

## RESEARCH ARTICLE

Diversity and Distributions WILEY

# Highway(s) overhead: Strong differences in wetland connectivity and protected status challenge waterbird migration along the four Palearctic-Afrotropical flyways

Evelien Deboelpaep<sup>1,2</sup>  | Lisa Partoens<sup>1,2</sup> | Nico Koedam<sup>2</sup> | Bram Vanschoenwinkel<sup>1,3</sup>

<sup>1</sup>Vrije Universiteit Brussel, Ecology & Biodiversity Research Group, Community Ecology Lab, Brussels, Belgium

<sup>2</sup>Vrije Universiteit Brussel, Ecology & Biodiversity Research Group, Plant Biology & Nature Management, Brussels, Belgium

<sup>3</sup>Centre for Environmental Management, University of the Free State, Bloemfontein, South Africa

## Correspondence

Evelien Deboelpaep, Vrije Universiteit Brussel, Ecology & Biodiversity Research Group, Community Ecology Lab, Pleinlaan 2, B1050 Brussels, Belgium.  
Email: evelien.deboelpaep@vub.be

## Funding information

Fonds Wetenschappelijk Onderzoek, Grant/Award Number: 11ZH516N

Editor: Trishna Dutta

## Abstract

**Aim:** Waterbirds that travel seasonally between Europe and Africa use wetlands along four major Palearctic-Afrotropical flyways. However, it is unknown to what extent the overall connectivity of these flyways may be threatened by ongoing habitat loss and degradation. Here, we contrasted the wetland connectivity along these four flyways, applying graph-theoretic connectivity metrics on an intercontinental scale. We also explored for which flyway connectivity is most at risk. We then identified the most important wetlands by their contribution to connectivity in each flyway.

**Location:** Western Palearctic, Afrotropics.

**Methods:** Based on high-resolution wetland maps, we calculated directional probabilistic connectivity metrics. Estimates of overall connectivity of each flyway were obtained, as well as the relative importance of wetlands, for birds with different migration strategies: short-distance hoppers and long-distance jumpers.

**Results:** The East-Atlantic flyway and Eastern Mediterranean flyway had higher overall functional connectivity than the two central routes, reflecting the larger barrier represented by the Mediterranean Sea and Sahara Desert. Fewer than 5% of all wetlands supported more than 70% of the total connectivity of the network in each flyway, regardless of the considered migration strategy. These wetlands were either large, strategically positioned or both. Removing non-protected wetlands from the analysis showed that the connectivity of some flyways could be jeopardized and that the East-Atlantic and Eastern Mediterranean flyway may be most vulnerable to additional habitat loss.

**Main conclusions:** Our results illustrate (i) the major contribution of unprotected wetlands to flyway connectivity, (ii) the importance of integrating migration ecology into site-based connectivity analyses and (iii) the utility of graph-based connectivity metrics to inform conservation prioritization under present and future scenarios.

Evelien Deboelpaep and Lisa Partoens have equal contribution.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd.

## KEYWORDS

flyways, functional connectivity, migratory waterbirds, probability of connectivity, protected areas, trans-Saharan migration, wetland networks

## 1 | INTRODUCTION

Migratory waterbirds spend much of their life travelling between scattered habitat patches in a largely inhospitable landscape matrix. Waterbirds ecologically link distant areas by performing these seasonal movements at large spatiotemporal scales (Bauer & Hoyer, 2014; Piersma & Lindström, 2004). Because of their migratory behaviour, avian migrants are sensitive to changes in the state of their habitat in every part of their range, and the quality and connectedness of paths and stopovers along migratory trajectories can culminate in strong differences in survival and reproduction (Aharon-Rotman et al., 2016; Bauer et al., 2008).

Cumulative effects of habitat deterioration and strong reductions in functional wetland area due to human disturbance and climate change may render migratory habits no longer ecologically tenable. Currently, 38% of all waterbird populations are declining, the majority of which are migratory (BirdLife International, 2018; Wetlands International, Mundkur, & Nagy, 2012). Some avian migrants can cross thousands of kilometres in a single non-stop flight, but all rely on stopovers that need to be sufficiently connected for replenishing their energy reserves (Kirby et al., 2008; Trierweiler et al., 2014; Xu et al., 2019). Nevertheless, whether currently used wetland networks are well-connected or not is unknown for the majority of the world's flyways.

The connectivity of suitable stopover sites such as wetlands is probably most important close to migratory barriers such as seas and deserts. Adequate resting and refuelling opportunities for birds in these barrier regions are scarce, and overall conditions can be more challenging for example, thermoregulation and maintaining internal water balance (Newton, 2008). Often, migratory waterbirds are classified into jumpers, skippers and hoppers based on their predominant migration strategy and the fat reserves they carry to fly longer distances (Piersma, 1987). However, currently we do not know how wetland networks along different flyways can facilitate efficient migration of birds with different migration strategies. Such knowledge could be important to better understand why birds follow certain routes and to analyse the extent to which different routes differ in facilitating bird migration.

Worldwide, eight (or nine) flyways are recognized that group similar migratory trajectories of different populations and species (Boere & Piersma, 2012; Boere & Stroud, 2006), though flyways can also be defined for individual birds. The flyway concept helps to better assess a wetland's function within the entire migratory trajectory and to coordinate international conservation efforts. More than 300 migratory bird species make use of the Palearctic-Afrotropical flyways and 255 of those rely mainly or exclusively on wetlands during at least part of the year (BirdLife International, 2010a, 2010b; UNEP/AEWA secretariat, 2018). Still, much remains unknown about

differences in connectivity of flyways and the relative importance of individual stopovers within them.

Globally, the Ramsar convention and Important Bird and Biodiversity Area (IBA) network are aimed at protecting wetland areas of international importance. In the Western Palearctic the Birds<sup>1</sup> and Habitats<sup>2</sup> Directives protect wetlands that are part of the Natura 2000 network within the European Union. However, a substantial fraction of wetlands used by migratory birds is not formally protected, let alone maintained in a favourable state of conservation, and it is not known to what extent such unprotected wetlands are essential to maintain connectivity (Runge et al., 2015). In the context of connectivity, not only a wetland's quality but also its position in relation to other wetlands and to migratory barriers should be taken into account when establishing conservation priorities (Amezaga et al., 2002; Dhanjal-Adams et al., 2017).

To better evaluate the suitability of stopover networks and prioritize wetland sites for bird migration, there is a need for practical metrics that can provide a reliable estimate of the connectivity of flyways and can assess which wetlands may be more important than others. This is not straightforward, as the concept of connectivity has different interpretations that are sometimes difficult to distinguish in practice (e.g. functional vs. structural connectivity; Taylor et al., 2006), and many different approaches exist that measure different types of connectivity (Keeley et al., 2021; Rayfield et al., 2011). Still, existing legal frameworks do not include quantitative measures that integrate a wetland's position in migratory networks during conservation prioritization.

Graph-theoretic metrics, which represent landscapes as a combination of nodes (habitat patches) and links between them, have emerged as an efficient tool for very large datasets in particular (Moilanen, 2011; Zetterberg et al., 2010). Graph theory has proven useful to assess the effects of sea level rise on migratory fluxes in shorebirds (Iwamura et al., 2013), or to directly relate connectivity losses to population declines in several migratory waterbird species (Xu et al., 2019). But thus far, applications to large-scale networks including a large number of patches are rare and have only addressed few flyways (Bellisario, 2018; Clauzel et al., 2018; Xu et al., 2020).

One of the most widely applied graph-theoretic connectivity metrics is the Probability of Connectivity (PC) index (Saura & Pascual-Hortal, 2007), which has been used to analyse the functional connectivity for a variety of ecosystems and species, including migratory birds (Engelhard et al., 2017; Xu et al., 2019; Zhao et al., 2014). PC is considered as one of the more sophisticated

<sup>1</sup>Directive 2009/147/EC of 30 November 2009 on the conservation of wild birds, the European Parliament and the Council of the European Union.

<sup>2</sup>Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora, Council of the European Union.

and versatile metrics (Laita et al., 2011), because the underlying model is sensitive to fragmentation and habitat loss of individual habitat patches. The importance of connections between patches is weighted by how easily they can be crossed by individual birds, which allows to include biological realism by simulating species with different migratory capacities (functional component of connectivity; Saura et al., 2014). The metric can incorporate the directional nature of migration, by downweighting connections that are directed away from the target destination (Saura et al., 2014) and can evaluate the importance of each habitat patch by comparing the loss in network connectivity if this patch would be removed from the network (Bodin & Saura, 2010; Saura & Pascual-Hortal, 2007). Combined, these traits render PC particularly suitable for identifying priority patches for different migratory species in different types of networks, which is a critical element for conservation planning and management (Keeley et al., 2021; Zetterberg et al., 2010). As such, it provides an excellent candidate method for comparative, large scale analyses of the connectivity of habitat networks and their sensitivity to habitat loss, especially given the development of wetland maps with a reasonable accuracy (Pekel et al., 2016).

Here, we present a quantitative comparison of the network structure and connectivity of the four major Palearctic-Afrotropical flyways for migratory waterbirds, based on high-resolution wetland maps: the East-Atlantic flyway (EAF), and the Black Sea-Mediterranean flyway split up in a Western (WMF), Central (CMF) and Eastern (EMF) flyway. Our main goals were (i) to reconstruct connectivity based on the network structure of the four flyways and the suitability for waterbirds with different migration strategies and (ii) to simulate the vulnerability of these flyways to habitat loss and degradation based on the current protected status of the wetlands along these flyways.

