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Note

Co-occurrence Patterns of Bird Species in the World

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Abstract In order to identify key nations and bird species of conservation concern we described multinational collaborations as defined using network analysis linked by birds that are found in all nations in the network. We used network analysis to assess the patterns in bird occurrence for 10,422 bird inventories from 244 countries and territories. Nations that are important in multinational collaborations for bird conservation were assessed using the centrality measures, closeness and betweenness centrality. Countries important for the multinational collaboration of bird conservation were examined based on their centrality measures, which included closeness and betweenness centralities. Comparatively, the co-occurrence network was divided into four groups that reveal different biogeographical structures. A group with higher closeness centrality included countries in southern Africa and had the potential to affect species in many other countries. Birds in countries in Asia, Australia and the South Pacific that are important to the cohesiveness of the global network had a higher score of betweenness centrality. Countries that had higher numbers of bird species and more extensively distributed bird species had higher centrality scores; in these countries, birds may act as excellent indicators of trends in the co-occurrence bird network. For effective bird conservation in the world, much stronger coordination among countries is required. Bird co-occurrence patterns can provide a suitable and powerful framework for understanding the complexity of co-occurrence patterns and consequences for multinational collaborations on bird conservation.

Key words: bird co-occurrence pattern, centrality, multinational collaboration, network analysis

INTRODUCTION

Birds have long been a major focus of public attention and research interest. In particular, multinational collaboration is now a major driver in bird conservation (Donald *et al*., 2007). Amongst researchers and environmental groups, the consensus about bird conservation is that a comprehensive and cooperative international effort is needed to conserve viable bird populations (Williams *et al*., 2013). Effective bird conservation globally will require far greater coordination amongst countries (Donald *et al*., 2007). The Individualistic implementation of bird conservation policies

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may fail if previously identified interactions within the network between countries are ignored (Runge *et al*., 2015), also contributing to the limited success of bird conservation at the national level, conservation policies are rarely implemented in a uniform manner and research interest is often patchy due to its dependency upon the researcher.

Although countries located along migratory routes have established networks for the protection of migratory birds, based on flyway concepts that emphasize political and governmental processes in multinational collaboration, non-migratory birds are not covered effectively in traditional flyway models. Spatial co-occurrences for both migratory and non-migratory birds, may reveal complex interactions in a network spanning many countries, based on the geographic patterns of bird co-occurrence among countries (Böhning-Gaese and Oberrath, 1999; Webb *et al*., 2002). The complexity of direct and indirect interactions linking birds amongst countries is so vast that their complete documentation is beyond reach. Using network analysis to understand the drivers affecting the distributional dynamics that facilitate bird conservation globally, as well as enable multinational collaboration, requires investigation using alternative approaches.

We use an approach based on network analysis to identify potential broad-scale interactions between birds from different countries, based on the geographical patterns of bird co-occurrence. Network analysis has traditionally had a strong synergy with business models in certain industries (Proulx *et al*., 2005), but we believe that it could be used to identify direct and indirect relationships linking birds from countries by analyzing the structure in the network (Scott, 2012).

Our specific objectives were to (i) propose multinational collaboration groups, defined by network analysis, that are linked by co-occurring birds, and (ii) to identify the key countries and birds of conservation concern in each network. First, we hypothesized that countries and birds with the potential to affect other countries and species will have higher closeness centrality scores. They can provide the clearest perspective of the state of the network. Second, we predicted that countries and birds that are important to the cohesiveness of the network would have a higher betweenness centrality score. Together, these indices can represent how each country can conduct bird conservation efforts independently and effectively relative to others.

METHODS

1. Data collection

We used 10,422 bird inventories from 244 countries and territories obtained from BirdLife International (2015, http://datazone.birdlife.org). The cumulative total contribution (in US Dollars) for 193 countries from 1973 to 2013 to the Environment Fund of UNEP (United Nations Environment Programme) was used to indicate conservation effort in each country including bird conservation.

