

Habitat- and species-mediated short- and long-term distributional changes in waterbird abundance linked to variation in European winter weather

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Abstract

Aim: Many species are showing distribution shifts in response to environmental change. We explored (a) the effects of inter-annual variation in winter weather conditions on non-breeding distributional abundance of waterbirds exploiting different habitats (deep-water, shallow water, farmland) and (b) the long-term shift in the population centroid of these species and investigate its link to changes in weather conditions.

Location: Europe.

Methods: We fitted generalized additive mixed Models to a large-scale, 24-year dataset (1990–2013) describing the winter distributional abundance of 25 waterbird species. We calculated the annual and long-term (3-year periods) population centroid of each species and used the winter North Atlantic Oscillation (NAO) index to explain the inter-annual and long-term shifts in their location.

Results: (a) Year-to-year southwestwards shifts in the population centroids of deep- and shallow-water species were linked to negative NAO values. Shallow-water species shifted northeastwards associated with positive NAO values and the distance shifted increased with increasing NAO. Deep-water species shifted northeastwards up to zero NAO indices, but showed no further increase at higher NAO values. (b) Deep-water species showed long-term northeastwards shifts in distributional abundance throughout the 1990s and the 2000s. Shallow-water species, on the other hand, shifted northeastwards during the 1990s and early 2000s, but southwestwards thereafter. There were no significant links between the NAO and year-to-year movements or long-term shifts in farmland species' population centroid.

Main Conclusions: We provide evidence for a link between both year-to-year and long-term changes in waterbird winter distributional abundances at large geographical scales to short- and long-term changes in winter weather conditions. We also show that species using shallow water, deep-water and farmland habitats responded differently, especially at high NAO values. As well as important ecological implications, these findings contribute to the development of future conservation measures for these species under current and future climate change.

KEYWORDS

abundance change, biodiversity conservation, climate change, density change, North Atlantic Oscillation, range shift, spatiotemporal analysis, waterbirds, wetlands, winter distribution

1 | INTRODUCTION

Understanding how species and populations respond to the spatiotemporal variability in their environment is a core feature of contemporary ecology (Begon, Harper, & Townsend, 1996). Most climate change scenarios predict alterations to natural climatic variability (e.g., variation in temperature and rainfall patterns) and increases in the frequency of extreme events in the next century (European Environment Agency (EEA), 2012, Intergovernmental Panel on Climate Change (IPCC), 2012). Accumulating evidence

shows that changes in climatic conditions have become a major threat to the maintenance of biodiversity (Parmesan & Yohe, 2003; Thomas & Williamson, 2012) and responses to such changes are already apparent among many taxa (Amano et al., 2016; Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Hughes, 2000; Knudsen et al., 2011; Parmesan, 2006). Common responses to climate change are, for example, adjustments to timing of phenological events, such as flowering (Frei, Ghazoul, Matter, Heggli, & Pluess, 2014; Menzel et al., 2006) or migration time (Kelly et al., 2016; Møller, Rubolini, & Lehikoinen, 2008; Møller, Rubolini, & Saino,

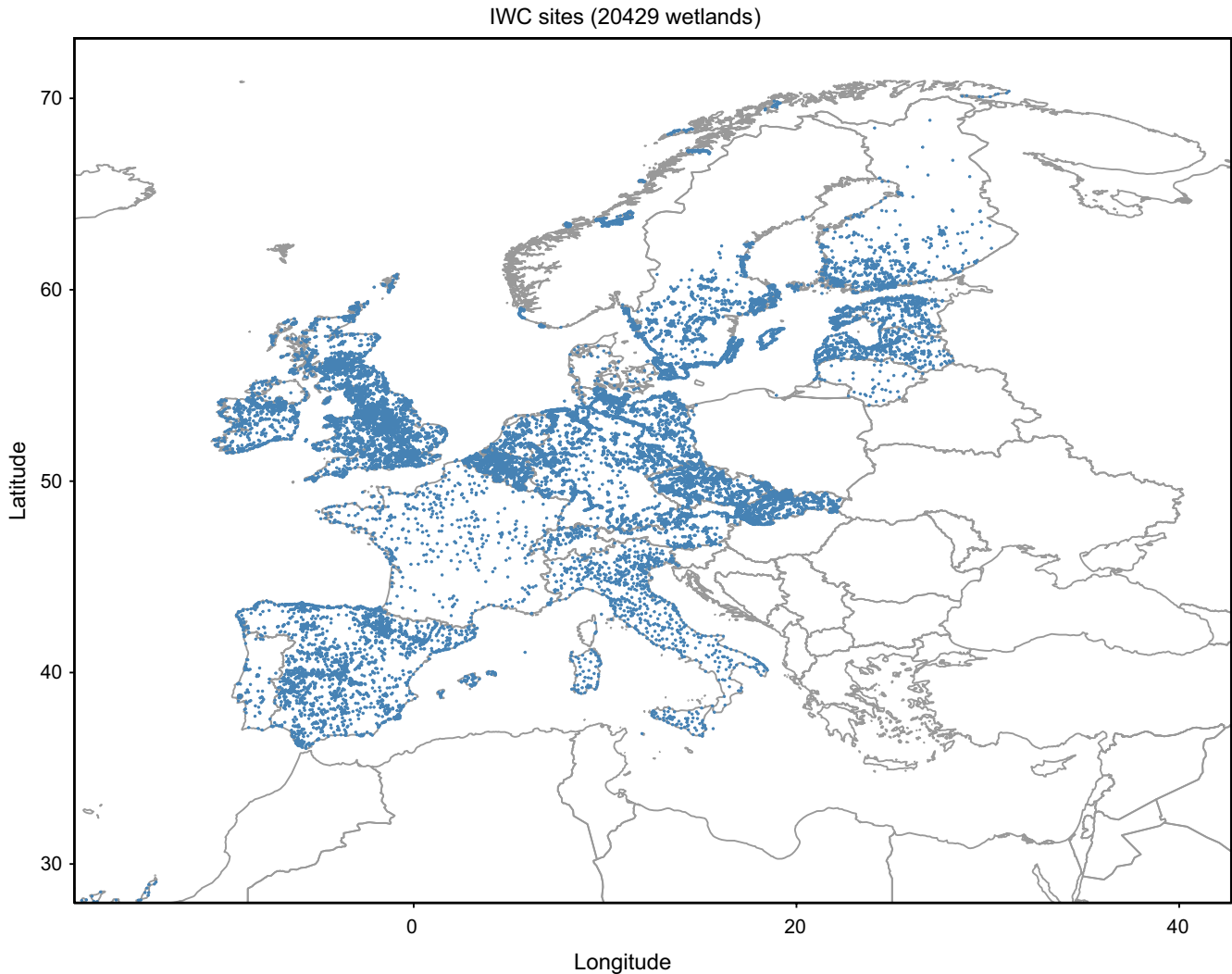


FIGURE 1 Spatial coverage of the study. Location of the 20 429 International Waterbird Count (IWC, mid-January) sites across the 21 European countries included in the analysis: Norway, Sweden, Finland, Estonia, Latvia, Lithuania, Poland, Denmark, Germany, Slovakia, Czech Republic, Austria, the Netherlands, Belgium, United Kingdom, Ireland, Switzerland, Italy, France, Spain and Portugal. Note the five sites in Poland at the Gulf of Gdansk and at the Odra river (on the border with Germany)

2017) or changes in distribution (Amano et al., 2016; Thomas et al., 2012).