Flyway connectivity was reconstructed using the directional graph-theoretic PC index. This metric assumes birds have a better chance of completing migration successfully for networks that consist of larger wetland areas and in which there is a higher potential movement between wetlands because there are fewer isolated or remote sites. This means that, depending on the network structure, smaller, well-connected sites may be more valuable for migratory birds than larger, isolated wetlands. Based on the wetland network structure, we assessed the suitability of each flyway for accommodating waterbird types with different migration strategies: short-distance hoppers and long-distance jumpers. We expected connectivity to be higher in the flyways along the Atlantic Coast and Nile River, where coastal wetlands and floodplains along the Nile River respectively provide more stopover opportunities. However, we hypothesized that differences in connectivity between flyways would be less pronounced for birds that employ a jumper migration strategy are able to fly longer stretches without visiting stopovers.

Second, we evaluated the extent to which the current network of protected areas can facilitate flyway connectivity. By simulating the disappearance of wetlands without formal protection, we assessed the flyways' sensitivity to wetland loss. Based on such information, we could identify at which exact locations extensions

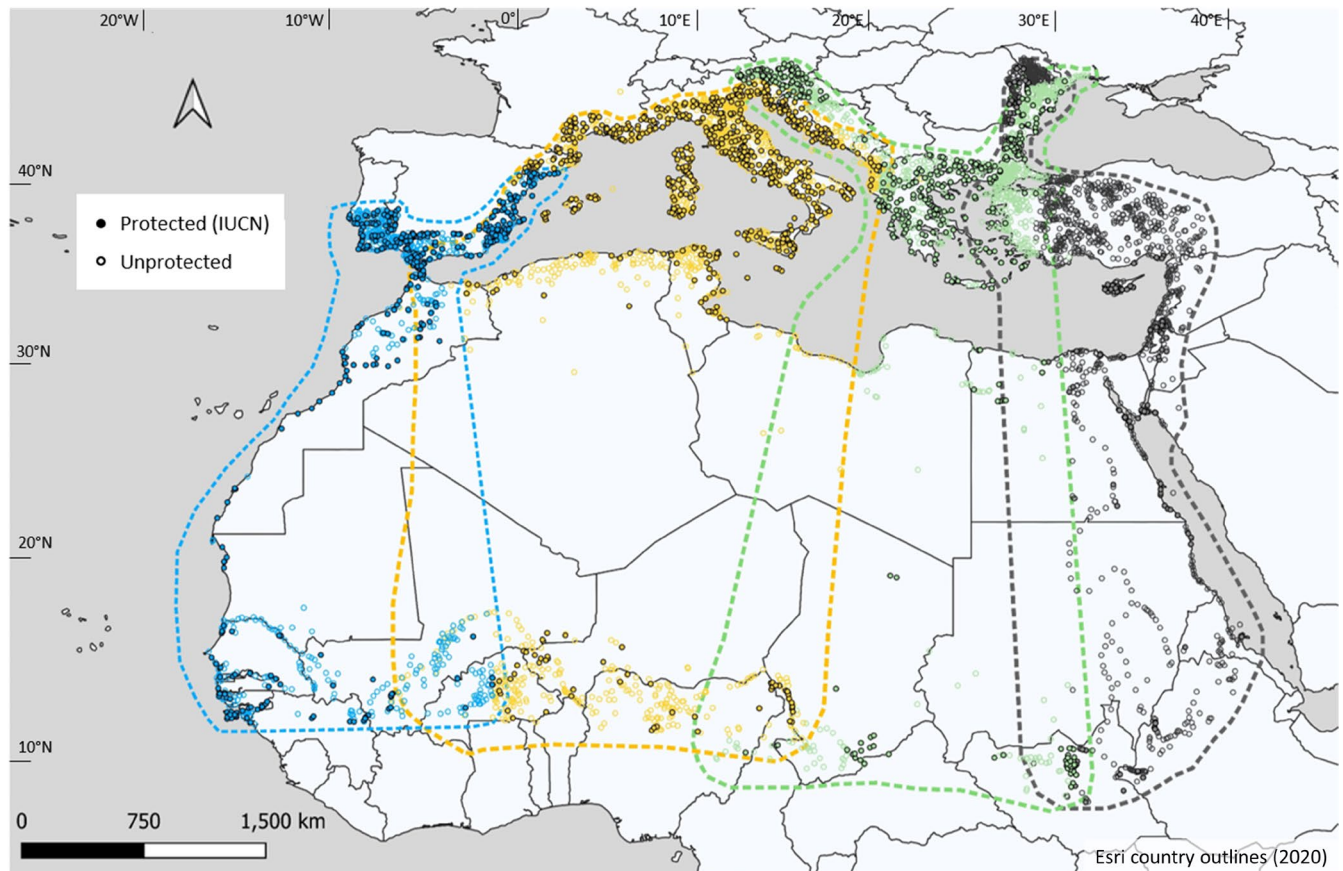
of legally protected wetland networks and improvements in the implementation of conservation policies may be most effective for migratory waterbirds. We hypothesized that particularly the flyway crossing the Balkan region might be sensitive to wetland loss, given that it covers European countries with a large fraction of unprotected wetlands. Third, we determined which (un)protected wetlands are disproportionately important for facilitating the crossing of major barriers. Larger wetlands with many connections to other wetlands are assumed to be more important for connectivity than smaller, isolated wetlands. Besides the surface area or the number of birds temporarily hosted by a site, a wetland's importance for overall flyway connectivity may be an additional motivation for allocating conservation resources to specific wetlands, especially when populations with different migration strategies depend on them.

## 2 | METHODS

### 2.1 | Study area

We analysed the connectivity of four major Palearctic-Afrotropical flyways. The study area stretches from the Syrian Desert and the Red Sea in the east to the Atlantic Ocean in the west, a longitudinal span of circa 22 degrees. At the northward border are mountain ranges of southern Eurasia (Pyrenees, Alps, Dinaric, Balkan and Pontic Mountains). The southward edge of the Sahel limits the study area up to approximately 10°N in the south (Figure 1). Geographic barriers that restrict the movement of migratory waterbirds and/or that represent important leading lines for orientation in the landscape were used to define the appropriate geographical borders. Because migration routes in the Mediterranean and northern and central African sections are better known than those in the northern regions of Eurasia and in southern Africa, we focused on the former.

Birds travelling to and from sub-Saharan Africa must cross the Sahara Desert, an area that spans up to 2000 km from north to south, where thermoregulation and replenishing energy reserves are particularly challenging (Fransson et al., 2017; Lok et al., 2015; Schmaljohann et al., 2007). The adjoining crossing of the Mediterranean Sea is another stretch of up to 700 km open water without stopovers. Mediterranean coastal wetlands in Southern Europe and Northern Africa provide relatively stable and suitable stopover habitats (Blondel et al., 2010). The study covers these wetlands where migrating waterbirds can build up or restore energy levels to overcome both geographical barriers, also for waterbirds travelling further north or south of the study area. In the southern part of the study area, the belt of Sahelian wetlands hosts many trans-Saharan migrants during migration or (part of) the non-breeding season (Bayly et al., 2012; Zwarts et al., 2009). Delineation of the East-Atlantic (EAF) and Black Sea-Mediterranean flyway was based on the global flyway concept (Boere & Stroud, 2006). The Black Sea-Mediterranean flyway was further split into in a western (WMF), central (CMF) and eastern (EMF) zone. The latter, EMF, incorporates a part of the West-Asian-East-African flyway. By subdividing the



**FIGURE 1** Map of flyway outlines (dotted lines) and wetland areas (circles) in different colours: EAF (blue), WMF (yellow), CMF (green) and EMF (grey). Blank circles with a coloured outline indicate unprotected wetlands, while legally protected wetlands are indicated by filled circles with a black outline. Wetlands that are located in the zones of overlap between the EAF-WMF (blue), WMF-CMF (yellow) and CMF-EMF (green) are included in both flyways. The datum used for mapping is the World Geodetic System 84 with a Mollweide equal area projection

Black Sea- Mediterranean flyway into three zones, we could compare the network structure of flight routes towards or from different Sahelian regions along different peninsular bridgeheads for crossing the Mediterranean Sea (between Corsica/Sardinia/Sicily/southern Italy and Tunisia/Western Libya, and between Greece/Turkey and Eastern Libya/Egypt), versus the Anatolia-Arabia land crossing (Figure 1).

## 2.2 | Wetland data

Wetland raster data were retrieved from the Global Surface Water Explorer (Pekel et al., 2016; <https://global-surface-water.appspot.com/>), developed by the European Joint Research Centre. This database integrates information on the extent of water bodies worldwide at a 30-m resolution. The water occurrence layer was considered most suitable for our purposes as it reflects the intra- and interannual dynamics of wetlands. To facilitate migration, waterbirds require stable wetland areas, with a predictable annual recurrence of resources during specific seasons (Newton, 2008; Woolf et al., 2003). All 30-m sided cells where water was present in

more than 75% of the observation period, that is, monthly records of water extent between 1984 and 2018, were considered as available wetland areas for migratory waterbirds. Raster cells where water was less regularly available were discarded. By allowing for temporal variation in the water extent of selected cells, we included permanent water bodies as well as temporary or seasonal wetlands that recurred during a large part of the study period. The water occurrence layer was processed in ArcGIS (ArcMap version 10.3, Esri) to create the vector-based input for the connectivity analyses (Figure S1.1); wetland maps and figures were created in QGIS (version 3.12, Bucureşti, Open Source Geospatial Foundation, 2020).