2. Network analysis

We used network analysis to examine the patterns of bird co-occurrence and the structure and level of bird connectedness. Network analysis uses a set of procedures to identify and measure the structural properties of social systems, based on relationships among entities in the system rather than on characteristics of the entities. A network can be thought of as a set of nodes with connections or links between them. In our study, the nodes are countries and birds while the links are undirected connections between each country and species.

Centrality indices describe the importance of specific nodes within the network (Newman, 2010). Different centrality indices measure different aspects related to the position of a node within its network. Closeness centrality expands the definition of degree by focusing on the distance between nodes. A central node is thus characterized in the networks by numerous short connections. Betweenness centrality represents a different aspect of centrality: based on the number of times a particular node is found on the shortest path between any pair of nodes in the network. Nodes that are highly central control information flow in the network and thus receive a higher score of betweenness centrality. A social network analysis and visualization software application, Gephi (which uses the ForceAtlas 2 algorithm as a type of force-directed layout algorithm, ver 0.9.2), was used to determine the position of the participants and develop network diagrams (sociograms) that indicate the relationship ties and information flow between the individual nodes. The different centralities among the groups were divided using the modularity index and were tested using a one-way ANOVA and Duncan's post-hoc test.

RESULTS

1. Bird co-occurrence

The average number of bird species for the 244 countries was approximately 403 species. The median number of birds per country was 311 species. Countries in South America, such as Columbia (1,827 species), Peru (1,807 species), and Brazil (1,753 species), had the highest number of bird species (Fig. 1a). In Asia, Indonesia (1,615 species) also showed a high number of bird species. A total of 7,586 species occurred in more than two countries, while 2,836 species (27.2% of total bird species) were only recorded in one country. *Arenariainterpres* (221 countries), *Hirundorustica* (213 countries), *Falco peregrinus* (210 countries), *Numeniusphaeopus* (209 countries), *Calidrisalba* (205 countries), and *Pandion haliaetus* (202 countries) had the broadest distributions across the world.

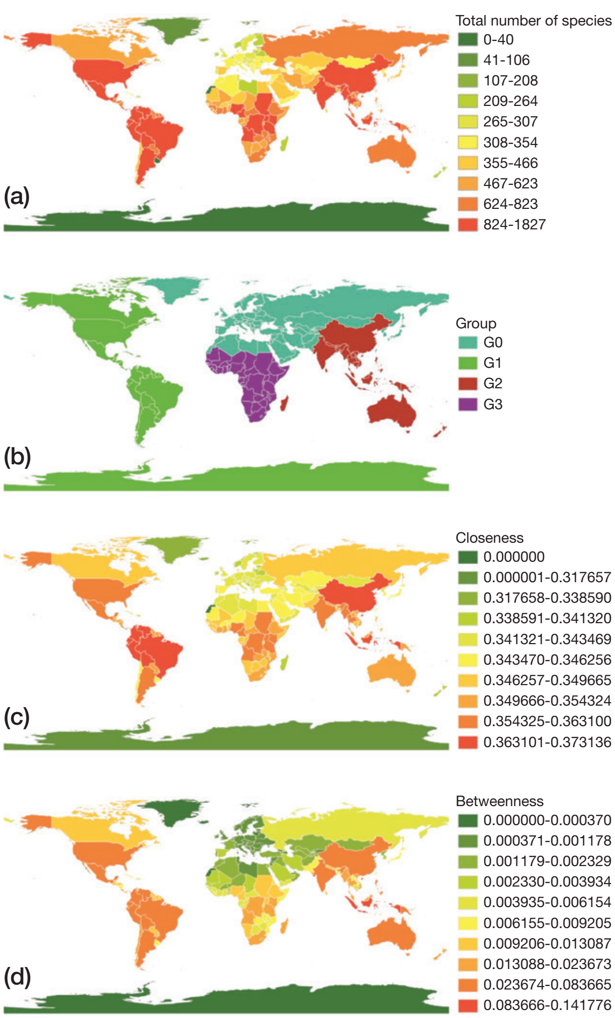

Fig. 1. Maps of (a) the total number of bird species, (b) groups based on modularity from network analysis, (c) closeness centrality and (d) betweenness centrality of countries.