Climate change impacts on distributions are expected to be more profound during winter than in the breeding season, especially for migratory species (Møller, Fiedler, & Berthold, 2010; Potvin, Välimäki, & Lehikoinen, 2016; Santangeli & Lehikoinen, 2017). This is because migratory species, in general, show more flexibility when settling at wintering areas compared to breeding sites (Newton, 1998) and because of the greater rate of change in weather conditions (e.g., temperature, rainfall and wind speed) during winter than in any other season (Intergovernmental Panel on Climate Change (IPCC), 2012). Typically, the northern edge of a species' wintering distribution is thought to be determined by climatic factors whereas interspecific interactions may play a more important role in shaping the distributions elsewhere (Newton, 1998). In this sense, climate change may favour colonization of new areas that formerly represented unsuitable habitat but have now become suitable and available along the

“cold” edge (Thomas et al., 2012; Fox et al., 2015; see also Cuervo & Møller, 2013). Moreover, climate change might render previously suitable habitats on the “warm” side of the wintering distribution unsuitable, for example through severe droughts, leading to local extinctions there (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Cuervo & Møller, 2013). In any case, both processes may ultimately contribute to changes in species' wintering distributions and densities (Brommer & Møller, 2010; Pearce-Higgins et al., 2015).

Here, we analyse a citizen science dataset that extends across Europe (Figure 1) and spans 24 years (1990–2013) to illustrate short- and long-term changes in winter distributional abundance of 25 waterbird species as a response to the inter-annual variation and long-term changes in large-scale weather conditions. Species with contrasting habitat requirements may respond differently to such changes in weather conditions (Clausen, Madsen, Cotaar, Kuijken, & Verschuere, 2018; Dalby, Fox, Petersen, Delany, & Svenning, 2013; Fox & Abraham, 2017; Lehikoinen et al., 2013). Thus, specifically, our

main objective is to investigate (a) the link between annual changes in winter weather conditions and the inter-annual variation in the location of the population centroid and (b) the long-term shifts in the population centroid of these species since 1990 linked to long-term changes in climatic conditions. In both analyses, we will explore how these relationships vary between groups of species with different habitat requirements.

The population flyways of the species considered in this study follow a north-east to south-west direction (Wetlands International 2017) corresponding also to the continental orientation and the general climatic gradient in Europe (e.g., Hurrell & Deser, 2010). In addition, due to the annual variability in winter weather conditions, we hypothesize that (a) the annual population centroid will move south-west relative to the preceding year in cold (and hence adverse) winter conditions in northern and western Europe due to the movement of large numbers of individuals further south-west along the north-east-south-west axis (Ridgill & Fox, 1990; Fox et al., 2016b; see also Maclean et al., 2008). Similarly, the centroid will shift towards the north-east relative to the preceding year in winters with mild weather conditions in northern and western Europe as more individuals are able to remain at sites closer to the breeding grounds (Elmberg, Hessel, Fox, & Dalby, 2014). These shifts represent the expected movement if distributions were mainly driven by weather (Rehfishch, Austin, Freeman, Armitage, & Burton, 2004; Maclean et al., 2008; see also Hurrell & Deser, 2010; Isaak & Rieman, 2013). In addition, we expect a longer-term directional shift of the population centroid. Hence, we also hypothesize that (b) the movement of the population centroid will show a long-term shift northeastwards over the study period as a direct consequence of a progressive increase in waterbirds' relative abundance in this region associated with a long-term increase in winter temperature (see Lehikoinen et al., 2013) and prolonged positive phase of the North Atlantic Oscillation (NAO) index (Hanna, Cropper, Jones, Scaife, & Allan, 2015; Hurrell & Deser, 2010).

Responses to climate change tend to be species-specific (Araújo et al., 2011), linked to species geographical range, habitat use and other ecological and life-history traits (Brommer, 2008; MacLean & Beissinger, 2017). Among waterbirds, species show strong adaptations for exploiting specific resources (Pöysä, Elberg, Nummi, & Sköberg, 1994) and such traits may explain differences in their specific responses to changes in climatic conditions (Dalby et al., 2013). For example, species that exploit deep-waters can be more flexible in terms of the choice of wintering grounds, because such a habitat may remain ice-free during most of the winter throughout the flyway. On the other hand, shorelines and farmland areas rapidly freeze during cold weather, and thus, species exploiting such habitats are forced to migrate to more south-western areas following the first days of freezing conditions. Thus, we hypothesize that (c) species exploiting shallow waters (hereafter, shallow-water species) or inland waters and agricultural habitats (hereafter, farmland species) will show stronger annual responses to cold weather conditions than species exploiting deep-waters (hereafter, deep-water species) (Dalby et al.,

2013). Consequently, we hypothesize that (d) deep-water species will show more marked long-term shifts northeastwards than shallow-water and farmland species (Fox et al., 2016b; Lehikoinen et al., 2013; Pavón-Jordán et al., 2015). Lastly, we expect that (e) species with more northerly wintering distributions will show stronger responses to inter-annual fluctuations in weather conditions than species with more southerly distributions (Dalby et al., 2013).

From a conservation point of view, effective evidence-based conservation of migratory waterbirds can only be achieved if there is a good understanding of the drivers of population change at local, country and global scales (Courchamp et al., 2015; Johnston et al., 2015; Stroud et al., 2004; Sutherland, Pullin, Dolman, & Knight, 2004). Previous studies have used the presence/absence data to investigate range shifts (Donald et al., 2007; MacLean & Beissinger, 2017; Thomas et al., 2012). However, exploring changes in populations using abundance data constitutes a better approach because it provides insights into processes occurring within the ranges, such as redistributions and changes in local abundances, which are impossible to detect using the presence/absence data (Dalby et al., 2013; Fox et al., 2016b; Johnston et al., 2015; Massimino, Johnston, Gillings, Jiguet, & Pearce-Higgins, 2017; Shoo, Williams, & Hero, 2005, 2006). Studies like the one presented here are essential to provide new evidence about large-scale responses of species to changing weather conditions, which help developing adaptive and evidence-based international conservation measures (Johnston et al., 2015; Mawdsley, 2011; Stroud et al., 2004; Whittaker et al., 2005).

