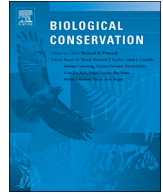




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Positive impacts of important bird and biodiversity areas on wintering waterbirds under changing temperatures throughout Europe and North Africa



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ABSTRACT

Migratory waterbirds require an effectively conserved cohesive network of wetland areas throughout their range and life-cycle. Under rapid climate change, protected area (PA) networks need to be able to accommodate climate-driven range shifts in wildlife if they are to continue to be effective in the future. Thus, we investigated geographical variation in the relationship between local temperature anomaly and the abundance of 61 waterbird species during the wintering season across Europe and North Africa during 1990–2015. We also compared the spatio-temporal effects on abundance of sites designated as PAs, Important Bird and Biodiversity Areas (IBAs), both, or neither designation (Unlisted). Waterbird abundance was positively correlated with temperature anomaly, with this pattern being strongest towards north and east Europe. Waterbird abundance was higher inside IBAs, whether they were legally protected or not. Trends in waterbird abundance were also consistently more positive inside both protected and unprotected IBAs across the whole study region, and were positive in Unlisted wetlands in southwestern Europe and North Africa. These results suggest that IBAs are important sites for wintering waterbirds, but also that populations are shifting to unprotected wetlands (some of which are IBAs). Such IBAs may therefore represent robust candidate sites to expand the network of legally protected wetlands under climate change in north-eastern Europe. These results underscore the need for monitoring to understand how the effectiveness of site networks is changing under climate change.

1. Introduction

The all-pervasive and continuous transformation of ecosystems by humans has caused extensive habitat loss and degradation, exacerbated in recent decades by rapid climate change, which have dramatically increased the extinction risk of many species globally (Parmesan and Yohe, 2003; Pimm et al., 2006). Many different taxa have already responded to climate change by, for example, altering phenology (Amano et al., 2010; Knudsen et al., 2011) and/or distributions (Amano et al., 2014; Chen et al., 2011; Stephens et al., 2016). As a result, our ability to maintain current levels of biodiversity largely relies on conservation interventions (Jones et al., 2018; Pimm et al., 2014), especially through the expansion and targeted management of protected areas (PA) (Araújo et al., 2011; CBD, 2010; Pouzols et al., 2014).

Under the prevailing dynamics of increasingly rapid environmental changes, conservation strategies must be under constant review to ensure that they continue to conserve biodiversity in the long-term (Alagador et al., 2014; Araújo et al., 2011; Hermoso et al., 2017). The Aichi Targets of the Strategic Plan for Biodiversity 2011–2020 (CBD, 2010) and Sustainable Development Goal 15 (SDG, 2018) require the regular, systematic assessment of the adequacy of international networks of PAs (Alagador et al., 2014; Mawdsley, 2011; Orlikowska et al., 2016). Given ongoing climate change-driven changes in the abundance and range of many species, there is debate about the effectiveness of protected area networks to conserve the species (and habitats) that they are designated to conserve (Hole et al., 2009; Johnston et al., 2013; Thomas et al., 2012). For instance, range shifts might push wintering birds into regions where the protected area network might not provide comprehensive protection (Alagador et al., 2014; Mawdsley, 2011; Pavón-Jordán et al., 2015; Virkkala and Rajasärkkä, 2011). It is therefore vital to investigate how species have responded to recent changes in climatic conditions within and outside the protected area

network as a basis for developing effective strategies to meet the challenges of future climate change (Hole et al., 2009; Johnston et al., 2013; Pavón-Jordán et al., 2015).

