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When and Where Do Waterbirds Need Water? A General Approach for Inferring Candidate Restoration Areas From Spatio-Temporal Variation in Surface Water Availability

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ABSTRACT

Aim: Globally, about 850 bird species depend on surface water habitats either year-round or during migration. However, large-scale analyses examining how different groups of waterbirds are associated with surface water across various regions and during different seasons are lacking. This study analyzes this relationship using high-resolution satellite imagery to determine when and where surface water and associated resources might be improved.

Location: Western Palearctic (Europe, Middle East, Northern Africa).

Methods: We correlated monthly counts of 40 waterbird species with surface water availability in the Western Palearctic at a 100×100 km grid cell resolution. We then identified where and when surface water or associated resources might be limiting for waterbird numbers, using waterbird count data and the most recent release of high-resolution satellite imagery from the Copernicus project.

Results: Surface water availability was higher in the East-Atlantic flyway than in the Black Sea–Mediterranean flyway, but differences were small, while bird abundances (after correction for observation effort) were comparable. The relationship between surface water and waterbird abundances was typically positive and slightly stronger in the East-Atlantic flyway. However, it was negative during summer in the northern regions, where many waterbirds breed. Correlations were stronger for ducks and other strictly wetland-dependent birds, reflecting their more exclusively aquatic feeding behaviour. Crowdedness, calculated as the number of birds per surface water area, was higher in autumn compared to spring migration.

Main Conclusions: Our results confirm that the importance of surface water availability for waterbirds varies seasonally and geographically. In addition, our maps integrating bird counts and surface water help to strategically prioritise regions where water availability could be limiting and high crowdedness implies a vulnerability for waterbirds, for example, in terms of resource

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Lisa Partoens and Vincent Dolmans contributed equally to this work.

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competition or disease transmission. These include parts of the Iberian Peninsula, the UK, northern-central Europe, the Levant and Northern Africa.

1 | Introduction

Waterbirds rely on wetlands during different stages of their life cycle. These wet habitats can be used for foraging or resting but also as nesting sites (Ma et al. 2010; Qiu et al. 2024). During migration, wetlands are important stopover sites and crucial staging areas for birds to replenish their energy reserves before crossing barriers such as mountain ranges, seas or deserts (Newton 2010; Deboelpaep et al. 2022). However, since 1700, 21% of the total global wetland area has been degraded or destroyed. Much of this wetland loss occurred in Europe, where more than half of the wetland area was lost (Fluet-Chouinard et al. 2023). Historically, wetlands were often drained since they were thought to be associated with disease (Xu et al. 2019) but more recent losses in the past 200 years are mainly due to agricultural intensification and urbanisation (Johnson et al. 2011; Meffert and Dziock 2013; Bairlein 2016).

Long-distance migration enables birds to avoid temporally unsuitable local conditions and exploit the opportunities provided by distant resources that are only available seasonally (Altizer et al. 2011). During their journeys, migratory birds traverse and use a range of different biotopes that together make up the migratory flyway (Boere and Stroud 2006). This makes them vulnerable to threats like habitat loss, degradation and fragmentation in this entire area (Deboelpaep et al. 2022; Vickery et al. 2023).

Approximately one fifth of all bird species are migratory (Kirby et al. 2008), and among these, about 360 are waterbird species (Birdlife International 2022). Waterbirds are defined by the Ramsar Convention as birds that are ecologically dependent on wetlands during at least one part of their life cycle (Ramsar Convention Secretariat 2013). Migratory birds are exposed to a growing number of threats leading to declining populations (Kirby et al. 2008; Birdlife International 2022; Lees et al. 2022). Notably, European migratory birds wintering in Africa are experiencing more rapid declines compared to non-migratory resident species. This decline has been mainly linked to habitat degradation and loss (Bairlein 2016). Despite substantial conservation efforts, the global decline of wetlands is still ongoing. A global study of 1250 Ramsar wetland sites found that 6000 km^2 of wetland area could be lost by 2100 because of global warming (Xi et al. 2021). However, where and during which part of the year wetland availability is most critical, for example, an important predictor for wetland bird abundances, is less clear.

For birds that migrate between the Palearctic and Afrotropics, two primary flyways can be identified: the East-Atlantic flyway and the Black Sea–Mediterranean flyway (Boere and Stroud 2006). The former links northern and northwestern European breeding grounds with African wintering grounds and mainly follows the Atlantic coast. The latter connects northern and (north)eastern Europe to North Africa, across the Black Sea and the Mediterranean Sea. The regions covered by these flyways experience contrasting climates. The East-Atlantic flyway has a temperate oceanic climate, while the Black Sea–Mediterranean flyway experiences a continental climate (Köppen and Geiger 1936). Yet, the extent to which these two major flyways differ in the abundance of wetlands, in seasonal wetland availability and in the number of waterbirds that use these wetlands has not been quantified.

Waterbirds by definition rely on surface water and associated terrestrial habitats such as marshland and reedbeds. However, quantitative analyses of links between wetland availability and waterbird counts are scarce and, when conducted, are typically restricted to small regions (Lorenzón et al. 2020; Ananin and Aiurzanaeva 2021; Frota et al. 2022). A complicating factor is that not all wetlands are consistently present or available for waterbirds year-round. Frost or drought can cause wetlands in a certain location to not provide aquatic resources such as water and foraging opportunities when birds need them (Ballard et al. 2021).

Satellite imagery is a valuable tool to study surface water availability (Pekel et al. 2016). However, up until very recently, high spatial and temporal resolution satellite imagery that allows assessment of how much surface water is present in a certain area and during different parts of the year was unavailable. Europe's wetland area, excluding the European part of Russia, is estimated to extend over 500,000 km^2 (Nivet and Frazier 2004), but high-resolution spatial and temporal data to determine when these wetlands are present throughout the year were lacking. In 2020, the global Copernicus Water Bodies database was expanded and now provides a monthly estimate of surface water distribution at a resolution of 100 m: a hundredfold increase compared to the earlier 1 km-resolution database (Copernicus 2020).

At the same time, there has been a substantial increase in the availability of bird count data from citizen-science based observations and continuous monitoring programs (Devictor et al. 2010; Follett and Strezov 2015; Hurlbert and Liang 2012; Sullivan et al. 2014), particularly in well-covered regions such as the Western Palearctic. This knowledge can be important for conservation managers to assess to which extent resources linked to wetland surface area may be limiting for waterbirds in different regions during specific time periods. For instance, a situation with high waterbird numbers relative to the available wetland area potentially signals crowdedness and may suggest that wetlands and their associated resources may be limiting. Additionally, crowdedness is also associated with other risks such as disease transmission (Møller et al. 2001; Rifkin et al. 2012) and a higher vulnerability to environmental disasters linked to specific sites (Pain et al. 1998; Yang et al. 2021). If areas experience crowding during certain parts of the year, this may be a reason to prioritise local habitat restoration.

The main goal of this study was to investigate when and where different groups of waterbirds may be limited by surface water availability within their flyway and during their annual migrations. This question has been frequently addressed at small spatial scales for a single wetland or a specific region (Maleki et al. 2016; Schaffer-Smith et al. 2017), but never at a subcontinental scale or at the scale of migratory flyways.

Spatiotemporal variation in the availability of surface water was mapped across the Western Palearctic (Europe, Northern Africa and part of the Middle-East) on a monthly basis for 2021 and 2022 using the Copernicus' Water Bodies 100 m database (Copernicus 2020). Forty waterbird species were selected that rely on wetlands during their life cycle but differ in their strict dependency on wetlands. Three functional groups were considered: ducks, which mostly use open water (i.e., wetlands that are permanently inundated and less densely vegetated, such as ponds, lakes and reservoirs), such as the Eurasian Teal (*Anas crecca*) and Mallard (*Anas plathyrhynchos*), strictly wetland-dependent birds that almost exclusively occur in wetlands such as the Common Snipe (*Gallinago gallinago*) or Eurasian Spoonbill (*Platalea leucorodia*), and wetland-associated birds that also feed in terrestrial habitats such as the Black-tailed Godwit (*Limosa limosa*) or White Stork (*Ciconia ciconia*). Bird count data for these 40 waterbird species in this region were compiled from the open-access Global Biodiversity Information Facility and corrected for observation effort (GBIF.org 2023).