2 | METHODS

2.1 | Waterbird data

In this study, we use 24 years (1990–2013) of spatially explicit winter abundance data (counts) of 25 common waterbird species across 21 European countries covering a large proportion of the European continent (Figure 1, Supporting information Appendix S2: Table S1 for details). These data are part of the International Waterbird Census (IWC), a standardized and synchronized survey carried out in January in all European countries by experienced volunteer birdwatchers which is coordinated by Wetlands International (Delany, 2005). The IWC started in 1967 in some countries but we here only use data from 1990–2013, as many states joined the monitoring programme after the 1980s. Overall, ca. 20,500 sites have been surveyed and over 213 million waterbirds counted during the study period (Supporting information Appendix S2: Tables S1 and S2 for details). We classified the 25 waterbird species included in this study into three main categories according to their main habitat preference: (a) shallow-water species (northern pintail *Anas acuta*, northern shoveler *Anas clypeata*, Eurasian teal *Anas crecca*, Eurasian wigeon *Anas penelope*, mallard *Anas platyrhynchos*, gadwall *Anas strepera*, shelduck *Tadorna tadorna*, grey heron *Ardea cinerea* and mute swan *Cygnus olor*), (b) deep-water species (common pochard *Aythya ferina*, tufted duck

Aythya fuligula, red-crested pochard *Netta rufina*, common golden-eye *Bucephala clangula*, goosander *Mergus merganser*, red-breasted merganser *Mergus serrator*, smew *Mergellus albellus*, coot *Fulica atra*, great cormorant *Phalacrocorax carbo* and great crested grebe *Podiceps cristatus*) and (c) those associated with inland water/farm-land (greater white-fronted goose *Anser albifrons*, greylag goose *Anser anser*, brent goose *Branta bernicla*, barnacle goose *Branta leucopsis*, Bewick's swan *Cygnus columbianus* and whooper swan *Cygnus cygnus*; see Supporting information Appendix S2: Table S1 for further details).

2.2 | Annual population centroid and annual northeasterliness

For each species, we calculated the distance (km) between the location of the population centroid (i.e., latitude and longitude weighted by count) in two consecutive winters. In order to properly measure such distance, we selected only those sites that were surveyed in both years of the comparison (24 years, 23 comparisons) and then calculated the population centroid for each year using that subset of the data. For example, we took all sites that were surveyed during 1990 and 1991 (in both years) and calculated the annual population centroid for both years. Note that the sites selected for the subsequent comparison (in this case 1991 and 1992) may differ, as only sites surveyed in both years will be represented in this subset, because not all sites were surveyed every year. The coordinates of the annual population centroid (weighted—by count—latitude and longitude) for each species are calculated as follows:

$$\text{Weighted Latitude}_t = \frac{\sum(\text{Latitude}_{i,t} \times \text{Count}_{i,t})}{\text{Total Count}_t} \quad (1)$$

$$\text{Weighted Longitude}_t = \frac{\sum(\text{Longitude}_{i,t} \times \text{Count}_{i,t})}{\text{Total Count}_t} \quad (2)$$

where “Latitude_{*i,t*}” and “Longitude_{*i,t*}” are the latitude and longitude of site *i* in year *t*, respectively. “Count_{*i,t*}” is the abundance (count) at site *i* in year *t*, and “Total Count_{*t*}” is the total abundance counted in year *t*.

The distance between the population centroids in two consecutive winters was measured as follows: First, we calculated how far the population centroid moved along a longitudinal (west–east) axis and then calculated how far it moved along a latitudinal (north–south) axis. If the population centroid moved towards the east, the distance would be positive, whereas if the movement was towards the west, the distance would have a negative value. Similarly, if the population centroid moved towards the north, the distance would have positive value and negative value if it moved southwards. The shortest distance between the population centroids in two consecutive years was calculated based on the “Vicenty (ellipsoid) great-circle-distance” in the “geosphere” package (Hijmans, 2017) in R3.3.2 (R Core Team 2015). Then, we summed these two distances to obtain a single value, which we hereafter define as “northeasterliness.” Positive northeasterliness means that the

population centroid had moved predominantly towards the north-east in year *t* relative to *t*–1, and negative northeasterliness means that it moved predominantly towards the south-west. We focused on northeastwards movements because the flyways described for the species considered in this study extend across Europe along a south-west–north-east axis (Wetlands International 2017). Thus, northeasterliness represents the natural direction of the shift along the flyway (Maclean et al., 2008; see also Hurrell & Deser, 2010). To differentiate this northeasterliness from the long-term movement in the population centroids (described below), we define this property as Annual Northeasterliness (AnnualNEness). We use the AnnualNEness as our response variable in the “short-term effect” model (see *Statistical analyses*).

In addition, we calculated the mean latitude during the study period (MeanLat) for each species by averaging the latitude of the eight long-term population centroids (see below). We used MeanLat to account for potential differences in the species response to changes in weather conditions (i.e., species with low MeanLat, which are regarded as southern species, might respond differently to changes in winter weather conditions than northern species).

2.3 | Long-term trend in northeasterliness

To assess whether there is a long-term movement in the population centroid northeastwards, we divided the data into eight periods of three years (period 1 = 1990 to 1992, period 2 = 1993 to 1995, ..., period 8 = 2011 to 2013). Then, we selected sites that were surveyed at least once in each of the eight periods. There are two main motivations for grouping the data in periods and not assessing long-term trends from the annual data: Firstly, in order to analyse a long-term trend across the entire study period (24 years), we would need to use only those sites that were surveyed every year from 1990–2013, which greatly reduced our potential dataset. By grouping the data into eight periods, we only needed to include sites that had been surveyed at least once during each of the eight periods. Secondly, averaging counts over three-year time periods reduced the variability in the data (because of the large inter-annual variation) that could reduce our ability to detect long-term trends.

We calculated the population centroid for each of the eight periods following the same rationale as before. However, in this case, if a site was surveyed more than once in a period, an average of the counts in that period was taken to calculate the weighted latitude and longitude in the population centroid (see Equations 1 and 2 above). We selected the mean abundance as it captures the overall situation at each site, whereas the use of maximum values would bias the value towards extreme observations. Once we had determined the population centroid for each of the eight periods, we calculated the northeasterliness (distance moved towards the north-east) for each period relative to period 1 (i.e., period 1 vs. period 1 to set the initial movement to 0, period 2 vs. period 1, period 3 vs. period 1, ..., period 8 vs. period 1). We used this long-term Northeasterliness (LongNEness) as our response variable in the “long-term trend” model (see below).

2.4 | Weather data

We used the winter North Atlantic Oscillation (NAO) index as a proxy of winter harshness (see MacKenzie & Köster, 2004). The NAO is closely associated with general weather conditions over the main wintering areas of the 25 species considered here (Hurrell & Deser, 2010; Wetlands International 2017). The NAO index is calculated as the difference between the normalized sea level pressures in Reykjavik (Iceland) and Lisbon (Portugal) since 1864 (Hurrell, 2016). Winters with high (positive) values of NAO reflect mild and wet winter weather conditions in western and northern Europe, which in turn can be associated with more benevolent winter conditions for waterbirds in these areas. Furthermore, positive values of NAO are also associated with drier winters in southern Europe compared to years with mean or negative NAO, as it is characterized by an atmospheric circulation that transports precipitation from the south-west towards the north-east (see Hurrell, 1995 for further details on the NAO index). Negative NAO, on the other hand, represents colder temperatures in northern and western Europe (Hurrell, 1995, 2016; Hurrell & Deser, 2010), which can be associated with more unfavourable winter conditions for waterbirds in these regions. Monthly NAO data were downloaded from <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml> (last access 10 July 2016).