Previous assessments of the effectiveness of protected area networks showed that breeding populations of bird species listed on Annex I of the Birds Directive (i.e. species in need of protection) were more likely to show more positive population trends than non-Annex I species in EU15 countries (i.e. old member states) after the implementation of the Directive (Donald et al., 2007). Moreover, Annex I species showed more positive trends in EU15 compared to non-EU15 countries (Donald et al., 2007), and in new member states compared to non-member states (Koschová et al., 2018). Gaget et al. (2020) also showed that the implementation of the Ramsar Convention as a conservation tool yielded positive benefits among wintering waterbird populations in the Maghreb region but not elsewhere in the Mediterranean region, depending on the extent to which the provisions of the Convention were implemented in each country. In addition, Amano et al. (2018) showed that the effectiveness of conservation interventions was strongly correlated to a country's governance, so wintering waterbird abundance only increased with increasing conservation effort (e.g. increasing area protected) in those countries with highly effective governance and not in countries with less effective governance. Hence, the degree of protection/management at each site throughout the network of protected areas coupled with the allocation of the limited funds to species and regions that are not of highest global priority (Hermoso et al., 2017) is a major factor affecting the delivery of optimal conservation outcomes.

It thus seems that while protected areas represent a successful mechanism to deliver biodiversity conservation, the concept can still benefit from a more evidence-based allocation of resources. Kukkala et al. (2016) showed that a relatively small expansion of the EU Birds Directive Special Protection Area (SPA) network would increase its effectiveness (from ca. 20% to 41% bird species represented within

SPAs). This would likely have wider taxa benefits if already identified Important Bird and Biodiversity Areas (IBAs) would be designated as protected areas because they also host relatively high numbers of amphibians, reptiles and mammals per unit area of land (Kukkala et al., 2016). This is especially the case if undertaken as part of an internationally coordinated, better-targeted expansion and redesign of the network to take account of current and predicted future climate and environmental change (Butchart et al., 2015; Guillemain and Hearn, 2017; Hermoso et al., 2017; Virkkala and Rajasärkkä, 2007).

IBAs are sites of international significance for the conservation of birds and other biodiversity; over 13,000 sites have been identified to date worldwide (Donald et al., 2018; Waliczky et al., 2019), although identification as an IBA does not imply formal designation as a PA. Nearly three quarters of all IBAs (72.7%) at least partially include areas protected by some mechanism, and 22.0% are completely protected (> 98% by area). On average, 49.3% of the area of all IBAs fall within PAs (Butchart et al., 2012; Waliczky et al., 2019). Nearly half of all identified IBAs (ca. 6,000) are inland wetland and coastal areas (Donald et al., 2018), underlining their critical importance and unique biodiversity (MEA, 2005; MWO, 2012), which also provide particular ecosystem functions and services (Gleason et al., 2011; Zedler and Kercher, 2005). However, wetlands continue to suffer the highest loss and degradation rate of all ecosystems (Amano et al., 2018; Zedler and Kercher, 2005). This is driven mainly by anthropogenic factors, such as pollution (Dudgeon et al., 2006; Gardner et al., 2015), climate change (Bellisario et al., 2014; Moss et al., 2011; Steen et al., 2016), and land-use change (Urban and Roehm, 2018; van Asselen et al., 2013).

Here, we aim to quantify spatio-temporal changes in migratory waterbird abundance under climate change, and assess the role of existing networks of PAs and IBAs in accommodating such changes. To achieve this, we first analyse a 26-year dataset on waterbird counts – the International Waterbird Census (IWC) – during the non-breeding (hereafter, ‘wintering’) season across Europe (including Turkey) and North Africa (Fig. 1). The impact of increasing winter temperatures on waterbirds and wetlands may differ geographically (e.g. droughts in southern Europe but mild and wet winters in northern Europe; Field et al., 2012; see also Hurrell, 1995). Thus, we first test the hypothesis that (i) the abundance of waterbirds increases with increasing winter temperature in wetlands located towards the north and east of species’ wintering ranges (‘cold edges’ in Europe) and decreases in wetlands located towards the south and west (‘warm edges’; Fox et al., 2016; Fox et al., 2019; Pavón-Jordán et al., 2019). Second, we investigate the