To assess the link between surface water availability and waterbirds, two metrics were calculated: (1) the Spearman-Rank correlation between surface water area and waterbird abundances during different months in three different latitudinal bands which span the northern, central and southern Palearctic and (2) a grid cell-based measure for crowdedness based on the number of waterbirds divided by the surface water area.

We tested four hypotheses. First, (H1) we expected that the correlation between waterbird abundances and surface water area would be weak in arctic and subarctic regions during the summer months since many waterbirds breed there in non-wetland habitat. We expect such correlations to be strongest in the Mediterranean region during the autumn migration, when many waterbirds pass through the area while many shallow wetlands may have dried out.

Second, (H2) when comparing the coastal East Atlantic with the more continental Black Sea–Mediterranean flyway, we expect that birds traveling via the latter flyway might be more limited by surface water availability, at least during some parts of the year. The continental climate of the middle latitudes of the Black Sea–Mediterranean flyway may result in more frozen wetlands in winter while the drier, hotter summers might ensure that many wetlands dry out. In contrast, the East-Atlantic flyway mostly follows the Atlantic coast and has a temperate climate, which may result in a more reliable surface water availability throughout the year.

Third, (H3) we hypothesise that the link with surface water availability will be strongest for ducks and strongly wetland-dependent bird species that strictly forage in wet habitats, and weaker for birds that also feed in terrestrial habitat.

Fourth, (H4) we expect that crowdedness (i.e., bird counts per area of available surface water) will be higher during the two main bird migration periods in spring and in autumn, in particular. Warm summer months with high evaporation and limited precipitation can ensure that less water is available in autumn, promoting crowdedness. In addition, the influx of newborn offspring after summer can result in higher bird abundances in autumn than in spring. In our analyses, crowdedness is a grid cell-based metric and reflects when and where bird densities are highest.

Understanding when and where waterbird species need water is crucial to inform policymakers and conservation planners where to conserve, create or restore wetland habitats globally. High correlation coefficients in specific regions and during certain time periods, combined with high population densities in local grid cells, may encourage nature managers to enhance surface water availability in these areas. This could help distribute migratory bird populations more evenly across the landscape, thereby reducing local population densities.

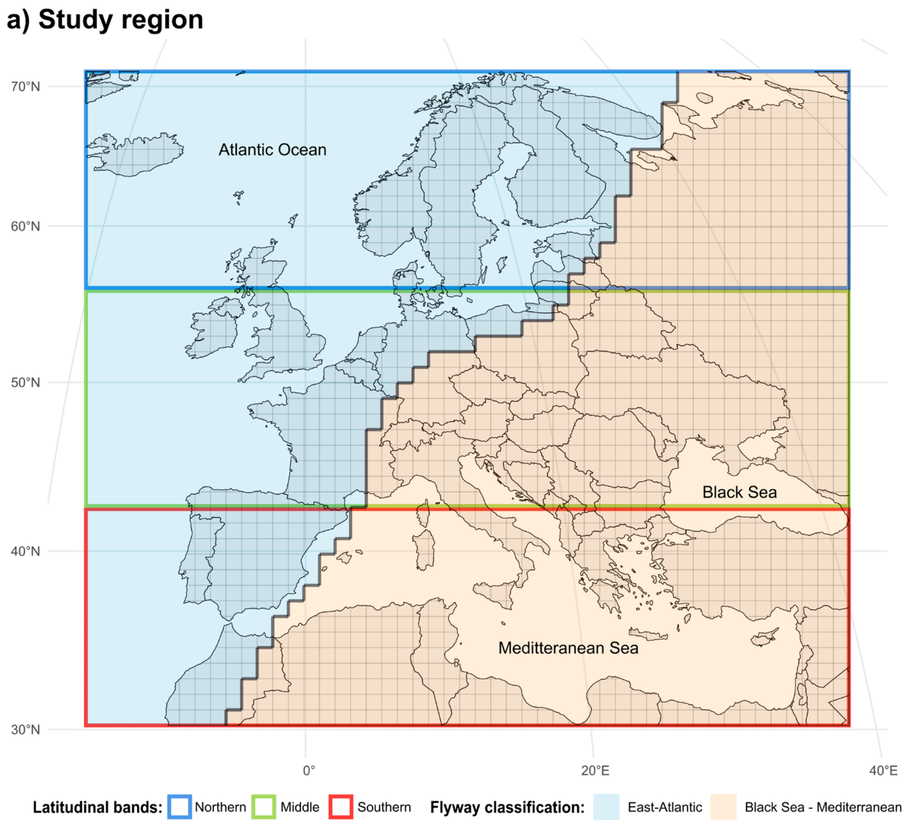
2 | Methods

2.1 | Study Area and Species

In this study, we investigated links between waterbird counts and surface water availability across the Western Palearctic (Europe, Middle East and Northern Africa), spanning the geographic coordinates between the westernmost point of Iceland (−28.8° W) and the easternmost point of the Black Sea (71.3° E) and from the southernmost tip of the Mediterranean Sea (30.2° N) to the top of the Scandinavian Peninsula (71.2° N). The study area encompasses two major migratory flyways: the East-Atlantic flyway and the Black Sea—Mediterranean flyway (Figure 1). These two flyways connect breeding grounds in northern and central Europe and wintering grounds in southern Europe and (sub-Saharan) Africa. The East-Atlantic flyway is positioned along the Atlantic coast, while the Black Sea—Mediterranean flyway extends along the eastern part of Europe, encompassing the Black Sea and Red Sea (Figure 1). Both flyways cross the Mediterranean Sea and Sahara Desert, notable barriers for migratory birds (Newton 2010).

The study region spans diverse climate zones. In the north, a subarctic climate prevails (Köppen-Geiger class D). In the mid-latitudes of Europe, there is a difference between the eastern and western regions. The eastern region has a continental climate (Köppen-Geiger class D), characterised by hot summers and at least 1 month with an average temperature below 0°C. In contrast, the western region has a temperate oceanic climate (Köppen-Geiger class Cw), marked by milder variations between winter and summer. In southern Europe, there is a Mediterranean climate (Köppen-Geiger class Cs, locally BS; Köppen and Geiger 1936).

Bird species were selected because (1) they rely on wetlands during their life cycle (foraging and/or breeding and/or resting), ranging from open water bodies to more terrestrial wet meadows, (2) they occur widespread throughout the study region and can be found both in the East-Atlantic and Black Sea–Mediterranean flyway and (3) sufficient count data for them are available (> 5000 data points per year). As such, the analysis is restricted to species that are relatively common for the whole study region. This resulted in a selection of 40 waterbird species (Table S1). These species were divided into three



b) Practical approach

1. Calculate correlation between (observer effort corrected) waterbird counts and surface water area for each month in three latitudinal bands.