After converting the raster to a vector layer, the resulting wetland polygons were aggregated if they were smaller than 75 000 m<sup>2</sup> and if they were situated within 5000 m from each other. Aggregating wetlands was required for rendering the number of nodes and calculation times manageable. The size and distance thresholds were selected to remain as close as possible to the way birds make use of wetland areas while travelling through flyway networks. Waterbirds easily cross 5000 m in their daily movements and are mostly attracted to larger wetland complexes, as these are more stable and host more diverse habitats in terms

of feeding opportunities and vegetation (Kirby et al., 2008; Ma et al., 2010). Also, smaller wetlands are considered of less importance for larger-scale patterns of connectivity. Different aggregation thresholds were explored and aggregating wetlands smaller than 75 000 m<sup>2</sup> resulted in a manageable network with the highest resolution (number of distinct wetlands).

Furthermore, special attention was paid to the linear elements that stretch out over a considerable part of the flyways, such as rivers. Rivers are considered important waterbird habitat, including the floodplains and oases associated with them, and they also function as visual cues for orientation in the landscape (Newton, 2008). To avoid bias in connectivity estimates, all rivers were fractionated into separate segments of 75 km at most (segmentation suggested by Erős et al., 2011). This north-to-south threshold was based on the north-to-south length of the largest wetlands. The segmentation of rivers does not have an influence on the connectivity of the network, as the flight abilities of migratory birds by far exceed this threshold distance. Without this segmentation step, rivers would appear as one large wetland regarding size but with only one centroid coordinate. This would distort the pattern of connections to other wetlands (i.e. the calculation of inter-wetland distances) within the flyway. The final result is a wetland vector layer for each flyway in which individual wetlands are defined as the (multipart) polygons that resulted from aggregating patches where water occurred for more than 75% of the months between 1948 and 2018, with river polygons divided into segments (Figure S1.1).

### 2.3 | Network structure and connectivity

For each flyway, we calculated the total surface area and size distribution of wetland patches and a proxy for general isolation of wetlands in each flyway. Average patch isolation was calculated as the average distance between two wetlands in each flyway. To analyse the overall connectivity of the four Palearctic-Afrotropical flyways and determine the relative importance of wetlands within these networks, an adapted, directional version of the PC index was used, implemented in R version 4.0 (Figure S2.1; R Core Team, 2020; Saura et al., 2014; Saura & Pascual-Hortal, 2007). Each wetland-to-wetland connection is defined by a distance and a direction in which the movement can occur. In our simulations, we modelled autumn migration, so movement is oriented southwards and inter-wetland connections opposite to the preferential direction are assigned a probability of zero to eliminate northward movements. Quantitatively, as no other parameters are changed in this model to reflect seasonality, PC results are identical for spring and autumn migration, yet very different from an undirected situation where both directions of inter-wetland movement would be allowed (Table S3.1).

We explored the effect of migration ecology on flyway connectivity by estimating connectivity for two types of migratory strategies. 'Hoppers' (e.g. Ruddy Turnstone *Arenaria interpres*,

Eurasian Spoonbill *Platalea leucorodia*) were assigned a median flight distance of 500 km, whereas 'jumpers' (e.g. Red Knot *Calidris canutus*, Black-tailed Godwit *Limosa lapponica*) were considered to easily fly 1500 km in one go (Dhanjal-Adams et al., 2017; Piersma, 1987; Warnock, 2010). The flight ranges of hoppers and jumpers were based on observed flight distances of species with a known migration strategy, shown in Figure S4.1b. These flight distances were linked to a probability of 0.5, which was assigned to the median non-stop flight distance, that is, a distance that is easily crossed in 50% of the cases by the migratory population. Given the exponentially decreasing relation between distance and the probability that this distance is crossed (Saura & Pascual-Hortal, 2007), this implies the maximal flight range of hoppers and jumpers is approximately 2200 and 6500 km respectively, with less than 5% of the population flying this distance easily in non-stop flight (Figure S4.1; Dhanjal-Adams et al., 2017). To explore robustness of the results, all analyses were repeated while implementing flight kernels based on gamma functions (i.e. where short-distance movements were assigned a lower probability). These represent scenarios where birds are more likely to fly intermediate distances than short distances during migration. The results of this gamma-based analyses are covered in Supporting Information (Figures S5.1, S5.2; Table S5.1).

For each flyway, network- and wetland-level connectivity estimates were obtained for both hoppers and jumpers. The network-level Equivalent Connectivity (EC<sub>PC</sub>) corresponds to the size of a single contiguous habitat patch that would have the same connectivity as the studied network (Saura & Torné, 2012). Larger EC<sub>PC</sub>-values indicate a higher connectivity of the network, i.e. more and/or stronger connections between habitat patches. Note that both EC<sub>PC</sub> and the summed wetland area represent a 'virtual' network where all wetlands of the flyway would form one coherent patch (Figure S6.1). The smaller the difference between the summed wetland area and the EC<sub>PC</sub>, the smaller the 'loss' of connectivity in the network due to spatial scattering of habitat patches as opposed to a network formed by a single uninterrupted patch.

The wetland-level dPC-value represents the importance of an individual wetland for overall network connectivity, which is the impact of the loss of this wetland on the flyway's connectivity. Wetlands are considered more important if their loss results in a larger decrease in connectivity of the flyway than if other wetlands are lost (Saura & Rubio, 2010).

The relative node importance (dPC) value can be subdivided into three fractions: intra, flux and connector. These components reflect the different ways in which wetlands and the connections between them contribute to connectivity (Figure S2.1). Intrapatch connectivity, dPC<sub>intra</sub>, is the potential movement within patches, depending on the available habitat area. Interpatch connectivity, or the contribution of connections between patches, is split up into the area-weighted flow via direct connections (dPC<sub>flux</sub>) and the movement through patches that function as steppingstones between other patches (dPC<sub>connector</sub>; Saura et al., 2014; Saura & Pascual-Hortal, 2007).



## 2.4 | Coverage of flyways by protected areas

To evaluate the robustness of each flyway against wetland habitat loss, we calculated how the overall connectivity ( $EC_{PC}$ ) of the flyways would change if only legally protected areas would remain. For this, we assumed that unprotected wetlands are less likely to be in a favourable state of conservation and more at risk for (future) habitat degradation and destruction than protected ones. Networks of protected wetlands were constructed from overlays of the Global Surface Water-derived wetland polygons and the IUCN's World Database on Protected Areas shapefile (version of June 2020). This way, we only selected wetland fragments that are currently legally protected at national or international level, without considering effectiveness of implementation of a favourable state of conservation. Because of the uncertainty involved in large-scale databases of this type for inferring a wetland's ecological condition, we opted for the most conservative approach by including all protected areas reported in the IUCN database. This implies the areas where information about the protection level was not reported, assigned or applicable were not discarded (Maiorano et al., 2015; Saura et al., 2019). Wetlands with multiple protection levels were included only once. For comparability with flyway networks in which both protected and unprotected wetlands were included, wetlands in the IUCN-layers were also aggregated if they were smaller than 75 000 m<sup>2</sup> and situated within 5000 m, followed by a segmentation step for river polygons.

To contrast these results with a more unfavourable scenario, we also assessed the connectivity of flyways in which we omitted wetlands for which information on protection level was lacking in the IUCN's database. Here, only protection categories I to VI were retained. Results of this analysis are reported in Supplementary Information, Appendix S7 (Figures S7.1, S7.2 and S7.3).

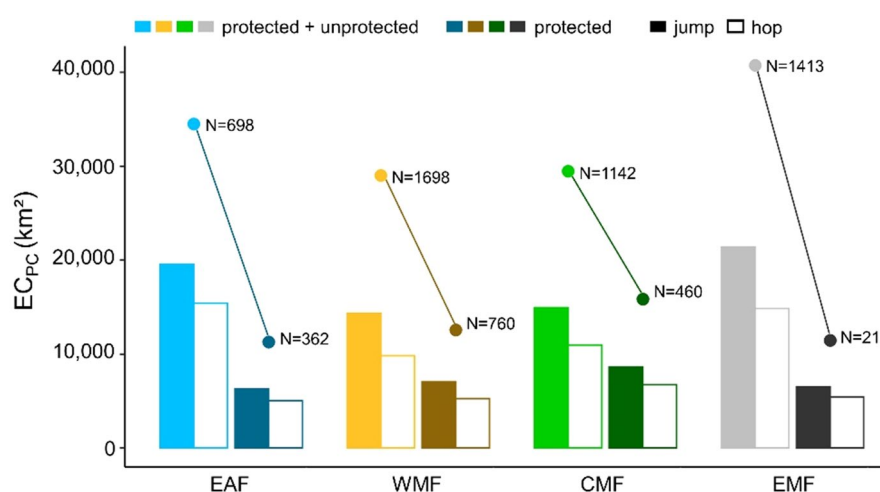
## 3 | RESULTS

### 3.1 | How connected are Palearctic-Afrotropical flyways?

The four studied flyways differed in network structure and overall connectivity (Figure 2, Figure S8.1). Based on the Equivalent Connectivity ( $EC_{PC}$ ), connectivity of the EAF and EMF was 24%–36% higher than the WMF and CMF. Although the WMF contained the largest number of wetlands, its total wetland surface area was lowest. The EAF had the lowest number of wetlands, but when combined these represented the second-largest total wetland surface area.