spatio-temporal dynamics of waterbird abundance in relation to four levels of wetland importance and protection by testing the hypothesis that (ii) wetlands identified as IBAs that also have legal protection (hereafter ‘IBA-PA’) accommodate the greatest waterbird abundance and show more positive long-term trends. According to this hypothesis, these are followed by wetlands designated as PA but not listed as IBA (hereafter ‘PA-only’), wetlands identified as IBA but not designated as PA (hereafter ‘IBA-only’), and lastly by wetlands that are neither an IBA nor a PA (hereafter ‘Unlisted’ wetland). We make the assumption here that (a) PAs are managed for biodiversity conservation, receiving management interventions to benefit waterbirds occurring within them and thus experience reduced threats from non-climate stressors. We also assume (b) that IBAs hold the largest concentrations of waterbirds, representing the most important sites for these species (Donald et al., 2018), many of which are managed for conservation even if not formally protected (Waliczky et al., 2019). We hypothesise that (iii) IBA-PA wetlands in north and east Europe will show most rapid increases in wintering abundance, being most attractive to species shifting their wintering distribution (Hiley et al., 2013; Thomas et al., 2012), followed by PA-only, IBA-only, and Unlisted wetlands. In addition, IBA-PA and PA-only wetlands situated towards the south and west will show less negative long-term trends than IBA-only wetlands as the legal protection and management plans should mitigate adverse drivers of population change. Lastly, we investigate the adequacy of IBAs as a guide to select important wetlands for potential expansion of the network of protected areas by comparing the trends in waterbird abundance in IBA-only wetlands with that in other wetland categories.

2. Materials and methods

2.1. Waterbird abundance data

We analysed a long-term dataset on site-based waterbird abundances spanning 26 years (1990–2015), part of the International Waterbird Census (IWC; Delany, 2005) coordinated by Wetlands International (www.wetlands.org). The IWC is carried out in winter (generally during mid-January) in over 100 countries worldwide. The data consist of site-specific counts of individuals (i.e. abundance) of all waterbird species during a single visit per winter. The IWC monitoring scheme aims to cover the entire range of natural and man-made wetland types available for wintering waterbirds (e.g. coastline, coastal marshes, inner lakes, rivers, fish ponds, reservoirs) as well as protected

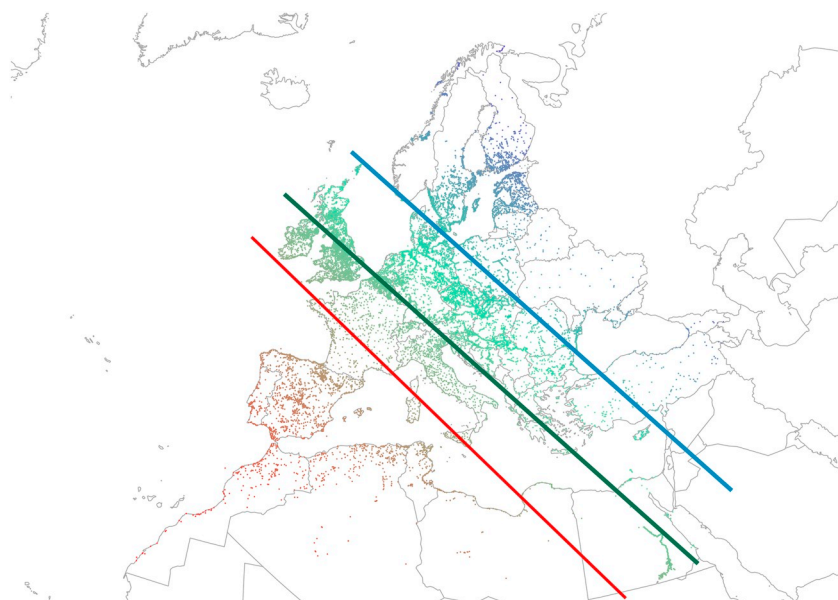


Fig. 1. All International Waterbird Census (IWC) sites ($n = 27,201$) surveyed at least once during 1990–2015 across Europe and North Africa. Northeasterliness. The colour gradient shows the northeasterliness values of each sites, ranging from -5.6 (red) to 3.8 (blue). The three solid lines denote northeasterliness values of -1 (red), 0 (green), and 1 (blue) corresponding to the southwestern (SW), central (C) and northeastern part of the study region, respectively. Northeasterliness is standardized to zero mean and one standard deviation (SD) prior running the models and thus 0 corresponds to the centre of the region, $+1$ SD to areas located towards the northern and eastern region, and -1 SD indicates wetlands located towards the southern and western region.