2. Calculate crowdedness (no. of birds [corrected for observation effort] / area surface water) in 100x100km grid cells.

FIGURE 1 | (a) Map of the study area. The study area is rasterised into grid cells of 100 × 100 km and was divided into three latitudinal bands: Northern, Middle and Southern. Two migratory flyways cross the study region: The East-Atlantic flyway (blue) and the Black Sea—Mediterranean flyway (orange). Maps are made using the World Geodetic System 84 with a Mollweide equal area projection (ESRI: 54009). (b) Schematic overview of the practical approach used and the calculations made.

distinct groups. The first group (G1) consists of six duck species (Anseriformes, Anatinae) commonly referred to as dabbling ducks such as the Eurasian Teal (*A. crecca*) and Mallard (*A. platyrhynchos*). These species employ a feeding strategy that involves dabbling and/or diving and are highly dependent on open water habitat (i.e., wetlands that are permanently inundated and less densely vegetated, such as ponds, lakes and reservoirs) (Svensson et al. 2022; Billerman et al. 2022). The second group (G2) includes 27 wetland-dependent species that wade in shallow wetlands and shores and are highly dependent on wetlands for foraging. These species primarily forage on insects, fish, amphibians, worms, small crustaceans and molluscs in the water column or in the mud. They are mostly found in or near water bodies such as mudflats, rivers and reedbeds (Svensson et al. 2022; Billerman et al. 2022). Examples are the Common Snipe (*G. gallinago*) and Eurasian Spoonbill (*P. leucorodia*). Lastly, the third group (G3) encompasses seven species that are associated with surface water but can also feed in other wet, but more terrestrial habitats such as meadows (Svensson et al. 2022; Billerman et al. 2022). Examples are the White Stork (*C. ciconia*) and Black-tailed Godwit (*L. limosa*).

2.2 | Data Collection

Data collection and manipulation was performed in R version 3.5 (R core team 2025), making use of the *terra* and *sf* packages for spatial operations (Hijmans 2025; Pebesma 2018), using *dplyr* for data manipulation (Wickham et al. 2023) and *ggplot2* for visualisations (Wickham 2016). Packages and functions used are denoted further within square brackets [package::function]. The full script is available in the Supporting Information. The study area was rasterised into 2058 grid cells (42 rows and 49 columns) [sf::st_make_grid], each of 100 × 100 km, ranging from the westernmost point of Iceland (−28.8° W) to the easternmost point of the Black Sea (71.3° E) and from the southernmost tip of the Mediterranean Sea (30.2° N) to the top of the Scandinavian Peninsula (71.2° N). Of these 2058 grid cells, 1452 remained when excluding grid cells with only marine cover. For each grid cell, (1) the number of waterbird observations, (2) the number of observations for all bird species as a proxy for observation effort, (3) the number of waterbirds corrected for observation effort (no. waterbirds/no. bird observations), (4) the surface water area and (5) the crowdedness as calculated by the number of waterbirds corrected for observation effort and divided by the area of surface water, were calculated. The analyses were performed at a monthly resolution for a total of 24 months from January 2021 until December 2022. The year 2021 was average in terms of precipitation, while 2022 was overall drier with severe droughts in spring and summer (Copernicus Climate Change Service 2021; Copernicus Climate Change Service 2022). Throughout the data processing, data originally in the Coordinate Reference System (CRS) WGS84 (EPSG: 4326) were transformed to the Mollweide equal area CRS (ESRI: 54009) [terra::project] before analysis.

Bird observation data for 40 waterbird species were retrieved from the Global Biodiversity Information Facility (GBIF) (GBIF.org 2023) using the 'rgbif' package for R (Chamberlain et al. 2025). GBIF is a platform that collects global biodiversity data from both moderator-verified citizen-science projects as well as research surveys. Observations were only included when coordinates were available and could be defined as observations, human observations, machine observations (e.g., camera trap observations) and occurrences. Tracking data were removed as they concern multiple occurrences of the same individuals. This was achieved by filtering out datasets published by 'This database consists of two classified layers: the Water Bodies layer (WB) and the Water Quality layer (QUAL), which together provide information about permanent and seasonal water body occurrence.' (Kays et al. 2022) as this was the only organisation publishing tracking data to GBIF in our temporal and spatial timeframe (Van Der Kolk et al. 2022). Focal waterbird species are listed in Table S1. The number of bird observations per month was calculated for each grid cell [sf::st_within]. Therefore, the number of individuals was used (individualCount). When 'individualCount' was not specified, it was assumed there was only one individual observed. Calculations were done for individual species and were grouped by the three functional species groups.

The surface water data were retrieved from Copernicus' Water Bodies 100 m database (Copernicus Global Land Operations 2020). This database provides global surface water data with a monthly temporal resolution and a spatial resolution of 100 m, starting from October 2020. The Water Bodies database collects from three primary sources: (1) Top of Canopy Sentinel-2 L1C MultiSpectral data, (2) the Joint Research Centre's Global Surface Water Explorer and (3) prior versions of CGLOPS Water Bodies Monthly databases (Copernicus Global Land Operations 2021; Pekel et al. 2016). This database consists of two classified layers: the Water Bodies layer (WB) and the Water Quality layer (QUAL), which together provide information about permanent and seasonal water body occurrence.

Surface water data were retrieved as raster .ncdf files in CRS WGS84 (EPSG:4326). Rasters were subsequently cropped to the study region [terra::crop](to save computation time), projected to Mollweide CRS [terra::project], cropped again to the study region in Mollweide CRS, and saved as .tif. The water quality (QUAL) data layer, which includes information about the type of data for each pixel, was used to exclude pixels with sea water (grid code: 0), no data (grid code: 251) and no observed water (grid code: 255). As such, only seasonal or permanent terrestrial and coastal water bodies were maintained [terra::classify]. Total water and land surface area for each grid cell was calculated [exactextractr::exact_extract]. For the land area, we used the Natural Earth land vector dataset [rnaturalearth::ne_download] at a 10 m resolution (Massicotte and South 2023).

Observation data from GBIF was first cleaned using the 'CoordinateCleaner' package [CoordinateCleaner::clean_coordinates] to remove any observations with faulty coordinate data (Zizka et al. 2019). For this, the 'capitals,' 'centroids,' 'seas,' 'equal,' 'zeros,' 'gbif,' 'institutions' tests were used with 1 km buffers for capitals, centroids and seas and 100 m for institutions. The 'seas' test also removed any observations not on land, and for this, we also used the Natural Earth land vector data at a 10 m resolution. Due to computational limitations, this layer was rasterised [terra::rasterize] to a 100 m resolution raster when counting observation effort as bird observations. Point vector layers for the waterbird occurrences and observation effort as bird observations were created [sf::st_as_sf] and reprojected to the equal-area projection Mollweide (ESRI:54009) [sf::st_transform]. To get the waterbird and observation effort counts, we intersected point data with our grid [sf::st_within]. Waterbird counts were first corrected for observation effort by dividing the number of waterbirds observed in each grid cell (no. observations × individualCount) by the number of observations of all bird species. Crowdedness was subsequently calculated as the observation effort corrected bird count divided by the surface water area per grid cell and per month. An overview of spatial bias in observer effort for birds on the GBIF.org platform can be found in Figure S1.

In this study, the strength of the correlation between waterbird counts and surface water area in three different latitudinal bands during different parts of the year was interpreted as a measure of surface water dependency (Figure 2). A positive correlation suggests that individuals of a certain bird species are distributed within this latitudinal band based on the availability of resources linked to total surface water area. A negative relationship suggests that cells with high surface water area tend to have fewer birds than cells with little water, implying that birds might prefer terrestrial habitats. An example would be the Golden Plover (*Pluvialis apricaria*), which does not associate with wetlands in the breeding season (Figure 2a,b). In terms of management, a positive correlation suggests that wetland creation or restoration might be effective in boosting local bird numbers. In turn, promoting wetland resources is less likely to have an effect on local bird counts when such a correlation is absent and might be counterproductive in situations where there is a negative correlation between counts of target bird species and surface water availability (Figure 2c).