### 3.2 | Are hoppers more affected than jumpers?

Connectivity, captured by  $EC_{PC}$ , was between 21 (EAF) and 31% (WMF) lower for hoppers than for jumpers, which can travel more easily through the network (Figure 2). In the EAF, the  $EC_{PC}$  was respectively 43 and 55% lower than the total wetland area for jumpers and hoppers. Although this difference between  $EC_{PC}$  and total wetland area is smaller than for the other flyways, the relatively large spatial distribution of wetlands causes functional connectivity to decrease with more than half compared to the imaginary situation when these wetlands would together form one contiguous habitat patch (Figure S6.1). In the other three flyways, the  $EC_{PC}$  was between 47 (EMF) and 51% (WMF) lower than the total area for jumpers, and between 63% and 66% for hoppers. The advantage of migration via the EAF compared to the WMF or CMF based on the connectivity of wetlands was more pronounced for hoppers than for jumpers. Also, the decrease in functional connected area ( $EC_{PC}$ ) compared to the



**FIGURE 2** Overview of the total wetland area (circles) and Equivalent Connectivity ( $EC_{PC}$ , bars) of the four flyways. Flyways are presented in different colours, with lighter and darker shades for the analyses in which networks contained all wetlands (both protected and unprotected), or only protected wetlands, respectively. Results for waterbirds with a jumping and a hopping migration strategy are respectively represented by filled and blank bars ( $EC_{PC}$ -values). Points indicate the summed wetland surface area of each flyway network, labelled with the total number of wetlands or wetland complexes (N) included in the analysis

summed wetland area was at least 4% and 8% smaller in the EAF compared to WMF, CMF and EMF for jumpers and hoppers respectively. Travelling via the EMF, however, had a slightly more distinct advantage for jumpers than for hoppers compared to the CMF route, as  $EC_{PC}$ -values were respectively 30% and 26% higher for the EMF than for the CMF (Table S3.1).

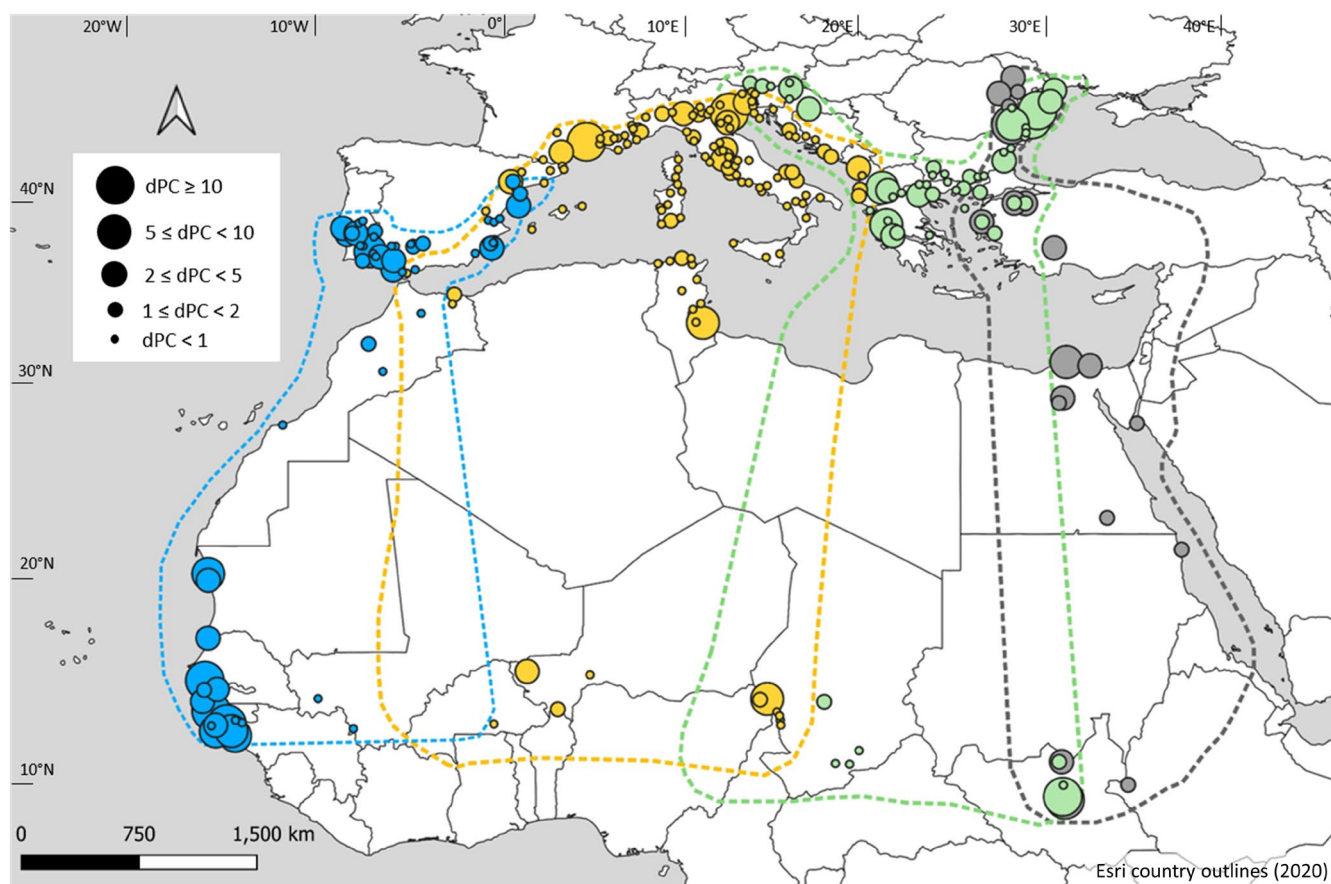
### 3.3 | Which wetlands are most important?

Wetlands and their relative importance value for connectivity are mapped in Figure 3. In all flyways, the 10 most important wetlands – those with the highest relative node importance (dPC) value – contributed to more than 40% of the total connectivity of the entire network and a similar proportion of the total available surface area (Table S3.1, conservation status in Table S9.1). Similarly, the 25 top-ranked wetlands accounted for more than 45% of flyway connectivity. Fewer than 5% of the wetlands accounted between 71% (WMF, jumpers) and 85% (EAF, hoppers) of the total connectivity and between 72% (WMF) and 80% (EMF) of the total surface area

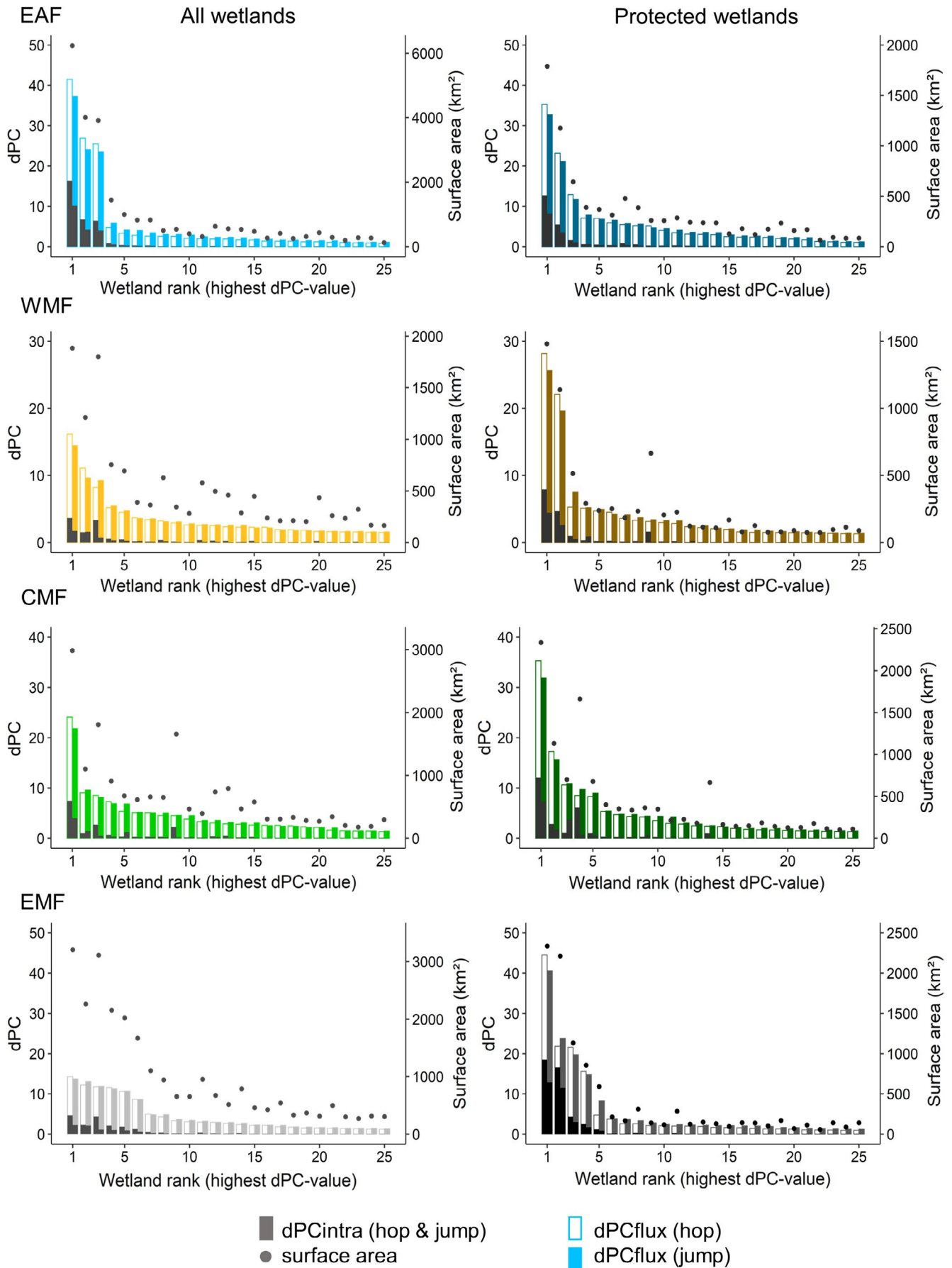
(Figure S10.1 and Table S10.1). More than 90% of the total surface area was covered by at most 15% of the wetlands, indicating that each flyway consisted of smaller wetlands for the greater part and few disproportionately large wetland areas (Table S10.1). In the EMF and WMF, the contribution of the 10 top-ranked wetlands to the overall connectivity was more evenly distributed than in the EAF and CMF, where fewer wetlands contributed dominantly to connectivity (Figure 4, Figure S10.1). The Danube Delta was the most important wetland area in both the CMF and the EMF. Lake Chad was one of the top three most important wetlands in the WMF as well as the CMF (Table S9.1). The rankings of the wetlands according to their importance for flyway connectivity were highly consistent for hoppers and jumpers, especially for the higher ranked wetlands.