We then calculated a mean winter NAO index for each winter to be included in the “short-term effect” model (see below) by averaging the NAO values for December and January in such a way that the NAO value for the winter in 1995 is the averaged NAO value of December 1994 and January 1995 (winter 1995 will be then associated with the species counts in January 1995). During our study period, a wide range of NAO index values have been recorded (mean and standard deviation: -0.03 ± 1.80 , total range: -3.45 to 2.60). We also calculated a mean winter NAO index for the “long-term trend” model (see below) by averaging the yearly NAO indices over each of the three-year periods.

2.5 | Statistical analyses

We built the “short-term effect” model to assess the impact of mean winter NAO, the preferred habitat of the species and the mean latitude of the species’ wintering range on the AnnualNEness. We fitted a generalized additive mixed model (GAMM) with Gaussian distribution (Zuur, Saveliev, & Ieno, 2014) and smoothing function for the interaction between NAO and Habitat Preference. Closely related species sharing a common ancestry may respond similarly to changes in weather conditions (Valimäki, Lindén, & Lehikoinen, 2016). Hence, to account for phylogenetic relatedness between some of the species included in the analysis, we ran one model with a nested random effect (species within subfamily) and another model with species as the only random effect (Fraixedas, Lehikoinen, & Lindén, 2015; Valimäki et al., 2016). The simpler model had lower AIC, and thus, we continued with the analysis with the model that included only species in the random part. In addition, to account for

temporal autocorrelation, we included an autoregressive term in the model (Pavón-Jordán et al., 2015).

$$\text{AnnualNEness}_{j,t} \sim f(\text{NAO}_t): \text{Habitat Preference}_j + \text{Habitat Preference}_j + \text{NEness} + \text{MeanLat}_j \\ \text{Species}_j \sim N(0, \sigma^2) \quad (3)$$

where AnnualNEness_{j,t} is the distance between the population centroid in year (winter) *t* and *t*–1 of species *j*, and *j* = 1, ..., 25. NAO_{*t*} represents the winter weather conditions during *t*. Habitat Preference_{*j*} is a categorical variable with three levels (deep water, shallow water or inland waters/farmland) indicating the main habitat exploited by species *j*. NEness is the autoregressive (AR) term that accounts for temporal autocorrelation (it represents the 1-year lagged northeast-ness). MeanLat_{*j*} is a continuous variable that accounts for potential differences between species with different wintering ranges. The smoothing function is applied to the interaction between NAO and Habitat Preference to test whether the relationship between NAO and AnnualNEness_{*j*} changes between species having different habitat requirements. Species_{*j*} is the random intercept, which is assumed to be normally distributed with mean of zero and variance σ^2 .

We also built the “long-term trend” model to investigate the long-term north-eastward shift in the population centroid over the study period and the impact of the NAO on such trend. We used the LongNEness as our continuous response variable. We fitted a GAMM with Gaussian distribution (Zuur et al., 2014) and used species as a random term. The mathematical notation for this model is

$$\text{LongNEness}_{j,t} \sim f(\text{Period}_t): \text{Habitat Preference}_j + \text{Habitat Preference}_j + f(\text{NAO}_t) \\ \text{Species}_j \sim N(0, \sigma^2) \quad (4)$$

where LongNEness_{j,t} is the distance between the location in the population centroid in period *t* and that of period 1 of species *j*, and *j* = 1, ..., 25. Habitat Preference is a categorical variable with three levels indicating whether species *j* exploits deep-waters, shallow waters or inland waters/farmland. The interaction between smoothing function period and the Habitat Preference of species *j* is denoted by (Period)_{*t*}: Habitat Preference_{*j*}. The smoothing function on the NAO main effect is denoted by *f*(NAO_{*t*}). Species_{*j*} is the random intercept, which is assumed to be normally distributed with mean of zero and variance σ^2 .

In order to estimate the overall effect of NAO on the inter-annual variation in AnnualNEness of the 25 species together, we ran the model in Equation 3 without the interaction. Accordingly, we also ran the model in Equation 4 without the interaction to assess the overall trend in the LongNEness of all 25 waterbird species (see Supporting information Appendix S1).

All continuous covariates included in these models were standardized in order to make all coefficients comparable by subtracting the mean and dividing by the standard deviation (Zuur et al., 2014). In addition, we looked for patterns in the residuals of our models to assess potential spatial and temporal autocorrelation following Zuur et al. (2014). Results of the correlogram and the autocorrelation function suggested low spatial and temporal autocorrelation, hence, introducing little bias in our results (see Supporting information

TABLE 1 Results of the “short-term effect” model (GAMM), where annual change in the population centroid (Annual Northeasterness) of 25 waterbird species in terms of northeasterness is explained by the interaction of the smoothing function of NAO and Habitat Preference (deep-water, shallow water or farmland), and mean wintering latitude of species

Smoother	Edf	F	p	
Winter NAO × Habitat: Deep	2.504	10.187	<0.001	
Winter NAO × Habitat: Shallow	2.304	16.004	<0.001	
Winter NAO × Habitat: Farmland	1	16.25	0.092	
Parametric coefficients	Estimate	SE	t	p
Intercept	82.972	74.449	1.114	0.266
Habitat: Shallow	-14.858	10.242	-1.451	0.147
Habitat: Farmland	4.313	11.619	0.371	0.711
Mean Latitude	-83.249	81.017	-1.028	0.305
NEness Lagged	-47.106	4.474	-10.528	<0.001

Notes. “NEness Lagged” is the autoregressive term accounting for temporal autocorrelation. Continuous covariates are standardized (subtracted the mean and divided by the standard deviation; Zuur et al., 2014). *F* denotes the results of the *F* test, and *Edf* indicates the effective degrees of freedom of the smoothers. In the section of *parametric coefficients*, *t* denotes the results of the *t* test. Statistically significant estimates are shown in bold (*p*).

Appendix S1). Lastly, we assessed whether the statistically significant smoothers of the interaction between habitat and NAO (see Equation 3) statistically differ from each other following the methodology described in Rose, Yang, Turner, and Simpson (2012). All analyses were carried out using the function `gamm` from the package “mgcv” (Wood, 2011) in R 3.3.2 (R Core Team 2015).

3 | RESULTS

3.1 | Inter-annual variation in the population centroid

Our analysis showed a significant nonlinear association between the inter-annual movement in the overall population centroid of waterbirds’ winter abundance and the winter NAO index (Supporting information Appendix S2: Figure S1, Supporting information Appendix S2: Table S3). A movement in the overall population centroid towards the south-west relative to the preceding winter was associated with harsh winters, characterized by negative NAO index values. Moreover, the distance shifted southwestwards relative to the preceding year increased with greater winter harshness (i.e., negative NAO index values of greatest magnitude). Year-to-year shifts northeastwards in the overall population centroid were associated with mild winters, characterized by positive or slightly negative NAO values. However, in contrast with harsh winters, the distance the centroid shifted northeastwards relative to the preceding year in mild winters was not closely related to the magnitude of the NAO index (Supporting information Appendix S2: Figure S1).