2.3 | Statistical Analyses

All statistical analyses were performed in R version 4.5 (R core team 2025). Analyses were performed for all 40 waterbird species

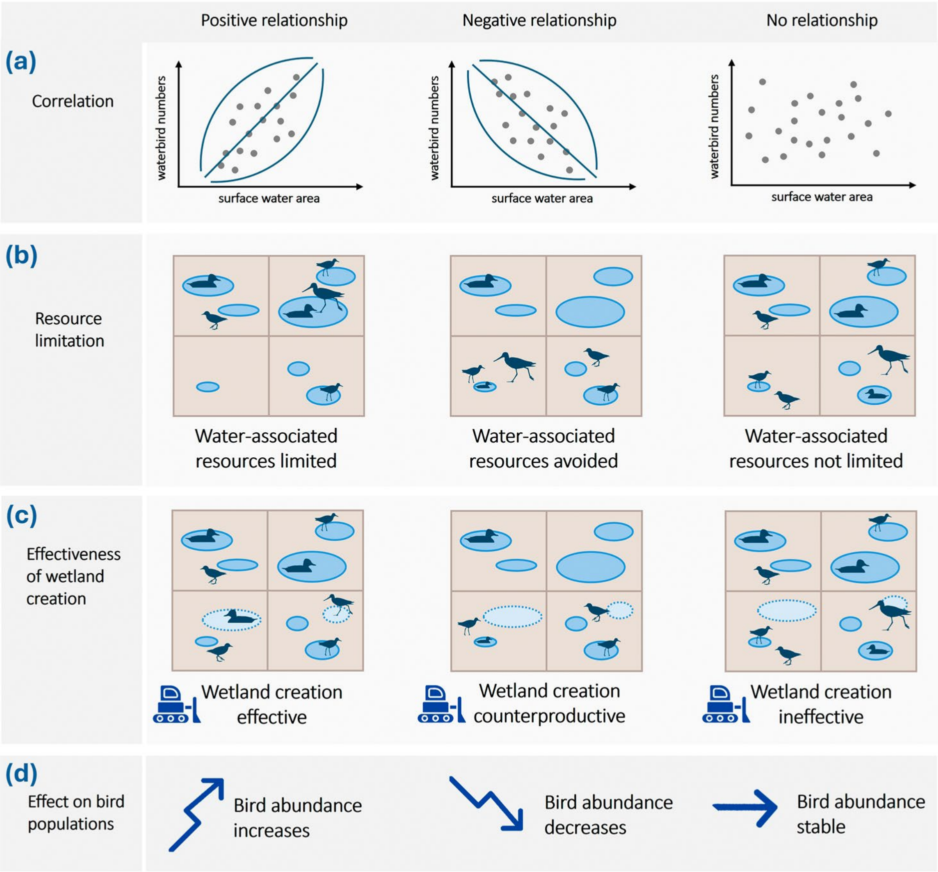


FIGURE 2 | Potential correlations between surface water and waterbird abundances. A positive correlation may indicate that wetland creation could lead to an increase in waterbird numbers in that region. A negative correlation may indicate that wetland creation might be an unproductive tool to increase waterbird numbers in that region. No correlation suggests that wetland creation may not be an effective tool to increase waterbird numbers in that region.

together (cumulative counts) and for each species individually, grouped in three functional species groups. Each grid cell was attributed to a latitudinal band (Northern, Middle or Southern) and to a flyway (East-Atlantic or Black Sea—Mediterranean flyway) (Figure 1).

Correlation tests were used to analyse the relationship between the number of waterbirds and surface water area per month and for different latitudinal bands and flyways [stats::cor.test]. Bird counts were not normally distributed, so Spearman-rank correlation tests were used. Correlation was considered strong if the correlation coefficient ρ was higher or equal to ±0.5, moderate when between ±0.5 and ±0.25 (included), and weak when lower than ±0.25. p-values for significance of the correlations were also extracted, and a Bonferroni correction for multiple testing was applied to them [stats::p.adjust(method = 'bonferroni')].

To examine how crowdedness varied spatially and temporally, hurdle generalised additive models (GAMs) were constructed for each flyway and latitudinal band using the *mgcv* package (Wood, 2017). Models were two-part consisting of a binomial regression model to predict the probability of crowdedness being non-zero and a GAM to predict the value of the crowdedness (log transformed). Binomial models [mgcv::gam(family = 'binomial')] used the number of bird observations (observation effort) as a linear explanatory variable. GAMs had a gaussian distribution as after observation effort correction our data followed a normal distribution after log transformation. GAMs were fitted with month as a cyclic cubic spline [mgcv::s(type = 'cc')] explanatory variable [mgcv::gam(family = 'gaussian')]. The number of knots for the spline was varied between 0 (linear) and 12 in steps of 2, and for each value, a model was fit. Only the model with the lowest AIC value [stats::aic] was retained. In the model with month as a linear predictor, a sine and cosine transformation of the radials was applied to make the variable circular (Pewsey et al. 2013). In addition, a null model without explanatory variables was added to the AIC selection. The model with the lowest AIC values was subsequently used to predict crowdedness together with the binomial model [mgcv::predict.gam]. Additionally, to visualise spatial variation of crowdedness in our study region, another hurdle GAM was fit for the entire dataset but with an additional thin plate regression spline for longitude and latitude of the centroids of the grid cells. For this model, only the partial predictions of the thin plate spline were extracted and subsequently visualised [mgcv::predict.gam(type = 'terms')] to show variation in crowdedness across the region. Assumptions for all the resulting models were checked visually for fit [gratia::draw.gam] and concurvity [mgcv::concurvity]. Model summaries were generated using the *gt* and *gtsummary* packages [gtsummary::tbl_regression] (Sjoberg et al. 2021; Iannone et al. 2025).

To test differences in water availability and bird counts between the different flyways and latitudinal bands, two GAMs were constructed in a similar process as before, where *K* values for a spline for month were varied between models, and only the lowest AIC model was retained. Explanatory variables consisted of a cyclic cubic spline for month and factors for flyway and latitudinal band. The model for water availability was fitted to a Gaussian distribution and log transformed, while the model for (observation corrected) bird counts was fitted to a negative binomial distribution [mgcv::negbin] and log(+1) [base::log1p] transformed.

2.4 | Chloropleth Maps

To visualise spatio-temporal variation in waterbird counts and surface water availability, chloropleth maps were made. These maps visualise the variation in quantitative variables between grid cells, through a graduated colour scale. Maps were made for each month visualising the total number of bird observations, the total surface water area and the crowdedness calculated as the number of birds per surface water area. Apart from monthly totals, the annual mean across months was also calculated.

3 | Results

A detailed descriptive overview of the distribution of surface water, waterbird abundances and densities across latitudes and flyways is provided in the Supporting Information. Figures and data on surface water availability, observation effort-corrected bird counts and correlations between the two in the main manuscript are shown for 2021. Figures for 2022 are included in the Supporting Information, as patterns between 2021 and 2022 were comparable.

The spatial distribution of surface water, waterbird abundances and densities during spring and autumn migration (April and October respectively), is shown in Figure 3. The complete time series is provided in Figures S17–S22.

