conservation frameworks. Y.X. led the manuscript writing, and all authors contributed to writing and gave approval for publication. All authors have read and agreed to the published version of the manuscript.

Funding: Y.X. was supported by China Scholarship Council (201600090128). A.J.G. was supported by Spanish National Plan projects CODISPERSAL CGL2016-76067-P and WATERZOO PID2020-112774GB-I00 (AEI/FEDER, EU).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We thank B.C. Sheldon, J.A. Firth for their insightful discussions about the functional aspects of connectivity in bird movement networks.

Conflicts of Interest: The authors declare no conflict of interest.

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