### 3.4 | Which aspect of connectivity matters most?

For nearly all wetlands, dPCflux, which captures the direct movement to other wetlands, accounted for more than 90% of a wetland's relative importance for flyway connectivity (Figure 4). In contrast,



**FIGURE 3** Map visualizing the relative importance of wetlands (circles) for connectivity in the four Palearctic-Afrotropical flyways, presented in different colours: the EAF in blue, the WMF in yellow, the CMF in green and the EMF in grey. The larger the circle, the more important a wetland is for connectivity within the flyway, based on its dPC-value (inset legend). Only wetlands that together account for at least 90% of overall network connectivity are indicated: 69 wetlands for the EAF, 272 for the WMF, 143 for the CMF and 126 for the EMF. Wetlands in the zones of overlap between the EAF and the WMF (blue), the WMF and the CMF (yellow), and the CMF and the EMF (green) are included in both flyways. Important wetlands are listed along with their protection status in Table S9.1. The datum used for mapping is the World Geodetic System 84 with a Mollweide equal area projection





**FIGURE 4** Contribution of different connectivity fractions to the importance of wetlands for overall functional connectivity of Palearctic-Afrotropical flyway networks, for two different migratory strategies (hoppers and jumpers) and two different network types (all wetlands and protected wetlands only). For the 25 most important wetlands according to the rank of their relative importance value for connectivity for hoppers, the contribution of dPCintra (bottom dark grey bars) and dPCflux (top blank and coloured bars) to the relative node importance (dPC) value is shown, with  $dPC_{intra} + dPC_{flux} = dPC$ , since  $dPC_{connector}$  is equal to zero for all wetlands. Together, these 25 wetlands account for 46%–81% (all wetlands) or 58%–92% (protected wetlands only) of overall flyway connectivity. Flyways are displayed in different colours, when all wetlands are included (left panels, lighter shades), or when only wetlands with a protected status according to IUCN are included (right panels, darker shades). Values for hoppers and jumpers are represented with blank and filled bars respectively. In each panel, the dark grey bars indicate the contribution of the dPCintra fraction to the dPC-value for each wetland, which differed between hoppers and jumpers. The surface area of each wetland is indicated with a filled circle (note the separate y-axis and units, km<sup>2</sup>). For both graphs of each flyway, the limits of the y-axes of relative importance values (dPC) are identical for analyses including all wetlands and protected wetlands to improve comparability

the component that indicates the value of wetlands as connecting elements between a pair of other wetlands ( $dPC_{connector}$ ) was zero or negligibly small. The contribution of the potential movement within patches ( $dPC_{intra}$ ) was at most 39%–50% for hoppers and 16%–27% for jumpers in the different flyways. Apart from five to six top-ranked wetlands in each flyway, where surface area also plays a prominent role, a wetland's position for facilitating migration through the network was the best indicator for a wetland's impact on connectivity (Figure S11.1).

### 3.5 | What is the impact of losing unprotected wetlands on flyway connectivity?

When comparing the overall connectivity ( $EC_{PC}$ ) of flyways in which only legally protected wetlands were included instead of all wetlands, the decrease in overall connectivity was largest in the EMF (70%) and EAF (68%), and smaller in the WMF (46%) and CMF (39%) (Figure 2, Table S3.1). Excluding unprotected wetlands reduced the number of wetlands in each flyway by at least 50% and drastically reduced the total wetland area, with a slight increase in the average wetland size (Figure 2, Table S3.1). While in the WMF and CMF protected wetlands covered nearly half of the total surface area (43% and 54% respectively), the contribution of unprotected wetlands in terms of area was substantially higher in the EAF and EMF (more than 23 000 and 29 000 km<sup>2</sup> or 67 and 72% respectively).

For jumpers, the  $EC_{PC}$ -value was between 43% (EMF) and 46% (CMF) lower than the summed wetland area and between 53% (EMF) and 58% (WMF) for hoppers, indicating that, overall, wetlands are interspersed with relatively large areas of unsuitable matrix in flyway networks (Figure S6.1). When comparing the two different migration strategies, decreases in overall connectivity were quite similar in the EAF, that is, 67% for hoppers and 68% for jumpers. However, for all three Black-Sea Mediterranean flyways – WMF, CMF and EMF – the reduction in connectivity that resulted from removing unprotected wetlands was 4%–6% stronger for jumpers than for hoppers, but in absolute terms connectivity is still much higher for jumpers than for hoppers. This suggests that longer distances that are considered more challenging for migrants are more common

in the WMF, CMF and EMF, and that the removal of unprotected wetlands leads to more and larger gaps in these flyways than in the EAF network.

Highest dPC-values were observed in the EMF, with the top-ranked wetland scoring 45, and whose removal from the network would correspond to a 45% decrease in flyway connectivity. Largest node importance values were accompanied by a relatively higher importance of  $dPC_{intra}$ , which contributed to the total dPC-value for up to 48% for jumpers (EMF) and 76% for hoppers (EMF). In contrast, for virtually all other wetlands,  $dPC_{flux}$  was the most important component for connectivity, accounting for more than 90% of the dPC-value. Lower ranked wetlands were of relatively similar value for flyway connectivity, with dPC-values mostly lower than 5 (Figure 4, Figure S12.1). A map of the protected wetlands that together account for 90% of flyway connectivity can be found in Supplementary Information (Figure S13.1).

## 4 | DISCUSSION

For Palearctic-Afrotropical migratory waterbirds, stopover opportunities greatly affect the success of their seasonal journeys. We reconstructed the wetland networks that support waterbird migration along four major flyways crossing two major biogeographic barriers: the Mediterranean Sea and the Sahara Desert. The situation was compared for two broad groups of waterbirds with contrasting migratory strategies: short-distance hoppers and long-distance jumpers. Consistent with our hypotheses, the functional connectivity of wetland networks was higher in the two peripheral (EAF, EMF) than the two central (WMF, CMF) flyways. A limited number of wetlands seems to influence the overall connectivity disproportionately. Overall, birds with a hopping migration strategy were more affected by the poorer connectivity of the two central flyways than jumpers, but differences were small. Reducing current networks by removing wetlands that lack formal protection strongly reduced the potential effectiveness of these networks for mediating bird migration, particularly in the flyways that originally had the highest connectivity (the EAF and EMF), and more so for birds with a jumping migration strategy.

#### 4.1 | Connectivity is highest in the EAF and EMF

Differences in connectivity between the four flyways can be attributed to the spatial distribution and surface area of wetlands in the respective networks. In line with our expectations, connectivity in the peripheral flyways was higher than in the central flyways. In the WMF, connectivity was lowest and the total wetland area was smallest, while the number of wetlands and inter-wetland distances were largest. This suggests migration along the WMF depends on large numbers of relatively small wetlands that are quite widely scattered. In the EAF, coastal wetlands along the Atlantic coastline provide frequent stopover opportunities. Such sites are much rarer at similar latitudes in the central flyways across the Sahara Desert, where birds need to travel longer stretches through unsuitable areas (Figure 1). Similarly, in the EMF, the Nile River is a visual reference for orientation and its associated floodplain wetlands provide a continuous chain of stopovers spanning this dry region (Newton, 2008). In addition, both peripheral flyways include important narrow sea straits and land bridges that minimize the crossing of the Mediterranean Sea, such as the Strait of Gibraltar along the EAF and the Levant along the EMF. This is especially helpful to larger birds such as storks and many raptors that use thermal air columns for soaring, as there are no favourable uplift conditions over the Mediterranean Sea in spring and adequate wind support is necessary for taking advantage of thermals over open water in autumn (Flack et al., 2016; Nourani et al., 2021; Phipps et al., 2019). In a recent broad-scale analysis of tracking data, European-African Passerine and near-Passerine populations could be subdivided in groups of migrants that either use the eastern (here: EAF and WMF) or western (here: CMF and EMF) migration corridors (Briedis et al., 2020). Routes that fringe the Sahara and those that cross it were not separated, yet it was suggested that the central routes are less used. Our analyses confirm that, from the perspective of connectivity, these central routes are indeed more challenging, while the peripheral routes along the coast and the Nile likely facilitate waterbird migration better.

#### 4.2 | Better connectivity for jumpers than hoppers, but similar ranking of wetlands

Connectivity was considerably higher for birds with a jumping migration strategy (+17%–31%) than for hoppers in all flyways. Jumpers can travel longer distances in non-stop flight, as they invest in extensive energy reserves (Piersma, 1987). In the Palearctic-Afrotropical flyway networks, wetlands are at most 5000 km apart, which can still be crossed by at least 1% of jumpers and 0.1% of hoppers in one go (Figure S4.1). Hoppers are less likely to migrate larger distances than jumpers, which translates into the observed lower flyway connectivity. Practically, this can be explained by the fact that the connectivity metric assigns higher probabilities to larger distances for jumpers than for hoppers. However, the ranking of wetlands based on their relative importance (dPC-value) for hoppers and jumpers was similar, indicating that both benefit from the same wetlands.