and unprotected (see also Fig. A1). In this analysis, we consider the 61 most common species of waterbirds reported in the IWC (see Table A1 for the complete list of species) that regularly winter within the two main flyways in the western Palearctic: The Atlantic flyway and the Black Sea–Mediterranean flyway (Nagy and Langendoen, 2018). We excluded all gull species as several countries do not report these species within the IWC monitoring scheme. During the 26-year study period, an aggregate total of more than 487 million individuals were recorded at 27,201 sites in 41 countries across Europe (including Turkey) and North Africa (Fig. 1).

2.2. Protected areas & Important Bird and Biodiversity Areas (IBAs)

We classified all the IWC sites into four categories based on their overlap with the polygons of PAs and IBAs: 1) *Unlisted Wetland* (IWC sites that do not overlap with a PA or an IBA), 2) *IBA-only* (IWC sites that fall inside wetlands identified as IBAs that is not formally designated as PA), 3) *PA-only* (IWC sites that fall inside wetlands designated under national or international legislation, which are not identified as IBAs), and 4) *IBA-PA sites* (IWC sites that fall in a wetland that is both listed as IBA and designated as PA). In order to assign one of the four above-mentioned categories to each IWC site, we made a 100 m buffer around each IWC site and then assess whether such buffer intersected with the IBAs and PAs polygons. All PAs established before 2014 were considered in the study and their polygons were downloaded from the World Database on Protected Areas (UNEP-WCMC et al., 2018; accessed October 2017). The polygons of IBAs were obtained from BirdLife International (2017; updated to September 2017. Available at <http://datazone.birdlife.org/site/requestgis>). The spatial overlap (intersection) between IWC sites and PAs and/or IBAs was assessed in ArcGIS ESRI© (version 10.3). Incorporating a buffer of 100 m instead of running a direct intersect between the IWC location and designated sites was deemed most conservative in light of possible inaccuracies in the coordinates of the IWC sites.

2.3. Northeasterliness

Because most waterbirds considered here migrate from wintering quarters back to their breeding areas along a southwest-northeast axis, we quantified “northeasterliness” to investigate the variation in the trends in wintering abundance throughout Europe and North Africa (Pavón-Jordán et al., 2019, see also Table A1). Northeasterliness represents the location of an IWC site relative to all the other sites along a southwest – northeast gradient in our entire study region. The Coordinate Reference System (CRS) used here is the European Terrestrial Reference System 1989 (ETRS89/LAEA; epsg:3035), in meter units. Northeasterliness was calculated as follows:

$$\text{Northeasterliness}_i = \frac{\text{Northing}_i - \text{MinN}}{\text{MaxN} - \text{MinN}} + \frac{\text{Easting}_i - \text{MinE}}{\text{MaxE} - \text{MinE}} \quad (1)$$

where $\text{Northeasterliness}_i$ is a continuous covariate representing the northeasterliness score of the IWC site i . Northing_i and Easting_i are the coordinates (epgs: 3035) of site i . MinN and MaxN denote the minimum and maximum northing coordinates found in the dataset, respectively. Similarly, MinE and MaxE denote the minimum and maximum easting coordinate, respectively. Higher values of northeasterliness occur towards northern and eastern Europe whereas lower northeasterliness values occur in western and southern Europe as well as northern Africa (Fig. 1).