Most interestingly, the relationship between the northeastwards shift of the population centroid and the NAO differed between species exploiting different habitats (Table 1, Figure 2). While the inter-annual movement of the population centroid was associated with changes in the NAO in shallow- and deep-water species, that of species exploiting farmland was not correlated with NAO during our

study period (Figure 2). Furthermore, we also found differences in the relationship between the NAO and the shifts between shallow- and deep-water species, especially in mild winters with high NAO index (Supporting information Appendix S2: Figure S2). At positive NAO index values, the north-eastward shift of the shallow-water species’ population centroid increased with increasing NAO (right panel in Figure 2, Supporting information Appendix S2: Figure S2). However, the magnitude (distance) of the shift of the deep-water species’ population centroid remained constant at positive NAO values (left panel in Figure 2). A north-eastward shift in the population centroid of deep-water species could be associated with mean or negative values of the NAO index (left panel in Figure 2), whereas that of shallow-water species was only linked to positive NAO (right panel in Figure 2).

Our results hence suggested that south-westward shifts of the population centroids of shallow- and deep-water species are associated with harsh winters (negative NAO index values) and that the increase in the distance shifted southwestwards increased with increasingly negative NAO index values (Figure 2). In addition, shifts were negatively associated with those in the preceding winter as depicted by the statistically significant effect of the autoregressive term. There were no statistically significant associations between species mean wintering latitude and centroid shifts.

3.2 | Long-term trends in the population centroid

The results from the model with only the main effects (i.e., no interaction term; Supporting information Appendix S1) revealed an overall long-term curvilinear trend in the movement in the population centroid of the 25 species considered in this study (Supporting information Appendix S2: Figure S3, Supporting information Appendix S2: Table S4). Specifically, a northeastwards shift in the overall population centroid only occurred during the mid-2000s (period 6 in Supporting information Appendix S2: Figure S3).

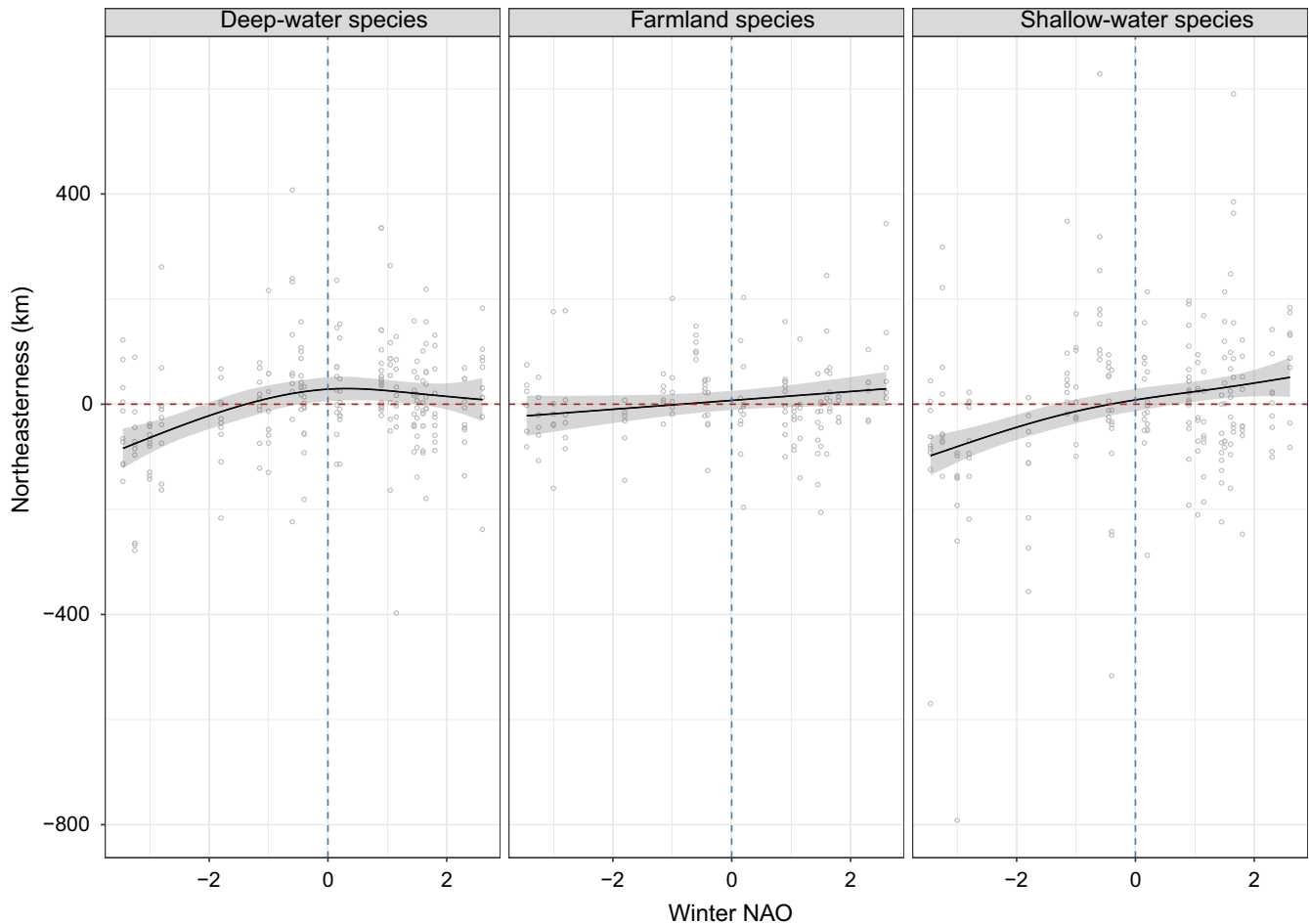


FIGURE 2 Results of the “short-term” GAMM (solid line). Smoothed inter-annual changes in the population centroid (mean latitude and longitude weighted by count) of species exploiting different habitats in response to changes in weather conditions (winter NAO): deep-water habitats (left panel), inland waters and farmland (central panel), and shallow-water habitats (right panel). Statistically significant smoother for species exploiting deep and shallow waters ($p < 0.001$) and not significant for species exploiting inland waters and farmland are shown (see also Table 1). The horizontal dashed line shows the northeasterliness = 0 (i.e., no inter-annual shift in the population centroid). Values above the dashed line represent movement northeastwards and those below the dashed line represent movement southwestwards. The vertical dashed line represents mean winter conditions (NAO index = 0; see Hurrell, 1995 for the description of the index). The 95% confidence interval is represented by the shaded area

The “long-term trend” GAMM also showed pronounced differences in the shifts between the groups of species exploiting different habitats (Figure 3, Table 2). The population centroid of deep-water species steadily shifted northeastwards since the 1990s (period 2; left panel in Figure 3) but levelled off in the 2010s (periods 7 and 8; left panel in Figure 3). The population centroid of shallow-water species showed a significant parabolic long-term trend. Despite showing an overall northeastwards shift during the 1990s and the early 2000s (corresponding to the first four periods; right panel in Figure 3) and southwestwards thereafter (periods 5 to 8, Figure 3), the overall location of the population centroid did not differ from that at the beginning of the study (confidence interval overlaps 0; Figure 3). Farmland species showed no significant long-term trend (central panel in Figure 3). Results also showed that the largest northeastwards shifts relative to the location at the beginning of the study period (i.e., period 1; 1990–1992) occurred in periods with the highest mean

winter NAO index (i.e., warm periods; Supporting information Appendix S2: Figure S4).