In line with our hypothesis (H2), the Black Sea—Mediterranean flyway had less available surface water compared to the East-Atlantic flyway (beta[flyway] = 0.69; $p < 0.001$) (Figure 4b; Figure S8). Surface water availability differed between latitudinal bands ($p < 0.001$) with the mid latitudes slightly lower (beta[Middle] = 0.78) and the southern Mediterranean substantially lower in available water (beta[Southern] = 0.29) compared to northern latitudes. Middle

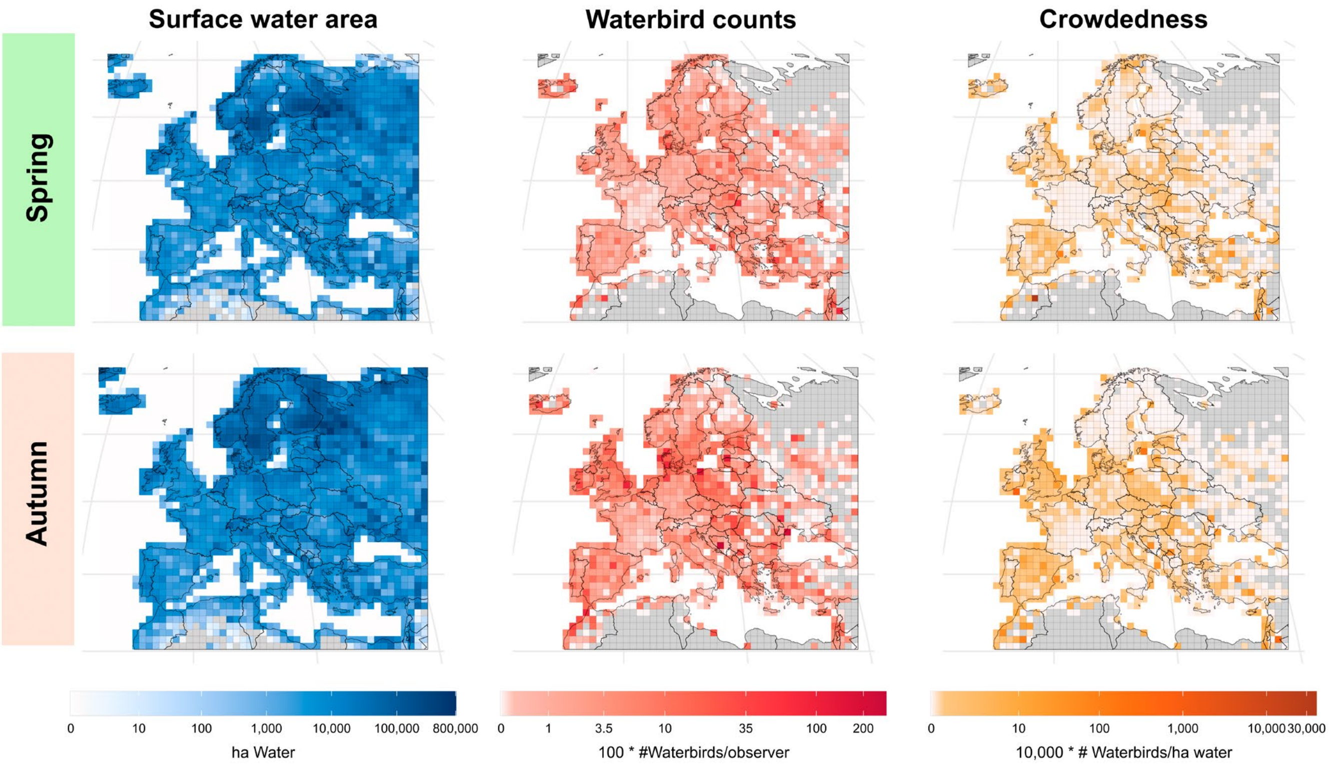


FIGURE 3 | Surface water area (ha) (left), observation effort corrected waterbird abundance (middle) and crowdedness (right) in April (top row) and October (bottom row) 2021, during spring and autumn migration, respectively. All three variables are visualised on a log + 1 scale. Shades of blue indicate surface area of water (in ha) per grid cell. Shades of red indicate the number of birds per grid cell. Shades of orange indicate crowdedness per grid cell, calculated as the number of birds per hectare surface water area. Uncoloured grid cells indicate there was no data for this grid cell. Each grid cell represents 100 × 100 km. Maps are made using the World Geodetic System 84 with a Mollweide equal area projection. The complete time series for 2021 and 2022 is provided in Figures S17–S22.

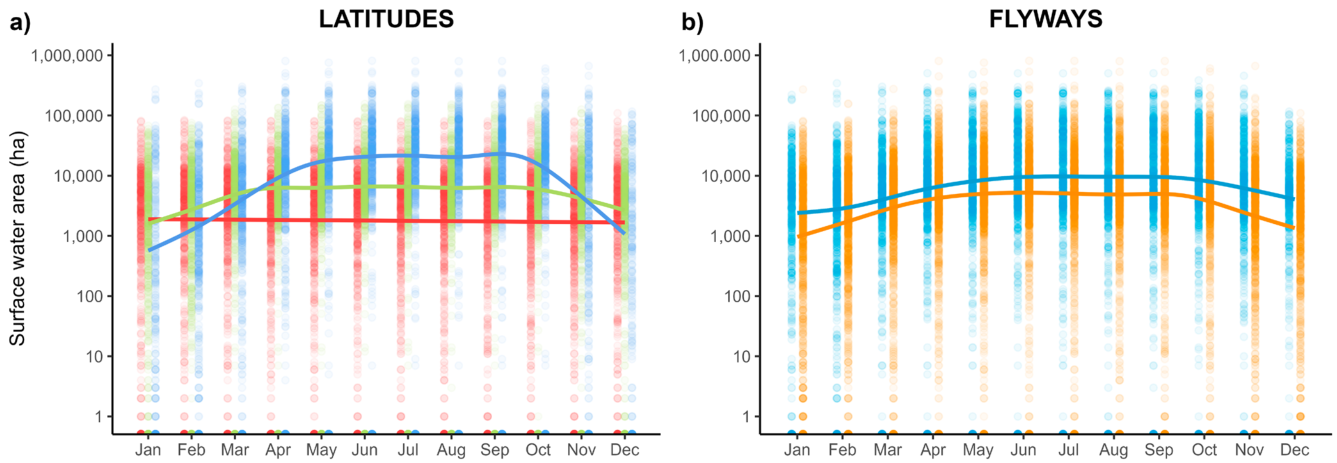


FIGURE 4 | Surface water area (ha) for each month of 2021 for 40 waterbird species in three latitudinal bands (Blue = northern latitudes, Green = middle latitudes and Red = southern latitudes; left panels) and the two major migratory flyways (Blue = East-Atlantic flyway, Orange = Black Sea—Mediterranean flyway, right panels) of the Western Palearctic. Data is visualised on a log+1 scale. Lines represent smoothed conditional means. The figure for the cumulative waterbird counts (corrected for observation effort) and The figure for 2022 is provided in the Supporting Information (Figures S2 and S3 respectively). The accompanying model summaries can also be found in the Supporting Information (Figures S8 and S9).

and northern latitudes were characterised by strong seasonal variation with most water in spring, summer and autumn. In the south, water availability was less variable throughout the year (Figure 4a; Figure S8). After correction for observation effort, bird counts also differed between flyways ($p < 0.001$) with the Black Sea—Mediterranean flyway having slightly less waterbirds (beta[flyway] = 0.80) most months in the year with numbers peaking during migratory seasons in spring and autumn (Figure S2a). Differences between latitudinal bands were small but significant ($p < 0.001$) with the middle and southern latitudes having higher waterbird abundances in general, mostly in winter (beta[Middle] = 1.12 and beta[Southern] = 1.20). Waterbird numbers in all the latitudinal bands of our study region drop in summer as birds migrate to central and southern Africa (Figures S2b and S9).

Consistent with our hypothesis (H1) we found generally weaker correlations between surface water and waterbirds at northern latitudes during the breeding season (May–July) until the onset of autumn migration (Figure 5). However, contrary to our expectations the correlations were only slightly stronger in the southern latitudes during the peak migration months in the Black Sea—Mediterranean flyway and weaker during spring migration in the East-Atlantic flyway. Hence these correlations do not support the idea that water availability is limited during those time periods in the Mediterranean. The correlation between surface water availability and waterbird counts was more often positive in the northern regions of the East-Atlantic flyway than in the northern parts of the Black Sea—Mediterranean flyway. In contrast, the correlation was generally less positive in the Black Sea—Mediterranean flyway than in the East-Atlantic flyway in the southern latitudes (Figure 5).