2.4. Temperature data

In order to investigate the link between changes in site abundances and those in local temperature, we downloaded monthly temperature (CRUTEM4) at 0.5×0.5 degrees grid resolution from the Climate Research Unit of the University of East Anglia (Osborn and Jones,

2014). Because waterbirds are able to change wintering site depending on the weather conditions experienced during autumn migration and early winter (Pavón-Jordán et al., 2019; Ridgill and Fox, 1990), we calculated an average early winter temperature (November–January) for each year in each grid. This average value was transformed into a *temperature anomaly* in each grid–year by subtracting the grid mean temperature during the entire study period from each year’s temperature value. The motivation for this was two-fold. First, we were interested in the link between changes in waterbird abundance and changes in temperature (rather than actual values of temperature, and, second, we wanted to reduce the high degree of collinearity between the absolute values of temperature and northeasterliness. Lastly, we assigned the local (grid) temperature anomaly value to all IWC sites falling within each grid.

2.5. Statistical analysis

Using count data models assuming Poisson or Negative Binomial was impossible for computing capacity reasons and the very high values of some counts (up to 300,000 individuals). We instead used a Gaussian distribution after log-transformation of our data (i.e. $\log(\text{Abundance} + 1)$). This Gaussian Linear Mixed Model (Zuur et al., 2009) was built using the package ‘*glmmTMB*’ (Magnusson et al., 2017) in R 3.6.1 (R Core Team, 2018). The fixed covariates included in the model were *temperature anomaly* (continuous covariate), *northeasterliness* (continuous), *year* (continuous; to estimate the temporal trend), and *site category* (categorical with four levels: IBA-PA, IBA-only, PA-only, Unlisted Wetland). In addition, we included a second order polynomial term for *year* (year^2) to explore potential non-linear (quadratic) trends in abundance. We also entered the two-way interaction terms *temperature anomaly* \times *northeasterliness*, *site category* \times ($\text{year} + \text{year}^2$), *site category* \times *northeasterliness*, and *northeasterliness* \times ($\text{year} + \text{year}^2$) and the three-way interaction term ($\text{year} + \text{year}^2$) \times *northeasterliness* \times *site category*. All continuous covariates were standardized to zero mean and one standard deviation (SD) prior the analysis. Lastly, to account for the dependency between observation of the same species and from the same site we included *species* and *site* as crossed random effects (Zuur et al., 2009). The generic mathematical notation of the model is:

$$\begin{aligned} \text{LogAbundance}_{i,j,s} \sim & \text{Temperature Anomaly}_{1,j} + \text{Northeasterliness}_j \\ & + \text{Site Category}_j + \text{Year}_i + \text{Year}_i^2 + \text{Site Category}_j \times (\text{Year}_i + \text{Year}_i^2) \\ & + \text{Site Category}_j \times \text{Northeasterliness}_j + \text{Northeasterliness}_j \\ & \times (\text{Year}_i + \text{Year}_i^2) + \text{Northeasterliness}_j \times \text{Temperature Anomaly}_{1,j} \\ & + (\text{Year}_i + \text{Year}_i^2) \times \text{Northeasterliness}_j \times \text{Site Category}_j + \text{Species}_s \\ & + \text{Site}_j \\ \text{Species}_s \sim & N(0, \sigma_s^2), \text{Site}_j \sim N(0, \sigma_j^2) \end{aligned} \quad (2)$$

where $\text{LogAbundance}_{i,j,s}$ is the i th observation in site j , and $j = 1, \dots, 27,201$ and Species_s and Site_j are the random effects, which are assumed to be normally distributed with mean zero and variance σ_s^2 and σ_j^2 , respectively.

To assess potential bias in the estimates due to spatial autocorrelation, we ran spatial correlograms based on the model residuals (Zuur et al., 2009). Correlograms showed low to moderate spatial autocorrelation (Fig. A2) and, thus, we used this model for further inference. To investigate potential differences in the estimated trends between the four site categories across a species wintering range, we carried out a post-hoc analysis of the three-way interaction at three values of northeasterliness using the functions *emttrends*, *emmeans*, and *contrast* from the ‘*emmeans*’ package (Lenth, 2019). Thus, we compared the estimated marginal means (EMM) and trends among the four site categories at northeasterliness values of -1 , 0 and 1 , which represent sites located in the south-western part of our study region (from France, Sicily and Libya; hereafter SW), central Europe (hereafter C), and north and eastern Europe (hereafter NE)(note that northeasterliness is

standardized to zero mean and one SD). Likewise, we also performed a post-hoc analysis of EMMs to investigate differences in the relationship between individual wetland waterbird abundance and the local temperature anomaly across these three regions.