4 | DISCUSSION

Like other species showing distributional changes in response to environmental change at different spatial scales (Parmesan, 2006; Thomas et al., 2012; Valimäki et al., 2016), our results provide strong evidence of the link between large-scale winter weather conditions (using the NAO index as a proxy) and the spatial distribution of abundances of 25 wintering waterbird species across 21 European countries. Firstly, we showed that the inter-annual differences in the location of the population centroid of these species correlated with winter conditions in Europe, but differed between groups of species exploiting different habitats. Secondly, we found contrasting long-term trends in the population centroids of groups

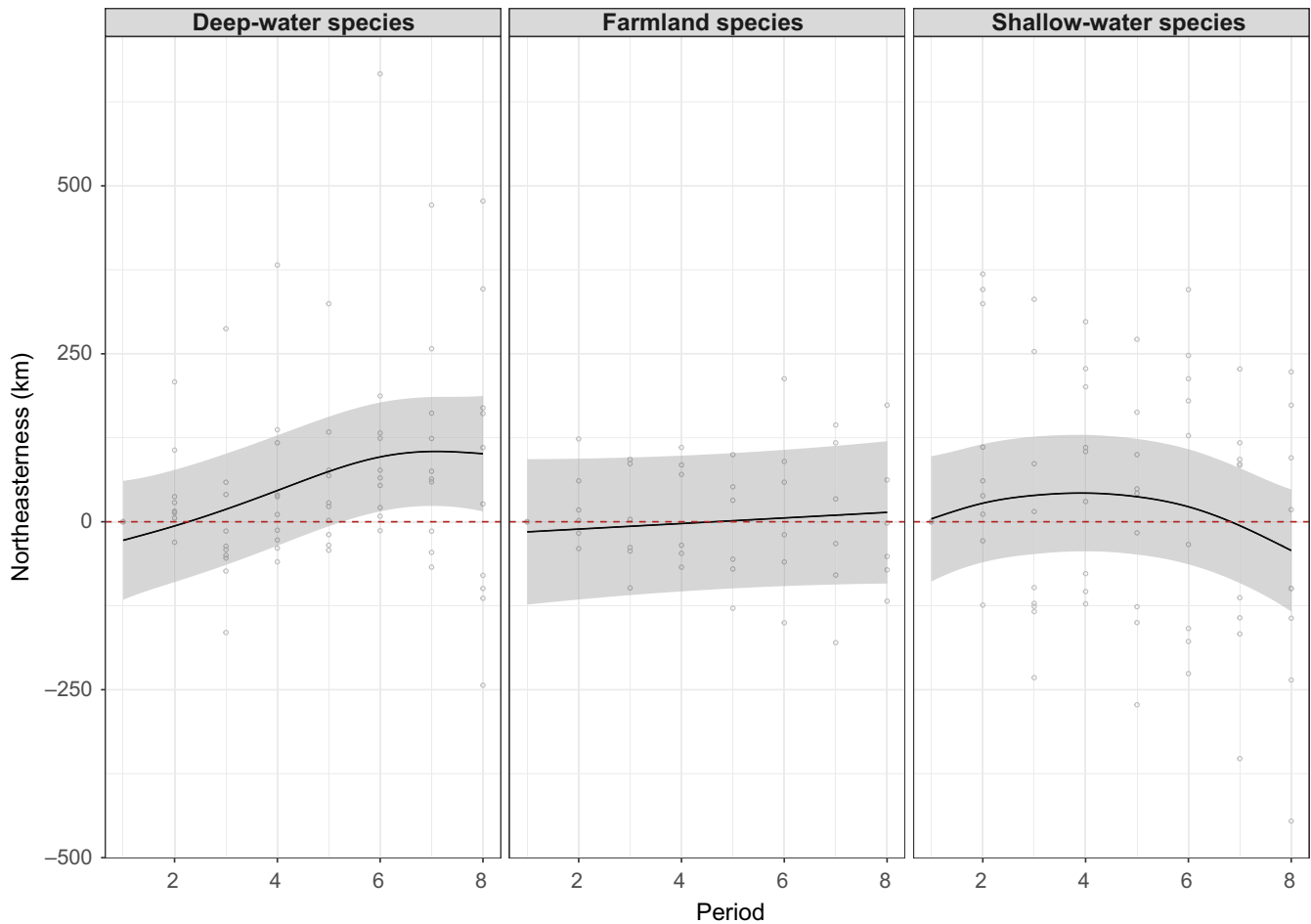


FIGURE 3 Results of the “long-term trend” GAMM (solid line). Smoothed long-term trend in the location of the population centroid (mean latitude and longitude weighted by count) relative to period 1 of groups of species exploiting different habitats: deep-water habitats (left panel), inland waters and farmland (central panel), and shallow-water habitats (right panel). Northeasterness (y-axis) indicates the difference between the location of the population centroid in each period relative to the initial period (i.e., period = 1) over time. Periods (x-axis) correspond to the 3-year groups: years 1990–1992 (period 1), 1993–1995 (period 2), 1996–1998 (period 3), 1999–2001 (period 4), 2002–2004 (period 5), 2005–2007 (period 6), 2008–2010 (period 7) and 2011–2013 (period 8). The horizontal dashed line shows the northeasterness = 0 (i.e., same location relative to period 1). Dots above the dashed line represent population centroids situated towards the north-east relative to period 1. Those below the dashed line represent movement southwestwards. The 95% confidence interval is represented by the shaded area

of species exploiting different habitats, associated with long-term changes in general climatic conditions (3-year average of the winter NAO index).

4.1 | Inter-annual variation in the population centroid

In general, year-to-year northeastwards and southwestwards movements of waterbirds’ population centroid seem to be associated with fluctuations in large-scale winter weather conditions, as characterized by the NAO index. Northeastwards shifts relative to the preceding winter of the overall distributional abundance of the 25 species considered in this study were generally associated with positive (high) NAO index. However, these were already evident during relatively colder winter weather conditions, characterized by negative NAO index values (Supporting information Appendix

S2; Figure S1). Despite this general pattern, the link between the variation in NAO and the inter-annual change in the relative abundance of waterbirds differed depending on the preferred habitats of the species.