Based on observed flight distances of hopping and jumping species, we included two extreme migration strategies, so the value of wetlands in the four flyways can be generalized for birds with a broad range of migration capacities – with the reservation that actual wetland use is still constrained by local habitat conditions and habitat preferences (Paracuellos, 2006).

As hoppers need more frequent stopovers, we expected the difference in connectivity between the central and peripheral routes to be more distinct for hoppers than for jumpers. Travelling via the coastal EAF was indeed relatively more advantageous for hoppers than for jumpers in terms of functional connectivity when compared to the other three flyways. For the EMF, however, connectivity metrics did not support the idea that flyway structure would facilitate migrating through the central part of the Sahara Desert more for jumpers than for hoppers. It also seems that, despite the presence of the Nile River and its associated wetlands, the coastal route is still superior to the EMF in terms of flyway connectivity. The size – as a possible proxy for resources – and position of wetlands in the northern (European) and southern (Sahelian) parts of the WMF and CMF likely compensate for the absence of wetlands at Saharan latitudes to support overall connectivity of the central trans-Saharan flyways. Since birds with different flight abilities rely on the same stopovers but not every flyway is equally suitable for different populations. Therefore, these findings may help to prioritize habitat conservation in regions where stopovers are crucial for successful migratory journeys of multiple populations. In those sites that are important to support the connectivity of their flyways, more specific targets for management can be formulated which integrate the ecological requirements of migratory birds relying on these wetlands.

#### 4.3 | Most connectivity is supported by few large wetlands

In each flyway, a small number of one to six top-ranked wetlands accounted for most of the total network area and connectivity. Wetland area and the population size supported by a site are widely accepted criteria for directing conservation efforts, and thus patch size is taken up as a central determinant of connectivity in the PC index (Saura & Pascual-Hortal, 2007).

The highest ranked wetlands were among the largest within each flyway, but not exclusively so. Facilitating the direct movement of migrants between wetlands (dPCflux) was by far the most important contribution of nearly all wetlands to flyway connectivity (>90% of dPC). This reflects the importance of wetland configuration for migratory populations (Dhanjal-Adams et al., 2017; Taylor & Norris, 2010). Exceptions were some of the larger top-ranked wetlands (dPC > 8), where a wetland's value for supporting connectivity was determined for up to 41% by its size (dPCintra). As hoppers are more restricted to fly from one wetland to another, dPCflux fractions were smaller, resulting in a larger influence of wetland size on connectivity for hoppers than for jumpers.

None of the wetlands in the four flyways was absolutely crucial to maintain connectivity between distant wetlands, as the connectivity fraction that traces steppingstones (dPCconnector) was equal to zero for all wetlands. This indicates that the disappearance or degradation of individual wetlands will not inhibit migration altogether, but will erode the overall ability of the network to facilitate functional flyway connectivity. A similar pattern of negligible dPCconnector fractions was observed in another study on an East-Asian – Australasian flyway for migratory waterfowl (Xu et al., 2019). The fact that no wetlands could be considered steppingstones, more narrowly defined as indispensable nodes, does however not imply that suitable stopovers are lacking from the flyway. According to the connectivity model, there is no mathematical need for migratory birds to make intermediate stops along the way, as they are able to fly long distances in one go. Instead, patches contribute to overall connectivity by facilitating direct movement between wetlands, as evidenced by high dPCflux-values. In the case of migratory birds, the dPCflux fraction can thus be used to identify important stopovers. For birds flying smaller distances or in networks where isolated patches are much more interspersed, moving between any two patches would be harder, with rather low probabilities assigned to links in the network. This would give rise to relatively lower dPCflux and larger dPCconnector fractions for some steppingstones that link sites between which a direct connection is not possible.

Dhanjal-Adams and coworkers (2017) suggested that the migratory flow of different wader species through the East-Asia – Australasia flyways could be affected by the loss of smaller wetlands. In that study, the ranking of wetlands according to maximum populations counts was compared to rankings based on a maximum flow model, that was calibrated with flight distance distributions derived from tracking data. For a number of sites, there was a discrepancy between both rankings: when accounting for the extent to which wetlands supported the flow or movement of the population, several wetlands that hosted fewer individuals were more important for connectivity than sites with a larger bird population (Dhanjal-Adams et al., 2017).

In our study, some of the wetlands were included in different flyways. When such wetlands were important for one flyway, this generally was also the case for the other. This suggests that these areas are not just important in their own right but could also act as junctions between flyways, particularly for migratory populations that use multiple flyways throughout their lifetime (Madsen et al., 2014). They might be hubs from which different trajectories could be selected by migrants depending on different cues.

#### 4.4 | Functional flyway connectivity is jeopardized when unprotected wetlands are lost

When wetlands without formal protection were removed from the analyses – as a rough and conservative proxy for discarding wetlands in an unfavourable condition or at increased risk of degradation – connectivity plummeted. The two peripheral flyways that originally had the highest connectivity, the EAF and EMF, suffered

the largest losses in overall connectivity (>63%). In the EMF, the number of wetlands was reduced by more than 85%. Smaller wetlands were more frequently discarded from flyways, because larger wetland areas were more often formally protected. Many of the wetlands with the most prominent roles in supporting overall flyway connectivity are at least to some extent protected by one or multiple conservation systems, such as the European Natura 2000 legislation or Ramsar, which acts worldwide (Table S9.1). European Union territory covers 23 (EAF), 40% (WMF), 26% (CMF) and 10% (EMF) of the total wetland area of the flyways. However, some of the most important European wetlands indicated by our analyses lack any protection, such as the Pagasitic Gulf (Greece, CMF), or are only partially protected (Albufeira do Alqueva (Portugal), EAF; Dniester Estuary (Ukraine), CMF). Many (coastal) wetlands in the Mediterranean Region are not designated as Ramsar sites at all, even though they host different waterbird species of conservation concern and/or a substantial population of wintering waterbirds (Popoff et al., 2021). It is striking that important gaps exist in protected areas, both when sites are prioritized for maintaining flyway connectivity as well as when they are listed because of the waterbird populations they harbour.

Because more than half of the wetlands were at risk of being lost in each flyway, many connections disappeared as well, resulting in overall larger inter-wetland distances in the protected flyways. Extended gaps led to a simulated loss of connectivity that was up to ten percent more severe for jumpers than for hoppers. This can be explained by the negative exponential distribution that is used to assign probabilities to distances, which declines more steeply at higher than at lower probabilities (Figure S4.1; Saura & Pascual-Hortal, 2007). The chances of moving between wetlands therefore dropped to a larger extent for jumpers than for hoppers, although jumpers travelled more easily through the network in absolute terms. In reality, hoppers visit more intermediate stopovers, but because of this, they can also compensate more easily for losses at a single stopover than jumpers. So, even though jumpers are at an advantage for reaching distant wetlands because of their flight abilities, they are more at risk when the few areas they rely on are degraded or in suboptimal condition (Both et al., 2010; Pakanen et al., 2018; Warnock, 2010).

#### 4.5 | Study limitations

The strength of the connectivity metrics applied here is that migration can be modelled at population level without the need for data-intensive estimates of individual birds' trajectories (Zetterberg et al., 2010) – which are lacking for most species. By including the complete wetland cover of the flyways we could identify the functional connectivity of different routes facilitating waterbird migration, without predetermined limitations on flight trajectories – which are quite dynamic and may vary between different seasons and years (Flack et al., 2016; La Sorte & Fink, 2017; Trierweiler et al., 2014). A downside is that, like in most models, optimal circumstances for

migration are assumed. Birds fly according to their theoretical or observed limits (Laita et al., 2011), while in reality adverse conditions *en route* such as bad weather or human disturbance can affect the birds' migratory performance (Grönroos et al., 2012; Koch & Paton, 2014; Palacín et al., 2017). Also, wetland patches are considered to consist entirely of suitable habitat that is predictably available during migration seasons. Seasonal or ephemeral wetlands were not included in our study. Such temporary wetlands may however be valuable for migratory waterbirds, but their interannual importance is less predictable. In addition, the actual state of wetlands is often unknown, some important wetlands are not legally protected, and adequate enforcement and monitoring is lacking in many protected wetlands (Keeley et al., 2021; Popoff et al., 2021). We know Palearctic-Afrotropical migratory bird populations are decreasing, especially within the Black Sea-Mediterranean flyway (Boere & Stroud, 2006; Vickery et al., 2014) and that natural wetland loss is alarmingly accelerating, amongst others due to effects of climate change and human hydrological engineering (Ramsar Convention on Wetlands, 2018). Our analysis shows which flyways may be most vulnerable, but we do not know how much additional habitat and connectivity we can afford to lose before the migration system would functionally collapse.