3. Results

3.1. Changes in local abundance in relation to local temperature

Our results showed that annual changes in the abundance of wintering waterbirds across Europe and North Africa in the past 26 years were positively correlated with changes in temperature anomalies, as depicted by local temperature anomalies (Table 1 Line 2). The association between site abundance and local temperature anomalies varied spatially, being most positive towards NE regions (statistically significant interaction *temperature anomaly* × *northeasterliness*; Table 1 L20, Fig. 2, Table A2). The post-hoc estimation of the effects (slopes) of this interactions showed that local abundance of wintering waterbirds increased with increasing local temperature anomaly (95% CI do not overlap with zero), with this effect being almost ten times larger in the NE than in the SW part of the study region (Fig. 2, Table A2).

3.2. Abundance and trends in relation to PAs, IBAs, and Unlisted Wetlands

The significant three-way interaction [(*Year + Year*²) × *Northeasterliness* × *Site Category*], suggested that the abundance of waterbirds in the four wetland categories varied across time and space in a predominantly non-linear way (Table 1 L21–26, Fig. 3). Overall, the abundance of wintering waterbirds was highest at IBA-PA and IBA-only wetlands during 1990–2015 (Table 1 L4 & L5, Fig. 3), especially in the central and north-eastern part of the study region (Table A3). PA-only wetlands hosted higher abundances than Unlisted wetlands during the 1990s, but this situation reverted at the end of the study period, especially in the SW part of the region (Table A3). The estimated (linear and quadratic) trends across the four wetland categories (post-hoc analysis) revealed statistically significant (CI not overlapping with zero) increasing trends in abundance in IBA-only, IBA-PA and Unlisted wetlands at the SW part of the study region but not in PA-only wetlands (linear trend in Table A4; see also Fig. 3). Moreover, pairwise comparisons (*contrasts*) of the estimated trends in winter waterbird abundance across the four site categories showed significantly more positive linear trends in IBA-PA and Unlisted wetlands than in IBA-only (comparison of linear trends in Table A5). However, in the SW part of the study region, the quadratic trends in abundance were similar in all four wetland categories (non-significant pairwise comparison of quadratic trends in Table A5).

A similar quadratic pattern was found at the C and NE part of the study region, with increasing trends in wintering abundance mainly from the 1990s until the mid-2000s (Fig. 3, Table A4, Table A5). However, at the NE the increasing trend in wintering numbers inside IBA-PAs continued throughout the entire study period (Fig. 3, Table A4, Table A5). Moreover, unlike in the SW region, the quadratic trend at the NE was more negative in IBA-only and Unlisted wetlands (i.e. unprotected) than in IBA-PA and PA-only wetlands (i.e. legally protected), reflecting that individuals wintering outside the network of protected areas may have a higher sensitivity to adverse drivers of abundance trends (Tables A4 & A5).

4. Discussion

We here provide evidence of the positive association between the overall local abundance of waterbirds during the wintering season and variation in local winter temperature over the past 26 years in more than 27,000 wetlands across Europe and North Africa. Furthermore, we show that the long-term trend in the winter abundance across the studied region differs spatially within species' wintering ranges and

between four wetland categories of protection level.