The relative abundance of deep-water species shifted northeastwards relative to the preceding year associated with NAO index values ranging from negative but close to zero (i.e., relatively cold winters in northern Europe) to positive values (i.e., warm and wet winters in northern Europe and dry conditions in southern Europe; see Hurrell & Deser, 2010). The magnitude (distance) of the northeastward shift increased as the NAO index changed from a negative to a positive phase (i.e., to more favourable winter conditions for waterbirds in northern Europe and detrimental conditions in the Mediterranean area) but remained relatively constant in winters characterized by positive NAO index values. Southwestwards shifts were associated with years with negative (low) NAO index and

TABLE 2 Results of the “Long-term trend” model (GAMM), where long-term change in the population centroid (long-term northeasterliness) is explained by the interaction of the smoothing function of Period and Habitat Preference (deep-water, shallow water or farmland), and NAO

Smoother	Edf	F	p	
Period × Habitat: Deep	2.302	10.654	<0.001	
Period × Habitat: Shallow	2.447	3.505	0.02	
Period × Habitat: Farmland	1	0.314	0.576	
Winter NAO	1.611	10.141	<0.001	
Parametric coefficients	Estimate	SE	t	p
Intercept	58.310	39.401	1.480	0.141
Habitat: Shallow	-35.432	57.248	-0.619	0.537
Habitat: Farmland	-51.596	64.341	-0.802	0.424

Notes. Period, which is a continuous covariates, is standardized (subtracted the mean and divided by the standard deviation; Zuur et al., 2014). *F* denotes the results of the *F* test, and *edf* indicates the effective degrees of freedom of the smoothers. In the section of *parametric coefficients*, *t* denotes the results of the *t* test. Statistically significant estimates are shown in bold (*p*).

the distance shifted southwestwards increased as the NAO index decreased.

Shallow-water species also shifted southwestwards associated with negative NAO index values. However, in contrast to deep-water species, northeastwards shifts were only apparent in years characterized by a positive NAO phase. Moreover, shallow-water species differed from deep-water species in that the distance shifted northeastwards relative to the preceding year increased with increasing NAO index and did not level off (Appendix S2: Figure S2).

The different response to increasing NAO index showed by the different group of species, especially in winters with high NAO (Supporting information Appendix S2: Figure S2), may be related to the direct impact of weather conditions on individuals (e.g., thermoregulatory cost) in synergy with indirect effects on habitat and food availability (Dalby et al., 2013). Shallow-water species typically have more northern and eastern breeding distributions (which are not suitable for waterbirds during winter) compared to deep-water species (Wernham et al., 2002). Many deep-water species, in contrast, breed in central Europe, where relatively modest amelioration in winter weather conditions (increasing NAO) can enable suitable wintering habitat to persist, allowing deep-water species to winter closer to their breeding grounds (Musilová, Musil, Zouhar, & Adam, 2018). However, further increases in NAO make little further difference to habitat availability and hence do not contribute to further distributional shifts to the north and east. On the other hand, shallow-water species tend to winter further south and west than deep-water species, far further from their breeding grounds (Wernham et al., 2002, Wetlands International 2017). The more northern and eastern breeding distribution of shallow-water species together with their typically more southern and western wintering areas means the potential for north-easterly shifts in the winter population centroid is greater than it is for deep-water species, which could explain their larger response to milder conditions, especially in winters characterized by high NAO.

The tendency of shallow-water species to winter further south and west of the zero degree isotherm than do deep-water species is probably associated with their respective habitat preference and food resources. While deep-water habitats may remain ice-free during winter offering the possibility for individuals exploiting such habitat to find sufficient food resources closer to the breeding grounds, shallow-water habitats are the earliest to be denied at subzero temperatures (Ridgill & Fox, 1990). Moreover, for shallow-water feeders such as the shoveler, their freshwater zooplankton prey populations can only renew themselves at temperature waters above 10°C, and, for the wigeon, which grazes short grassland adjacent to shallow water, net growth of greenswards begins above 3°C (Dalby et al., 2013 and references therein). In contrast, for deep-water species' feeding on fish and bivalves, such food resources remain available in colder conditions as long as waters remain ice-free (conditions which may persist even well below subzero air temperatures, Waldeck & Larsson, 2013). Hence, it seems also logical that shifts in deep-water species may be apparent at lower NAO index values than would be the case for shallow-water species.

As expected, we also found that the population centroid of shallow-water and deep-water species moved southwestwards in winters characterized by low NAO. During such harsh winters, large numbers of individuals of these species that traditionally winter around the Baltic Sea and the North Sea undertake cold weather movements due to the absence of suitable habitat to forage, causing the population centroid to shift southwestwards (Fox et al., 2016b; Pavón-Jordán et al., 2015; Ridgill & Fox, 1990).

We did not detect any link between the winter NAO and the shift in the population centroid of goose and swan species that exploit farmland habitats. Previous studies at smaller spatial scales have shown that the wintering distribution of the Greylag goose is undergoing change in response to changing weather conditions (Podhrázský et al., 2016; Ramo et al., 2015). However, our results suggest that this is not the general response of other species with similar life-history and ecological traits (after accounting for phylogenetic relatedness)

such as *Branta*, *Cygnus* and other *Anser* species (considered as farmland species in this study, see Supporting information Appendix S2: Table S1). Almost ad libitum food resources (e.g., fields of intensive grassland and cereal production) close to safe roosting sites in traditional core wintering areas permit large aggregations of these species occur in winter in areas of a suitable climatic template (Fox & Abraham, 2017). It is thus not surprising that the shift of marginal wintering numbers (compared to the core wintering areas) from sites at the edges of the distribution does not significantly contribute to a shift in the population centroid of these species (Fox et al., 2016b). Such over-winter environmental conditions, coupled with large population increases (Fox & Abraham, 2017) and the strong family bounds that are characteristic of these species and reinforce winter site fidelity (Owen & Black, 1990), may partly explain the weak association between north-eastern shift in the population centroid and the winter NAO found in this study (but see Ramo et al., 2015; Clausen et al., 2018). Nevertheless, our result suggests a positive, but not statistically significant (at the 5% level), linear relationship between northeastwards shifts of farmland species and NAO.

4.2 | Long-term trend in the population centroid

One of the main consequences of ongoing climate change is the poleward shift of species' distributions as their optimal climatic conditions no longer characterize their former geographical range and/or new suitable habitat becomes available under the new climatic conditions (Amano et al., 2016; Araújo et al., 2011; Parmesan, 2006; Thomas et al., 2012). Here, we show a modest long-term northeastwards shift in the overall population centroid of 25 waterbird species during the mid-2000s (period 6).