#### 4.6 | Opportunities for future studies

The recent availability of high-resolution wetland data has enabled researchers to map and model migratory networks at an unprecedented resolution. This study shows the potential insights that can be generated from such bottom-up reconstructions that start from habitat availability, while also accounting differences in migration strategies. At the same time, much progress has been made in tracking actual migratory movements of birds, looking at the habitats used by a limited set of individual birds but neglecting the full availability of different habitat types in the landscape. In the future, it would be valuable to merge both perspectives and couple actual migration patterns with a thorough analysis of the network structure of flyways based on habitat that is used such as wetlands (Briedis et al., 2020; Dhanjal-Adams et al., 2017). For instance, we may evaluate whether there is a match between the migratory strategy adopted by a population and its preferred flyway, based on the spatial configuration of the wetland network. Connectivity assessments can be a practical tool for conservation planners (Foltête et al., 2014; Zetterberg et al., 2010) to help determine where efforts are needed to create wetlands or improve the ecological conditions of existing wetlands. It will also be interesting to incorporate additional levels of complexity in connectivity models, such as the bio-energetic constraints of refuelling and energy expenditure during flights, and more specific habitat requirements. This way, wetland protection for migratory birds can become more targeted by incorporating the needs of waterbird populations with different ecological requirements and migration strategies.

#### ACKNOWLEDGEMENTS

We thank J. Van der Straeten for contributing to a supporting analysis in which different Global Surface Water data layers were compared for their use in this study. M. Kellens optimized the R script of the PC metric to facilitate processing larger networks, which was of great help for advancing the analysis. ED is supported by a PhD fellowship 11ZH516N from the Research Foundation – Flanders (FWO). The authors would like to thank the editor and two anonymous reviewers for their feedback and constructive comments for improving this manuscript.

#### CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

#### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13508>.

#### DATA AVAILABILITY STATEMENT

Data are openly available in a public repository that issues datasets with DOIs (DOI: <https://doi.org/10.5061/dryad.vt4b8gtsn> – accessible after review).

#### ORCID

Evelien Deboelpaep  <https://orcid.org/0000-0001-5834-4031>

#### REFERENCES

- Aharon-Rotman, Y., Bauer, S., & Klaassen, M. (2016). A chain is as strong as its weakest link: Assessing the consequences of habitat loss and degradation in a long-distance migratory shorebird. *Emu*, 116(2), 199–207. <https://doi.org/10.1071/MU15029>
- Amezaga, J. M., Santamaría, L., & Green, A. J. (2002). Biotic wetland connectivity: Supporting a new approach for wetland policy. *Acta Oecologica*, 23(3), 213–222. [https://doi.org/10.1016/S1146-609X\(02\)01152-9](https://doi.org/10.1016/S1146-609X(02)01152-9)
- Bauer, S., & Hoyer, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344(6179), 1242552. <https://doi.org/10.1126/science.1242552>
- Bauer, S., Van Dinther, M., Høgda, K.-A., Klaassen, M., & Madsen, J. (2008). The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *Journal of Animal Ecology*, 77(4), 654–660. <https://doi.org/10.1111/j.1365-2656.2008.01381.x>
- Bayly, N. J., Atkinson, P. W., & Rumsey, S. J. R. (2012). Fuelling for the Sahara crossing: Variation in site use and the onset and rate of spring mass gain by 38 Palearctic migrants in the Western Sahel. *Journal of Ornithology*, 153(3), 931–945. <https://doi.org/10.1007/s10336-012-0823-5>
- Bellisario, B. (2018). Conserving migration in a changing climate, a case study: The Eurasian spoonbill, *Platalea leucorodia leucorodia*. *Biological Conservation*, 217, 222–231. <https://doi.org/10.1016/j.biocon.2017.11.013>
- BirdLife International (2010). *Spotlight on flyways: East Atlantic flyway factsheet*. Retrieved from <http://datazone.birdlife.org/sowb/spotFlyway>
- BirdLife International. (2010). *Spotlight on flyways: Mediterranean/Black sea flyway factsheet*. Retrieved from <http://datazone.birdlife.org/sowb/spotFlyway>



- BirdLife International. (2018). *State of the world's birds: Taking the pulse of the planet*. Cambridge, UK: BirdLife International.
- Blondel, J., J. Aronson, J.-Y. Bodiou, & G. Boeuf (Eds.) (2010). *The Mediterranean region: Biological diversity in space and time* (2nd ed). Oxford University Press.
- Bodin, Ö., & Saura, S. (2010). Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. *Ecological Modelling*, 221(19), 2393–2405. <https://doi.org/10.1016/j.ecolmodel.2010.06.017>
- Boere, G. C., & Piersma, T. (2012). Flyway protection and the predicament of our migrant birds: A critical look at international conservation policies and the Dutch Wadden Sea. *Ocean & Coastal Management*, 68, 157–168. <https://doi.org/10.1016/j.ocecoaman.2012.05.019>
- Boere, G. C., & Stroud, D. A. (2006). The flyway concept: What it is and what it isn't. In G. C. Boere, C. A. Galbraith & D. A. Stroud (Eds.), *Waterbirds around the world* (pp. 40–47). The Stationery Office.
- Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J., & Foppen, R. P. B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 277, 1259–1266.
- Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Krist, M., Liechti, F., Lisovski, S., Meier, C. M., Procházka, P., & Hahn, S. (2020). Broad-scale patterns of the Afro-Palaearctic landbird migration. *Global Ecology and Biogeography*, 29, 722–735. <https://doi.org/10.1111/geb.13063>
- Clauzel, C., Jeliakzov, A., & Mimet, A. (2018). Coupling a landscape-based approach and graph theory to maximize multispecific connectivity in bird communities. *Landscape and Urban Planning*, 179, 1–16. <https://doi.org/10.1016/j.landurbplan.2018.07.002>
- Dhanjal-Adams, K. L., Klaassen, M., Nicol, S., Possingham, H. P., Chadès, I., & Fuller, R. A. (2017). Setting conservation priorities for migratory networks under uncertainty. *Conservation Biology*, 31(3), 646–656. <https://doi.org/10.1111/cobi.12842>
- Engelhard, S. L., Huijbers, C. M., Stewart-Koster, B., Olds, A. D., Schlacher, T. A., & Connolly, R. M. (2017). Prioritising seascape connectivity in conservation using network analysis. *Journal of Applied Ecology*, 54(4), 1130–1141. <https://doi.org/10.1111/1365-2664.12824>
- Erős, T., Schmera, D., & Schick, R. S. (2011). Network thinking in riverscape conservation: A graph-based approach. *Biological Conservation*, 144(1), 184–192. <https://doi.org/10.1016/j.biocon.2010.08.013>
- Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., Aghababayan, K., Fakriadi, I., Makrigianni, E., Jerzak, L., Azafzaf, H., Feltrup-Azafzaf, C., Rotics, S., Mokotjomela, T. M., Nathan, R., & Wikelski, M. (2016). Costs of migratory decisions: A comparison across eight White stork populations. *Science Advances*, 2(1), e1500931. <https://doi.org/10.1126/sciadv.1500931>
- Foltête, J.-C., Girardet, X., & Clauzel, C. (2014). A methodological framework for the use of landscape graphs in land-use planning. *Landscape and Urban Planning*, 124, 140–150. <https://doi.org/10.1016/j.landurbplan.2013.12.012>
- Fransson, T., Karlsson, M., Kullberg, C., Stach, R., & Barboutis, C. (2017). Inability to regain normal body mass despite extensive refuelling in Great reed warblers following the trans-Sahara crossing during spring migration. *Journal of Avian Biology*, 48(1), 58–65. <https://doi.org/10.1111/jav.01250>
- Grönroos, J., Green, M., & Alerstam, T. (2012). To fly or not to fly depending on winds: Shorebird migration in different seasonal wind regimes. *Animal Behaviour*, 83(6), 1449–1457. <https://doi.org/10.1016/j.anbehav.2012.03.017>
- Iwamura, T., Possingham, H. P., Chadès, I., Minton, C., Murray, N. J., Rogers, D. I., Treml, E. A., & Fuller, R. A. (2013). Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 280(1761), 20130325. <https://doi.org/10.1098/rspb.2013.0325>
- Keeley, A. T. H., Beier, P., & Jenness, J. S. (2021). Connectivity metrics for conservation planning and monitoring. *Biological Conservation*, 255, 109008. <https://doi.org/10.1016/j.biocon.2021.109008>
- Kirby, J. S., Stattersfield, A. J., Butchart, S. H. M., Evans, M. I., Grimmett, R. F. A., Jones, V. R., O'Sullivan, J., Tucker, G. M., & Newton, I. (2008). Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International*, 18(S1), S49–S73. <https://doi.org/10.1017/S0959270908000439>
- Koch, S. L., & Paton, P. W. C. (2014). Assessing anthropogenic disturbances to develop buffer zones for shorebirds using a stopover site. *The Journal of Wildlife Management*, 78(1), 58–67. <https://doi.org/10.1002/jwmg.631>
- La Sorte, F. A., & Fink, D. (2017). Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations. *Global Ecology and Biogeography*, 26(2), 216–227. <https://doi.org/10.1111/geb.12534>
- Laita, A., Kotiaho, J. S., & Mönkkönen, M. (2011). Graph-theoretic connectivity measures: What do they tell us about connectivity? *Landscape Ecology*, 26(7), 951–967. <https://doi.org/10.1007/s10980-011-9620-4>
- Lok, T., Overdijk, O., & Piersma, T. (2015). The cost of migration: Spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*, 11(1), 20140944. <https://doi.org/10.1098/rsbl.2014.0944>
- Ma, Z., Cai, Y., Li, B., & Chen, J. (2010). Managing wetland habitats for waterbirds: An international perspective. *Wetlands*, 30(1), 15–27. <https://doi.org/10.1007/s13157-009-0001-6>
- Madsen, J., Tjørnløv, R. S., Frederiksen, M., Mitchell, C., & Sigfússon, A. T. (2014). Connectivity between flyway populations of waterbirds: Assessment of rates of exchange, their causes and consequences. *Journal of Applied Ecology*, 51(1), 183–193. <https://doi.org/10.1111/1365-2664.12183>
- Maiorano, L., Amori, G., Montemaggiore, A., Rondinini, C., Santini, L., Saura, S., & Boitani, L. (2015). On how much biodiversity is covered in Europe by national protected areas and by the Natura 2000 network: Insights from terrestrial vertebrates. *Conservation Biology*, 29(4), 986–995. <https://doi.org/10.1111/cobi.12535>
- Moilanen, A. (2011). On the limitations of graph-theoretic connectivity in spatial ecology and conservation: Limitations of graph-theoretic connectivity. *Journal of Applied Ecology*, 48(6), 1543–1547. <https://doi.org/10.1111/j.1365-2664.2011.02062.x>
- Newton, I. (2008). *The migration ecology of birds*. Elsevier/Acad. Press.
- Nourani, E., Bohrer, G., Becciu, P., Bierregaard, R. O., Duriez, O., Figuerola, J., Gangoso, L., Giokas, S., Higuchi, H., Kassara, C., Kulikova, O., Monti, F., Pokrovsky, I., Sforzi, A., Therrien, J.-F., Vansteelant, W. M. G., Viana, D. S., Yamaguchi, N. M., & Safi, K. (2021). The interplay of wind and uplift facilitates over-water flight in facultative soaring birds. *BioRxiv, preprint*, 26. <https://doi.org/10.1101/2020.09.04.282939>
- Pakanen, V.-M., Jaakkonen, T., Saarinen, J., Rönkä, N., Thomson, R. L., & Koivula, K. (2018). Migration strategies of the Baltic dunlin: Rapid jump migration in the autumn but slower skipping type spring migration. *Journal of Avian Biology*, 49(1), jav-01513. <https://doi.org/10.1111/jav.01513>
- Palacín, C., Alonso, J. C., Martín, C. A., & Alonso, J. A. (2017). Changes in bird-migration patterns associated with human-induced mortality. *Conservation Biology*, 31(1), 106–115. <https://doi.org/10.1111/cobi.12758>
- Paracuellos, M. (2006). How can habitat selection affect the use of a wetland complex by waterbirds? *Biodiversity and Conservation*, 15(14), 4569–4582. <https://doi.org/10.1007/s10531-005-5820-z>
- Pekel, J.-F., Cottam, A., Gorelick, N., & Belward, A. S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature*, 540(7633), 418–422. <https://doi.org/10.1038/nature20584>
- Phipps, W. L., López-López, P., Buechley, E. R., Oppel, S., Álvarez, E., Arkumarev, V., Bekmansurov, R., Berger-Tal, O., Bermejo, A.,