Correlations between surface water availability and waterbird counts varied between ducks, wetland-dependent and wetland-associated species and also showed seasonal differences (Figures S5 and S6). The correlations were generally weak to moderately positive ($0 < \rho < 0.5$), apart from summer and autumn months in northern latitudes in the East-Atlantic flyway. Here, weak to moderately negative ($-0.5 < \rho < 0$) correlations were found in several strictly wetland-dependent species and wetland-associated species, as well as some weak negative correlations ($-0.25 < \rho < 0$) for ducks. In the northern latitudes, many bird species are absent during winter. A few species also exhibited weak negative correlations with surface water in the south during the summer months, especially in the Black Sea–Mediterranean flyway.

Crowdedness, defined as the number of birds per surface water area, varied between latitudes and flyways (Figure 6). Overall, models predicted the same temporal pattern for both flyways, with crowdedness decreasing in late spring, summer and early autumn ($p < 0.001$). The duration of this seasonal crowdedness drop differs between latitudinal bands, with the northern bands having a longer dip in crowdedness compared to the southern bands. This seasonal lower crowdedness likely reflects both an increase in water availability when the ice melts (see Figure 4a) and a drop in association with water when birds are breeding (see Figure 5). While the Black Sea–Mediterranean flyway had lower crowdedness generally, the seasonal increase in crowdedness observed in the middle and northern latitude during winter was much higher. This is likely the result of the observed differences in water availability between the flyways (see Figure 4b), where, with less water available in general, crowdedness starts to shoot up when the smaller water supply starts to freeze over winter.

Crowdedness also varied significantly in space ($p < 0.001$) with generally lower crowdedness in the Scandinavian Peninsula and Russia due to the abundance of water in the summer and the absence of birds in winter. Other regions with low crowdedness are the Ionian Peninsula, SE France and the Alpine region, likely due to extensive available wetlands, for example, the Camargue wetlands and numerous coastal wetlands along the Greek islands. The areas with the highest crowdedness were situated in northern Africa, particularly the Saharan region. Other regions with elevated crowdedness were the UK,

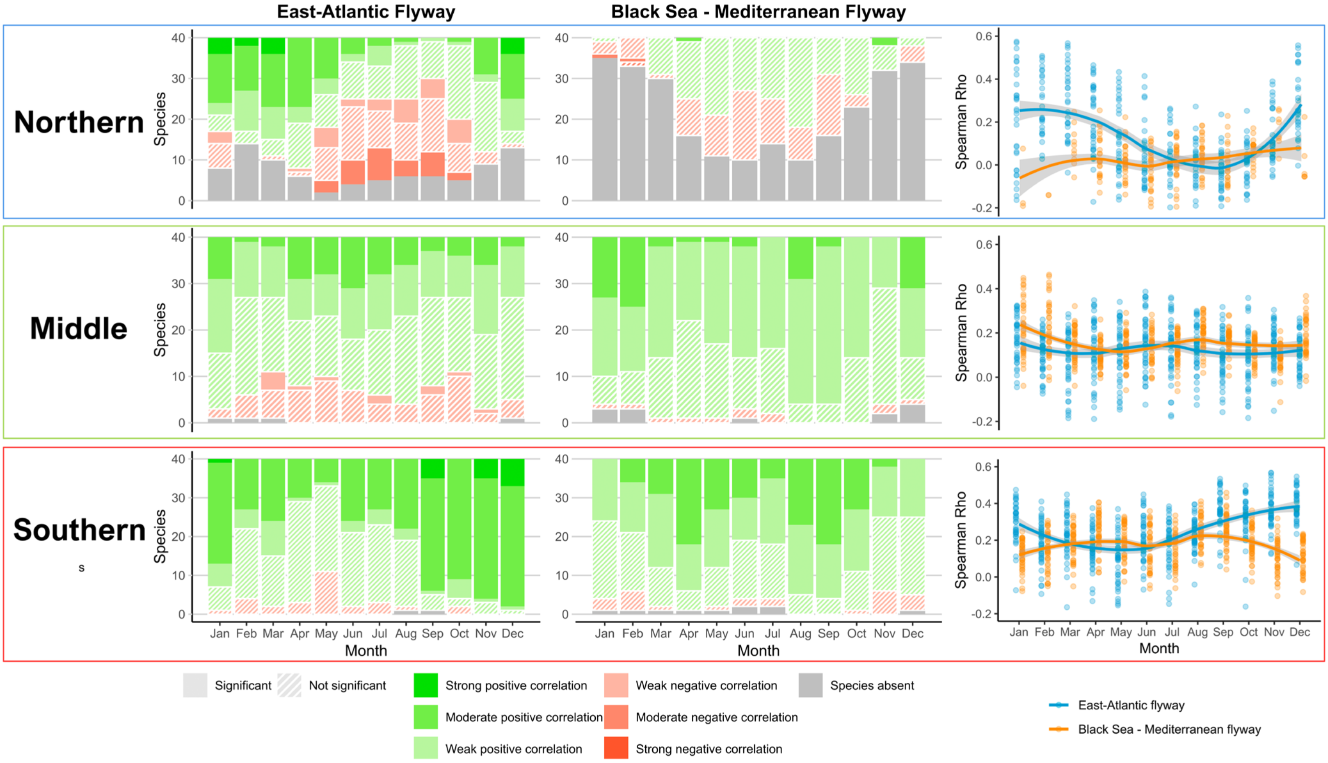


FIGURE 5 | Correlations (Spearman ρ) between surface water availability and waterbird counts for each month of 2021 for 40 waterbird species for three latitudinal bands in the Western Palaearctic: Northern latitudes (above), middle latitudes (middle) and southern latitudes (below). Left panels show the East-Atlantic flyway, middle panels the Black Sea—Mediterranean flyway. Right panels show correlation between surface water area and bird counts for each bird species per month averaged for all species for both flyways (blue = East-Atlantic flyway, orange = Black Sea—Mediterranean flyway). The correlation is calculated as a non-parametric Spearman-Rank ρ coefficient. Stacked bars show the relative proportion of bird species with positive or negative correlations with water availability. Shades of green or red indicate positive or negative correlations between surface water area and the number of waterbirds, respectively. Striped patterns indicate non-significant correlations ($p > 0.05$). Grey means the species is absent in the particular month so no correlation could be calculated. Lines represent smoothed conditional means. The figure for 2022 is provided in the Supporting Information (Figure S4).

northern central Europe, Iceland, the Levant and the Iberian Peninsula.

4 | Discussion

Waterbirds are birds that, by definition, rely on wetlands for feeding, resting and/or breeding (Ramsar Convention Secretariat 2013). However, comprehensive large-scale analyses to quantify how this dependency varies among different groups of waterbirds, across geographical regions and throughout different times of the year are currently lacking. To resolve this knowledge gap, we integrated state-of-the-art high-resolution satellite imagery data with citizen science bird observation data and reconstructed spatio-temporal variation in surface water dependency for 40 waterbird species across the two major migratory flyways of the Western Palearctic. Overall, we found clear differences in the seasonal surface water dependency of three functional groups of waterbirds. This relationship was similar for the two major Palearctic–Afrotropical flyways. By analysing correlations between waterbird counts and surface water availability and spatio-temporal patterns of crowdedness, we pinpointed vulnerable regions where resources linked to surface water may be currently limiting for waterbirds.

4.1 | Differences in Surface Water Dependency Between Flyways and Between Waterbird Species

Initially, we expected that waterbirds would be more strongly correlated to surface water in the Mediterranean compared to northern latitudes (H1), but this hypothesis is only partially confirmed. Most waterbird species had weak or moderate positive correlations with surface water availability during different parts of the year. Consistent with our hypothesis, stronger positive correlations were most common in the Mediterranean in autumn, but this pattern was only clear in the East-Atlantic flyway. During the summer in northern latitudes, certain species exhibited a weaker or even negative correlation with surface water availability.