The nature of this shift differed between species with different habitat requirements. Wintering numbers of deep-water species have progressively increased in north-eastern Europe since the 1990s compared to other regions in Europe, causing a steady shift northeastwards in the population centroid. This shift, however, ceased in the 2010s (periods 7 and 8), suggesting that the relative winter abundance in north-eastern regions did not increase further compared to other regions across Europe. This pattern is strongly linked to the long-term decadal climatic conditions experienced in the 1990s and the 2000s. The 1990s was a decade of predominantly high NAO (mild winter conditions), especially in the first half of the 1990s (Hurrell & Deser, 2010) allowing deep-water species to exploit newly available wintering sites in north-eastern Europe (see Fox et al., 2015; Guillemain et al., 2013; Lehikoinen et al., 2013; Pavón-Jordán et al., 2015). However, since the late-1990s, the variability in winter weather condition has increased (Hurrell & Deser, 2010), especially following the mid-2000s when record minimum NAO values were registered. Interestingly, the cessation of the rapid increase in deep-water species' relative abundance in north-eastern regions compared to other regions in Europe coincided with this period of greater winter weather instability, which included some very cold winters (Taws, Marsh, Wells, & Hirschi, 2011; Hanna et al., 2015; the mean NAO index for the last two periods of our study, 2008–2013,

was -0.22). Correspondingly, shallow-water species also showed a northeastwards shift during the 1990s and early 2000s (periods 1 to 4), which match the period of milder weather conditions (Hurrell & Deser, 2010). After this period, and coinciding with the period of colder winters, the population centroid shifted southwestwards, which suggests such conditions have contributed to the resumption of more conservative patterns of winter distribution for both sets of species.

There is, thus, strong evidence of the link between winter severity and long-term changes in distributional abundances in the past decades. This, coupled with the increase in winter mildness (and continuation of a positive phase in NAO) predicted under many climate change scenarios (Visbeck, Hurrell, Polvani, & Cullen, 2001; Intergovernmental Panel on Climate Change (IPCC), 2012), suggests that full shifts of wintering ranges (sensu Elmer et al., 2014) of many waterbird species are likely to occur in the future. However, our results also suggest that shifts may not be driven solely by weather conditions but will occur in synergy with ecological and life-history traits (Dalby et al., 2013; MacLean & Beissinger, 2017; Møller et al., 2017), changes in species wintering habitats (e.g., restoration of wetlands and novel food sources due to invasive species) and in relation to species breeding distributions.

4.3 | Conservation and management implications of distributional abundance shifts

Our findings highlight the need to maintain a comprehensive network of protected areas throughout species' entire potential wintering distributions. On one hand, the availability of new wintering areas in the northern Baltic Sea (previously rendered inaccessible by ice cover three decades ago, when the network of protected areas was established in that region) requires major reassessment, because some of these sites may become internationally important for certain waterbird species (Lehikoinen et al., 2013; Johnston et al., 2013; Pavón-Jordán et al., 2015; see also Guillemain & Hearn, 2017). We found that large numbers of individuals, especially of shallow-water species, may adapt wintering sites at the north-eastern edge of their wintering distribution, causing large increases in the local abundance on these sites. This should be taken into account in future planning and management of the protected area network for each of the populations (Guillemain & Hearn, 2017). On the other hand, despite the long-term tendency shown here that some species are shifting their range northeastwards, the responsiveness of some waterbirds to inter-annual changes in winter weather conditions continues to make traditional wintering sites in the south-western part of the range of high conservation importance as "cold weather refuges" (Dalby et al., 2013; Guillemain, Mondain-Monval, Johnson, & Simon, 2005; Koffijberg, van Winden, & Clausen, 2013; Pavón-Jordán et al., 2015; Ridgill & Fox, 1990). Furthermore, the predicted increasing trend in winter mildness (Hanna et al., 2015; Visbeck et al., 2001), stochasticity and frequency of extreme events (European Environment Agency (EEA), 2012, Intergovernmental Panel on Climate Change (IPCC), 2012) may result in an increased inter-annual variation in the local

abundance of wintering waterbirds within Europe, which reinforces the need to maintain a cohesive and comprehensive site-safeguard network throughout the entire flyway.

The contrasting changes in distributional abundances between waterbird species with different habitat requirements may contribute to significant changes in community composition in the short- and long-term. While species interactions do not seem to be the main driver of changes in the distribution of abundances at large spatial scales, they could have important consequences for the functioning of ecosystems at smaller scales. This signals the need for further analyses to assess the effectiveness of the current protected areas network to accommodate these changes (Fox et al., 2015; Guillemain & Hearn, 2017; Guillemain et al., 2013; Johnston et al., 2015). Here, we showed that the population centroid of some waterbird species can shift more than 100 km in some years. This may appear modest compared to the geographical scale of this study but suggests that dramatic changes in relative abundances may be occurring at the edges of the range, while the vast majority wintering in the central part of the range may not be responding so strongly (see also Fox et al., 2016b).

4.4 | Monitoring and detection of distributional abundance shifts

Extensive monitoring schemes are critical to detect shifts in distributional abundance and to be able to adapt conservation and management interventions to these changing circumstances. The IWC maintains very effective extensive site coverage and because we analysed data from 21 countries, covering a large proportion of the main wintering areas within Europe, we believe that the patterns presented here reflect realistic responses shown by most waterbird species considered in this study. However, it is the case that by counting birds on wetlands, the IWC does not cover some populations (such as geese) very effectively. Geese typically leave wetlands to feed on agricultural fields (Fox & Abraham, 2017), which are not counted by the IWC, and hence, important numbers of geese might be missed during the counts. This, coupled with very rapid population increases in the last four decades, may partly explain the lack of statistical significance of the large-scale distributional changes linked to changes in weather conditions among species favouring field foraging, which have been shown to be currently ongoing in Europe (Podhrázký et al., 2016; Ramo et al., 2015).

Furthermore, differences between local breeding population dynamics across Europe may interfere with our ability to detect shifts in the population centroid and core wintering range. For example, in species with large breeding distributions, higher productivity of populations breeding in southern Europe (which most likely winter around their breeding areas) may mask the overall tendency of more migratory individuals (breeding at higher latitudes) to winter at the north-eastern part of the wintering range. This may even result in a shift southwards of the overall species population centroid, unrelated to weather, if the differences in trends in local breeding populations across the entire range are large enough. Future research

should focus also on assessing the effect of different population trends on the direction and the speed at which species shift their distributional abundance.

In conclusion, we here provide evidence of two complementary processes with important ecological and conservation implications; the inter-annual and the long-term northeastwards shift in the population centroid of waterbird species. We believe that these differences in the response to changes in weather conditions must be taken into consideration when developing targeted conservation actions and management plans. For example, while the future well-being of some species may rely on the maintenance of good cold weather refuges throughout the flyway, the protection of new wintering sites in north-eastern Europe may be critical for other species adjusting their wintering distribution to ongoing climate change (see also Guillemain & Hearn, 2017). These findings constitute a firm basis for a re-analysis of the effectiveness of the EU site-safeguard network in the context of varying responses of waterbirds to climate change and for providing a better advice to allocate conservation resources and to propose new evidence-based conservation measures (Fox et al., 2016a; Guillemain & Hearn, 2017; Johnston et al., 2015; Mawdsley, 2011; Stroud et al., 2004).

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DATA ACCESSIBILITY

The waterbird count data used in this study were provided by Wetlands International, coordinator of the International Waterbird Census (IWC), with the approval of all national coordinators of the countries included in this study. These data are available upon request from <https://www.wetlands.org/>. NAO data are freely available to download from <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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