- Bounas, A., Alanís, I. C., de la Puente, J., Dobrev, V., Duriez, O., Efrat, R., Fréchet, G., García, J., Galán, M., García-Ripollés, C., ... Vallverdú, N. (2019). Spatial and temporal variability in migration of a soaring raptor across three continents. *Frontiers in Ecology and Evolution*, 7, 323. <https://doi.org/10.3389/fevo.2019.00323>
- Piersma, T. (1987). Hink, stap of sprong? Reisbeperkingen van arctische steltlopers door voedselzoeken, vetopbouw en vliesnelheid. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening and flight speed. *Limosa*, 60, 185–194.
- Piersma, T., & Lindström, Å. (2004). Migrating shorebirds as integrative sentinels of global environmental change. *Ibis*, 146(suppl. 1), 61–69. <https://doi.org/10.1111/j.1474-919X.2004.00329.x>
- Popoff, N., Gaget, E., Béchet, A., Dami, L., du Rau, P. D., Geijzendorffer, I., Guelmami, A., Mondain-Monval, J.-Y., Perennou, C., Suet, M., Verniest, F., Deschamps, C., Taylor, N. G., Azafaz, H., Bendjedda, N., Bino, T., Borg, J. J., Božič, L., Dakki, M., ... Galewski, T. (2021). Gap analysis of the Ramsar site network at 50: Over 150 important Mediterranean sites for wintering waterbirds omitted. *Biodiversity and Conservation*, 30(11), 3067–3085. <https://doi.org/10.1007/s10531-021-02236-1>
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from: <https://www.R-project.org/>
- Ramsar Convention on Wetlands (2018). *Global wetland outlook: State of the world's wetlands and their services to people*. Ramsar Convention Secretariat.
- Rayfield, B., Fortin, M.-J., & Fall, A. (2011). Connectivity for conservation: A framework to classify network measures. *Ecology*, 92(4), 847–858. <https://doi.org/10.1890/09-2190.1>
- Runge, C. A., Watson, J. E. M., Butchart, S. H. M., Hanson, J. O., Possingham, H. P., & Fuller, R. A. (2015). Protected areas and global conservation of migratory birds. *Science*, 350(6265), 1255–1258.
- Saura, S., Bertzy, B., Bastin, L., Battistella, L., Mandrici, A., & Dubois, G. (2019). Global trends in protected area connectivity from 2010 to 2018. *Biological Conservation*, 238, <https://doi.org/10.1016/j.biocon.2019.07.028>
- Saura, S., Bodin, Ö., & Fortin, M.-J. (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, 51(1), 171–182. <https://doi.org/10.1111/1365-2664.12179>
- Saura, S., & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83(2–3), 91–103. <https://doi.org/10.1016/j.landurbplan.2007.03.005>
- Saura, S., & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, <https://doi.org/10.1111/j.1600-0587.2009.05760.x>
- Saura, S., & Torné, J. (2012). Conefor 2.6 user manual.
- Schmaljohann, H., Liechti, F., & Bruderer, B. (2007). Songbird migration across the Sahara: The non-stop hypothesis rejected! *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 274(1610), 735–739. <https://doi.org/10.1098/rspb.2006.0011>
- Taylor, C. M., & Norris, D. R. (2010). Population dynamics in migratory networks. *Theoretical Ecology*, 3(2), 65–73. <https://doi.org/10.1007/s12080-009-0054-4>
- Taylor, P. D., Fahrig, L., & With, K. A. (2006). Landscape connectivity: A return to the basics. In K. R. Crooks, & M. Sanjayan (Eds.), *Connectivity conservation* (pp. 29–43). Cambridge University Press. <https://doi.org/10.1017/CBO9780511754821.003>
- Trierweiler, C., Klaassen, R. H. G., Drent, R. H., Exo, K.-M., Komdeur, J., Bairlein, F., & Koks, B. J. (2014). Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 281(1778), 20132897. <https://doi.org/10.1098/rspb.2013.2897>
- UNEP/AEWA secretariat. (2018). Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA): Agreement text and annexes as amended at the 7th Session of the Meeting of the Parties to AEWA 4–8 December 2018, Durban, South Africa (p. 62). Bonn, Germany.
- Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpišová, J., & Gregory, R. D. (2014). The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, 156(1), 1–22. <https://doi.org/10.1111/ibi.12118>
- Warnock, N. (2010). Stopping vs. staging: The difference between a hop and a jump. *Journal of Avian Biology*, 41(6), 621–626. <https://doi.org/10.1111/j.1600-048X.2010.05155.x>
- Wetlands International, Mundkur, T., & Nagy, S. (2012). *Waterbird population estimates, fifth edition*. Wetlands International. Retrieved from Wetlands International website: 978-90-5882-000-6
- Woolf, A., Nawrot, J. R., Kirk, L., & Elliot-Smith, E. (2003). Habitat preferences of migratory shorebirds and waterfowl on the east shoreline of Rend Lake Refuge (No. Federal Aid Project W-141-R-1). Cooperative Wildlife Research Laboratory, SIUC.
- Xu, Y., Si, Y., Takekawa, J., Liu, Q., Prins, H. H. T., Yin, S., Prosser, D. J., Gong, P., & de Boer, W. F. (2020). A network approach to prioritise conservation efforts for migratory birds. *Conservation Biology*, 34(2), 416–426. <https://doi.org/10.1111/cobi.13383>
- Xu, Y., Si, Y., Wang, Y., Zhang, Y., Prins, H. H. T., Cao, L., & de Boer, W. F. (2019). Loss of functional connectivity in migration networks induces population decline in migratory birds. *Ecological Applications*, 29(7), e01960. <https://doi.org/10.1002/eap.1960>
- Zetterberg, A., Mörtberg, U. M., & Balfors, B. (2010). Making graph theory operational for landscape ecological assessments, planning, and design. *Landscape and Urban Planning*, 95(4), 181–191. <https://doi.org/10.1016/j.landurbplan.2010.01.002>
- Zhao, H., Liu, S., Dong, S., Su, X., Liu, Q., & Deng, L. (2014). Characterizing the importance of habitat patches in maintaining landscape connectivity for Tibetan antelope in the Altun Mountain National Nature Reserve, China. *Ecological Research*, 29(6), 1065–1075. <https://doi.org/10.1007/s11284-014-1193-7>
- Zwarts, L., Bijlsma, R. G., van der Kamp, J., & Wymenga, E. (2009). *Living on the edge: Wetlands and birds in a changing Sahel*. KNNV Publishing.

## BIOSKETCH

The PhD research of LP and ED under supervision of BVS and NK aims at investigating wetland suitability and connectivity for waterbird migration at different spatial scales, with a focus on the governance aspect of connectivity conservation. In their work, they combine field observations as well as different modelling approaches.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Deboelpaep, E., Partoens, L., Koedam, N., & Vanschoenwinkel, B. (2022). Highway(s) overhead: Strong differences in wetland connectivity and protected status challenge waterbird migration along the four Palearctic-Afrotropical flyways. *Diversity and Distributions*, 28, 1067–1080. <https://doi.org/10.1111/ddi.13508>