These results align with the known breeding behaviour of waterbirds in these regions, such as Black-tailed Godwit (*L. limosa*) and Northern Lapwing (*Vanellus vanellus*), which often nest away from open water (Svensson et al. 2022; Billerman et al. 2022). In the northern section of the Black Sea–Mediterranean flyway,

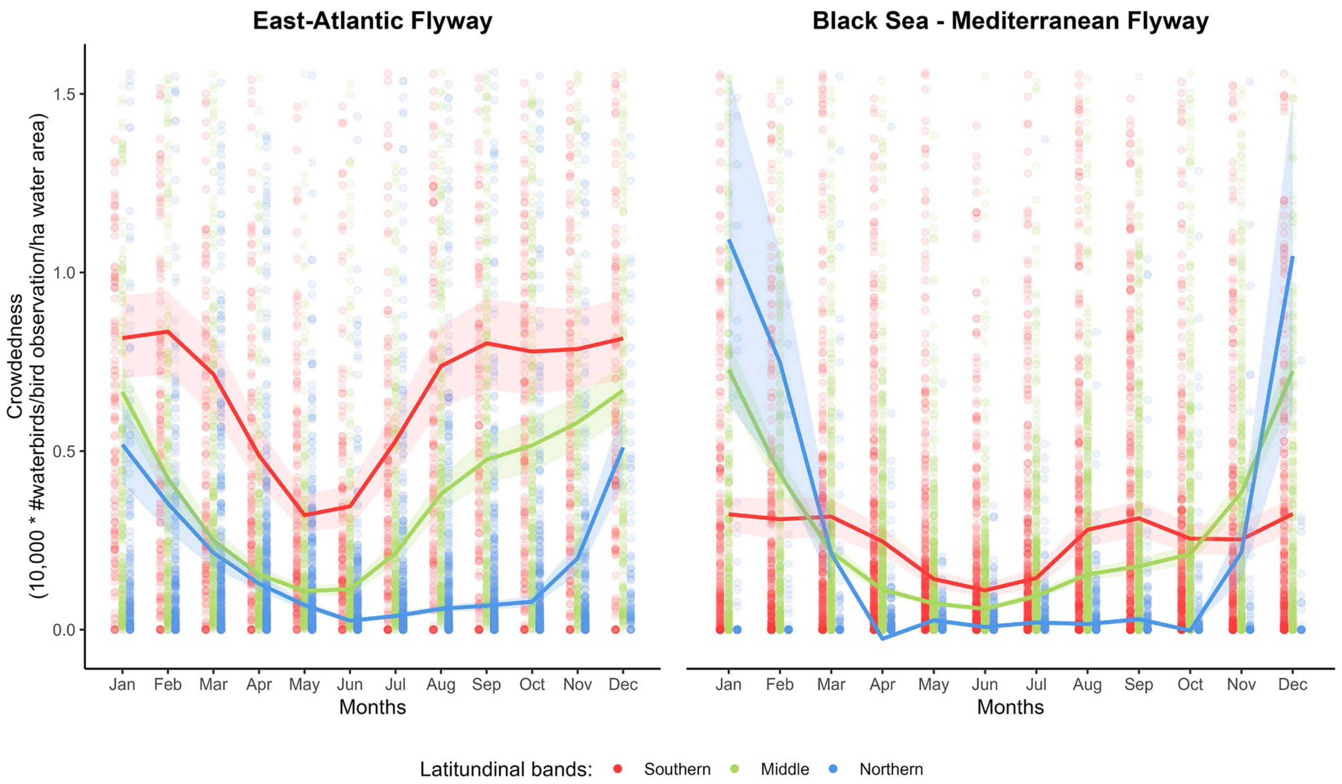


FIGURE 6 | Seasonal variation in crowdedness of waterbirds (total no. birds per observation effort per ha of surface water) for 40 selected waterbird species in individual 100 × 100 km grid cells. Lines represent predictions of Hurdle Generalised Additive Models (GAMs). Separate patterns are reconstructed for three latitudinal bands: Northern latitudes (blue), middle latitudes (green) and Southern latitudes (red) and for the two Palearctic-Afrotropical flyways: The East-Atlantic (EA) flyway (left) and the Black Sea—Mediterranean (BSM) flyway (right). Data points with crowdedness higher than 1.5 are not shown. Spatial variation between grid cells is visualised in the Supporting Information (Figure S7). Model outputs are summarised in the Supporting Information (Figures S11–S16).

which comprises Finland, the Baltics and part of Russia, negative correlations between birds and surface water were less clear. Although speculative, this might be explained by an overabundance of surface water (seasonally) to the point where waterbird numbers are no longer congregated in space to areas with high surface water.

We also expected (H2) that local counts of birds travelling via the Black Sea–Mediterranean flyway, which is characterised by colder winters and drier summers, would be more constrained by surface water availability. Our results did not confirm this hypothesis, with generally weaker bird correlations with surface water and lower crowdedness throughout the year with the exception of the winter months when crowdedness increases to higher levels than in the East-Atlantic flyway. Additionally, the Black Sea–Mediterranean flyway also appears to have more areas of low crowdedness compared to the East-Atlantic flyway. While the Black Sea–Mediterranean flyway did have less available surface water, it also had fewer waterbirds (after correction), and thus the low prevalence of surface water might only lead to higher crowdedness in winter in the northern and middle latitudes.

Consistent with our third hypothesis (H3), we found that surface water dependency was strongest for ducks and birds that forage in wetlands only, and weaker for birds that also feed in terrestrial habitats. This provides empirical support for the current perception of water dependency in these groups (van de Kam et al. 2004; Ma et al. 2010).

As anticipated (H4), crowdedness of waterbirds (i.e., the number of birds per surface area of water) was highest during autumn migration. In addition to surface water declines in the northern regions, autumn migration includes more birds due to the addition of the new cohort of juveniles produced in that year while surface water availability remains comparable to spring conditions. Potentially, these extra birds can lead to more crowdedness at stopover sites. Crowdedness was on average higher in the East–Atlantic flyway, which also had slightly higher bird counts in general than the Black Sea–Mediterranean flyway. Regions with high crowdedness include the UK, Iceland and the Iberian Peninsula, as well as increasing crowdedness in North Africa towards the Sahara desert due to increasing drought and precipitation seasonality. A potential explanation for the observed flyway differences could be that the former includes a single land bridge for shorter sea crossing, that is, the Strait of Gibraltar. The latter includes several crossings through Mediterranean islands such as Sicily and Crete and a larger land surface area which may allow for broader, more spatially diffuse migration routes and less crowding along this flyway. Along the Black Sea–Mediterranean flyway, high crowdedness was detected in the Levant, which represents an important coastal corridor for many migratory waterbirds to bypass the Mediterranean. We detected less crowdedness at northern latitudes. This might be due to the high abundance of surface water (e.g., vast numbers of glacial ponds and lakes) available there in spring when most birds arrive to breed, although seasonal fluctuations in surface water are more pronounced here. Another explanation is that many waterbirds such as godwits and curlews are not strongly linked to wetlands in the breeding season and build their nests away from open water (Svensson et al. 2022; Billerman et al. 2022). Besides, depending on the species, bird densities can be variable and low in the breeding ranges, which might cause lower crowdedness in the summer (Svensson et al. 2022; Keller et al. 2020).