2. Bird network

The country-bird network consisted of 10,585 nodes and 97,419 edges (average degree, or node, connectivity = 18.4, Fig. 2). The average network distance between all node pairs (average path length) was 3.63 (the longest distance was 6 edges). The modularity index was 0.596 (values > 0.4 suggest that the network has a strong modular structure).

Nodes were divided into 4 groups based on their modularity. Co-occurrence networks for four groups of birds reveal different relationships with biogeographical organization (Fig. 2). Group 0 (G0) accounted for 8.68% of the network; it included 93 countries and 826 species in Europe, North Africa, the Middle East, and East Asia. Group 1 (G1) consisted of 60 countries and 4,220 species in America. G1 was the largest group in the network, with 40.44% of total nodes and edges. Group 2 (G2) accounted for 34.59% of the network, and included 48 countries and 3,613 birds in Asia, Australia and the South Pacific. Group 3 (G3) accounted for 16.29% of the network, and included 43 countries and 1,681 species in Sub-Saharan Africa.

Fig. 1c and 1d show that several countries within middle latitudes had higher centrality scores for both closeness and

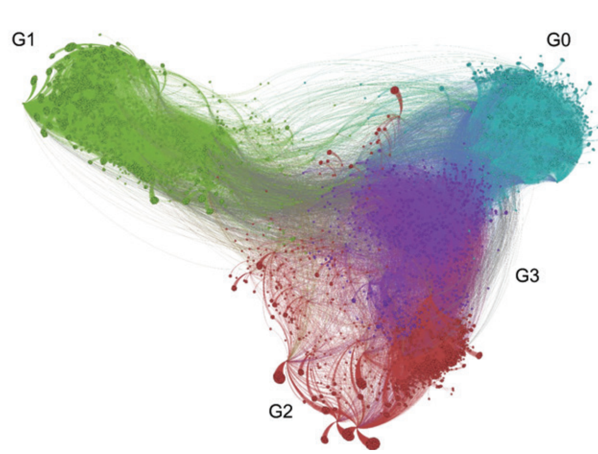

Fig. 2. The network diagram for countries and birds. Each node (dot) represents a country or a bird. Nodes of same color belong to the same group. An edge (line) represents the relationship between two individuals.

betweenness centrality. Closeness centrality of countries in G3 was significantly higher than in the other groups (Post-hoc test, $P<0.001$) while betweenness of countries in G2 were higher than in the other groups (Post-hoc test, $P<0.05$). Pakistan (G0), Brazil (G1), Indonesia (G2), and Congo (G3) had the highest closeness centrality in each group. Highest betweenness centralities were recorded in Japan (G0), Brazil (G1), Indonesia (G2), and Tanzania (G3) in each group.

Among all bird species, closeness and betweenness centralities of G0 were significantly higher than they were for the other groups (Post-hoc test, $P<0.001$). *Porphyrio porphyria*, *Dendrocygnaviduata*, *Cisticolajuncidis*, *Elanuscaeruleus*, and *Rostratulabenghalensis* had the highest scores for closeness centrality. Comparatively, *D. viduata*, *P. porphyria*, *Nettaerythrophthalma*, *Laruscirrocephalus*, and *C. juncidis* had the highest scores for betweenness centrality. *Arenariainterpres* (G0), *Butoridesstriata* (G1), *Fregata minor* (G2), and *P. porphyrio* (G3) had the highest values for closeness centrality for each each group. *A. interpres* (G0), *B. striata* (G1), *F. minor* (G2), and *D. viduata* (G3) had the highest values for betweenness centrality for each each group.

The allocation to the Environment Fund of the UNEP from each country was not an appropriate measure of the importance of each country, based on centralities in the network. Many countries with high-level centrality values made small contributions (Fig. 3). This result presents a paradox and emphasizes the importance of multinational collaboration in bird conservation (Donald *et al.*, 2007; Butchart *et al.*, 2010).

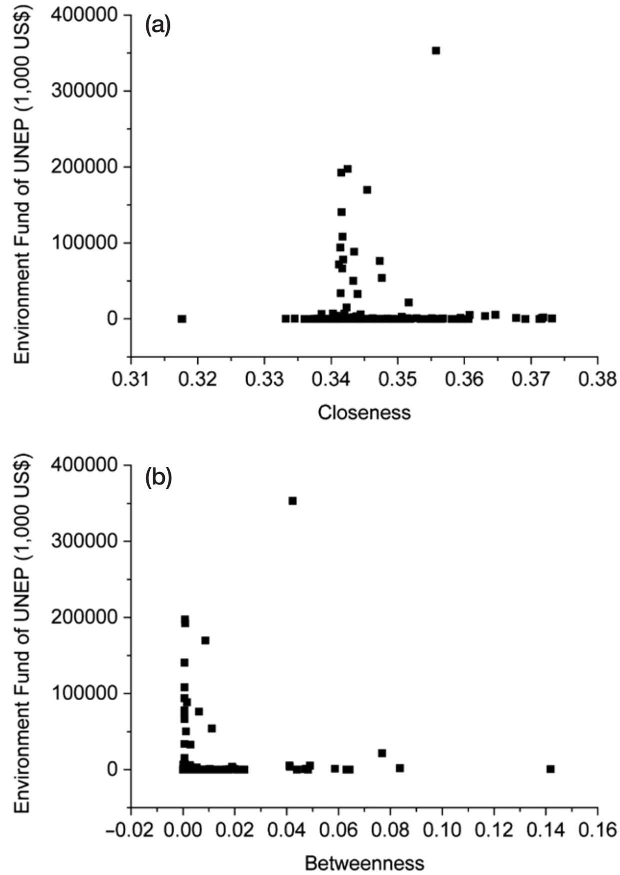

Fig. 3. Relationships between centralities and their contributions to the Environment Fund of UNEP, which represent bird conservation efforts in each country.

DISCUSSION

The present study identifies groups of birds that can be targeted for multinational collaboration, using network analysis. In addition, we identify several countries and bird species that provide important links and are crucial for multinational bird conservation in the four regional groups and globally. The geographical distribution of the groups, based on bird co-occurrence patterns, corresponds with large zoogeographic regions such as Nearctic, Neotropical, African, Palearctic, Oriental, and Australian regions. The zoogeographic region construct has already been used to highlight areas of the world that are most distinctive or represent high "value" and are, therefore, worthy of greater attention (Olson and Dinerstein, 1998; Olson *et al.*, 2001). A large multinational group can be more appropriately conceptualized as an international bird conservation group rather than a representation of local conservation (Sodhi *et al.*, 2011). Each group in the network may overcome a limitation of the migratory bird flyway concept, in which east-west migration is not well-recognized (Favell, 2008). However, conservation policies that are implemented across large biotic regions or hotspots often fail to discern smaller but highly distinctive areas; this can result in these areas receiving insufficient conservation attention (Olson *et al.*, 2001). Bird conservation at the local level should also be strongly recommended, as careful attention to bird habitat may be improve the efficiency of conservation efforts.

Countries and species with high scoring closeness and betweenness centrality may act as excellent sentinels or indicators of trends in co-occurrence bird networks, although countries in mid-latitudes had high centralities that strongly correlated with the number of species. Bird species with high score centralities had extensive distributions across the world. Generalist birds that have broad distribution with large population are often not important issues in bird conservation. However, these species could be important for identifying the current state of bird diversity and conservation effectiveness at the local level, for these species have the great role of connecting habitats and countries (Cassey *et al*., 2004).

Sustained economic support for coherent global bird conservation is essential to improve the effectiveness of these responses. We believe that a bird co-occurrence network provides a suitable and powerful framework to address the complexities of co-occurrence patterns and can pave the way to improving worldwide bird conservation.

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