4.2 | Study Limitations

In these analyses, we assumed that a strong positive correlation between surface water availability and waterbird abundances during specific months and within separate latitudinal bands might indicate that surface water associated resources are limiting for waterbirds and that more birds could be supported locally in a region if the surface water area were increased. However, this correlation does not necessarily imply that wetland creation would ensure that the overall waterbird populations will grow as well. More water may also result in a more even distribution of birds among different wetlands in a region, resulting in lower crowdedness (Figure 2). High bird densities concentrated in a few sites can be disadvantageous for several reasons. For instance, it can facilitate the transmission of diseases like avian influenza (Olsen et al. 2006). Diseases often become more prevalent during autumn after breeding, at migratory stopovers, and in winter when many birds gather for wintering (Verhagen et al. 2021), although outbreaks can also occur in summer in birds that form breeding colonies (Wille and Waldenström 2023). Strong crowding also makes the overall population more vulnerable to local disturbances or habitat degradation at specific sites, such as those caused by droughts or environmental disasters (Pain et al. 1998; Yang et al. 2021). In the long run, expanding wetland areas and reducing local crowding could benefit populations by lowering mortality rates (e.g., through reduced disease transmission) and promoting higher fecundity (e.g., by providing more abundant food sources). In regions with a weak or absent correlation between waterbird counts and water availability, other non-water-related factors such as disturbance or predation risk are likely more important determinants of bird numbers (Bauer et al. 2010).

The correlation between surface water availability and waterbird counts is interpreted here as a proxy for water dependency. However, it is important to realise that it is not the surface water area itself per se that is affecting the birds. More water can mean more birds, but the area of open water detected on satellite images may not be the limiting factor. Besides surface area, other factors such as nutritional quality, water depth and local microhabitat quality and diversity will influence which bird species and how many birds occur, as different species have different habitat preferences, diets and feeding strategies (Svensson et al. 2022; Billerman et al. 2022; Deboelpaep et al. 2024).

Besides conceptual limitations, our approach also has some technical limitations. The spatial resolution of the data means that water bodies smaller than 100 m × 100 m are not incorporated in the analyses. Such smaller water bodies can be important habitats for waterbirds as well. A potential underrepresentation of small water bodies in some areas could bias our results to some extent and might explain the presence of significant numbers of waterbirds in areas with little detected water. Additionally, wetlands that are partially or entirely covered by vegetation are difficult to detect, further limiting the detection of smaller, vegetated water bodies. We acknowledge that because grid cells are used as replicates in our correlation analyses, neighbouring cells are not fully independent. Given the large scale of the cells (100 × 100 km), we believe the bias this introduces will be very limited. However, if similar analyses would be performed over smaller spatial scales with smaller grid cells and for specific bird species, corrections for spatial autocorrelation can be important, as bird counts in a focal cell can reflect conditions in nearby cells.

Surface water availability might be underestimated in this study because satellite imagery is distorted by cloud cover, especially in winter months, in high-latitude regions and at higher elevations. The somewhat higher crowdedness detected in winter in northern latitudes is most likely the result of this bias. In addition, counting efforts of migratory birds are considered to be higher in Western than in Eastern Europe (Wetzel et al. 2018), which implies that we probably somewhat underestimate crowdedness in the Black Sea–Mediterranean Flyway. However, the species selected for this study are common throughout the whole study region and only included in the data analysis when enough (> 5000 data points) were available. Therefore, we excluded species that were too rare or for which data availability was too limited to make meaningful conclusions. However, some more obscure or elusive species, such as the Black Stork (*Ciconia nigra*), might still be underdetected in citizen-science-based observation data, which could affect our results and the crowdedness estimates in our study region.

The patterns reported in this paper reflect the 2 years that have passed since the high-resolution monthly surface water data became available. In the future, reconstructions over longer time scales will be possible as new data come out that will lead to more robust conclusions. Yet, for the 2 years of available data, we found that our results were remarkably consistent. The year 2021 was average in terms of precipitation, while 2022 was characterised by severe droughts in spring and summer (Copernicus 2021; Copernicus 2022).

4.3 | Perspectives and Conclusions

Our study provides a first quantitative exploration of spatiotemporal variation in the link between waterbirds and surface water in the Western Palearctic flyways, one of the world's most important migratory systems. We find that birds that are commonly considered waterbirds indeed tend to be linked to water, but this dependency differs among different functional groups of birds and also depends on the location and the time of the year.

Numerous studies show shifts in the timing of bird migration, primarily in response to rising temperatures in the departure regions (Parmesan and Yohe 2003; Saino et al. 2011; Bairlein 2016; Van Doren 2022). Birds may depart earlier and, as a result, be confronted with different wetland and resource conditions during their trajectory compared to what they currently experience. It is possible that moments with high levels of crowdedness could become more common in the future due to such mismatches between water presence and bird migration phenology. However, longer time series data will be needed to confirm this.

Our study shows that integrating satellite-based water observations with citizen-sourced bird data is an effective approach to identify when and where surface water and related resources may be insufficient for waterbirds, and where high bird densities relative to available surface water indicate crowding. According to our analyses, such regions are found in the UK, Poland, Iceland, the Iberian Peninsula, the Suez region and locally in Northern Africa. As such, these results may assist in prioritising broad regions for wetland conservation or restoration. Within the regions prioritised by our analyses, a thorough assessment of various costs and benefits should be conducted during site selection for conservation or restoration. These considerations include land prices, stakeholder resistance and trade-offs between the costs and benefits for different species, ecosystems and their associated services or disservices. Such analyses are essential to determine the optimal locations within these prioritised regions for wetland restoration or creation.

Additionally, as illustrated in Figure 2, it may be beneficial to not limit wetland restoration to regions that currently have the highest densities of waterbirds. Instead, wetland creation and restoration could be prioritised in (1) regions where water-associated resources are likely limiting during critical parts of the year for waterbirds and (2)—within such regions—to sites that currently have lower densities of waterbirds but a substantial surface area that could be restored. This view emphasises the importance of a spatial insurance strategy by developing alternative stopover sites within landscapes. For instance, Deboelpaep et al. (2022) showed that the connectivity of wetland networks across the Mediterranean for migratory waterbirds tended to disproportionately rely on a limited set of large, high-quality wetlands. As such, to enhance the effectiveness of wetland restoration for waterbird conservation, spatial prioritisation should ideally be tackled at a transnational level and, if possible, at a flyway level. This might ensure that enough wetland resources are present when and where birds need them.

The analyses in this paper indicate that wetland-associated resources could be limiting for waterbirds in specified regions and during migratory seasons. However, this does not mean that water is the most critical factor explaining the current population trend of the species. For instance, wide-scale illegal killing of waterbirds during migration and breeding seasons may be more important (Brochet et al. 2016, 2019; Kirby et al. 2008). It is notoriously difficult to assess the value of wetlands for waterbirds, as information on limiting factors such as predators including poachers, food availability and quality and external sources of disturbance are very difficult to quantify. Analyses such as ours may be coarse but can already provide much-needed directions for the large-scale wetland restoration projects that are planned, for instance via the Nature Restoration Law recently adopted by the European Union (European Union 2024).

Author Contributions

Conceptualisation: L.P. and B.V. Methodology: L.P., V.D. and B.V. Conducting the research, data analysis, data interpretation, preparation of figures and tables: L.P., V.D. and J.B. Writing the manuscript: L.P., V.D., J.B., E.D., N.K. and B.V.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used is publicly available from the Copernicus and GBIF websites. The R script for the data collection, analyses and creation of the figures used in this study is available at DOI: https://doi.org/10.5061/dryad.41ns1rnsw.

Peer Review

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Biosketch

L.P. is a doctoral researcher interested in the availability and connectivity of wetlands for waterbirds across different spatial scales. Her work integrates remote sensing, field data and modelling to advance the conservation and governance of waterbird habitats. V.D. is a doctoral researcher investigating how wetland availability and habitat quality for waterbirds vary across space and time. He combines field observations with modelling approaches to support the conservation and management of waterbird habitats. Their supervisor, B.V., is a community ecologist focused on understanding the factors that shape patterns of species diversity and abundance across spatial scales.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ddi70107-sup-0001-Supinfo.docx.