4.1. Temperature-driven changes in species' abundance

Here, we demonstrated that, at an individual wetland level, the overall abundance of waterbirds is linked to temperature anomalies at the local scale (0.5 × 0.5 degrees grid cells). Our results also showed that the relationship between variation in local winter temperature (i.e. temperature anomaly) and changes in species' local winter abundance differed geographically over the period 1990–2015. These findings are in line with previous studies that have shown the link between increasing winter temperature or North Atlantic Oscillation index and increasing abundance of wintering waterbirds in the northern part of their distribution and declines in the southern edge (Fox et al., 2016; A. Lehikoinen et al., 2013; Pavón-Jordán et al., 2015; Pavón-Jordán et al., 2019). In general, overall waterbird abundance increased with increasing local temperature anomaly. However, this relationship varied across Europe and North Africa, showing the strongest association in wetlands situated in NE Europe. We found the lowest abundance of waterbirds in the NE during cold winters, compared to the C and SW regions. However, the abundance of waterbirds wintering in the NE

Table 1

Results of the Gaussian Linear Mixed Model (eqn 2) fitted to the International Waterbird Census (IWC) data. The overall abundance of 61 waterbird species ($\log(\text{abundance} + 1)$) was modelled as a function of the environmental covariates shown in this table. Continuous covariates (i.e. 'Temperature Anomaly', 'Year', and 'Northeasterliness') are standardized (zero mean and one standard deviation). 'Site Category' is a categorical variable with four levels: 1) not an IBA nor protected area (i.e. Unlisted wetland) as the baseline category, 2) IBA-only, 3) PA-only, and 4) IBA-PA (see methods section for further details on these categories). SE, Z and P are the standard error, Z-statistic and the associated P-value, respectively (significance level, $\alpha = 0.05$). The column 'Line' is a running number to facilitate understanding with Results section.

Line	Variables	Estimate	SE	Z	P
1	Intercept	0.8567	0.0965	8.87	< 0.001
2	Temperature Anomaly	0.0352	0.0011	33.1	< 0.001
3	Northeasterliness	-0.0514	0.0061	-8.48	< 0.001
4	Site Category (IBA-only)	0.2735	0.0258	10.58	< 0.001
5	Site Category (IBA-PA)	0.2831	0.0198	14.25	< 0.001
6	Site Category (PA-only)	0.0302	0.0289	1.05	0.2955
7	Year	0.0974	0.0013	72.58	< 0.001
8	Year ²	-0.0504	0.0014	-34.85	< 0.001
9	Site Category (IBA-only) x Year	-0.0437	0.0046	-9.45	< 0.001
10	Site Category (IBA-PA) x Year	-0.0369	0.0034	-10.91	< 0.001
11	Site Category (PA-only) x Year	-0.0773	0.0057	-13.19	< 0.001
12	Site Category (IBA-only) x Year ²	0.0047	0.0052	0.91	0.3647
13	Site Category (IBA-PA) x Year ²	0.0335	0.0037	9.02	< 0.001
14	Site Category (PA-only) x Year ²	0.0300	0.0063	4.72	< 0.001
15	Northeasterliness x Site Category (IBA-only)	0.1479	0.0188	7.85	< 0.001
16	Northeasterliness x Site Category (IBA-PA)	0.0698	0.0174	4	< 0.001
17	Northeasterliness x Site Category (PA-only)	0.0694	0.0276	2.51	0.012
18	Northeasterliness x Year	-0.0241	0.0014	-16.82	< 0.001
19	Northeasterliness x Year ²	0.0036	0.0015	2.37	0.0179
20	Temperature Anomaly x Northeasterliness	0.0268	0.0010	25.85	< 0.001
21	Northeasterliness x Site Category (IBA-only) x Year	0.0160	0.0034	4.69	< 0.001
22	Northeasterliness x Site Category (IBA-PA) x Year	-0.0021	0.0032	-0.66	0.5075
23	Northeasterliness x Site Category (PA-only) x Year	0.0343	0.0059	5.74	< 0.001
24	Northeasterliness x Site Category (IBA-only) x Year ²	-0.0018	0.0038	-0.47	0.638
25	Northeasterliness x Site Category (IBA-PA) x Year ²	0.0200	0.0035	5.63	< 0.001
26	Northeasterliness x Site Category (PA-only) x Year ²	-0.0009	0.0066	-0.14	0.89

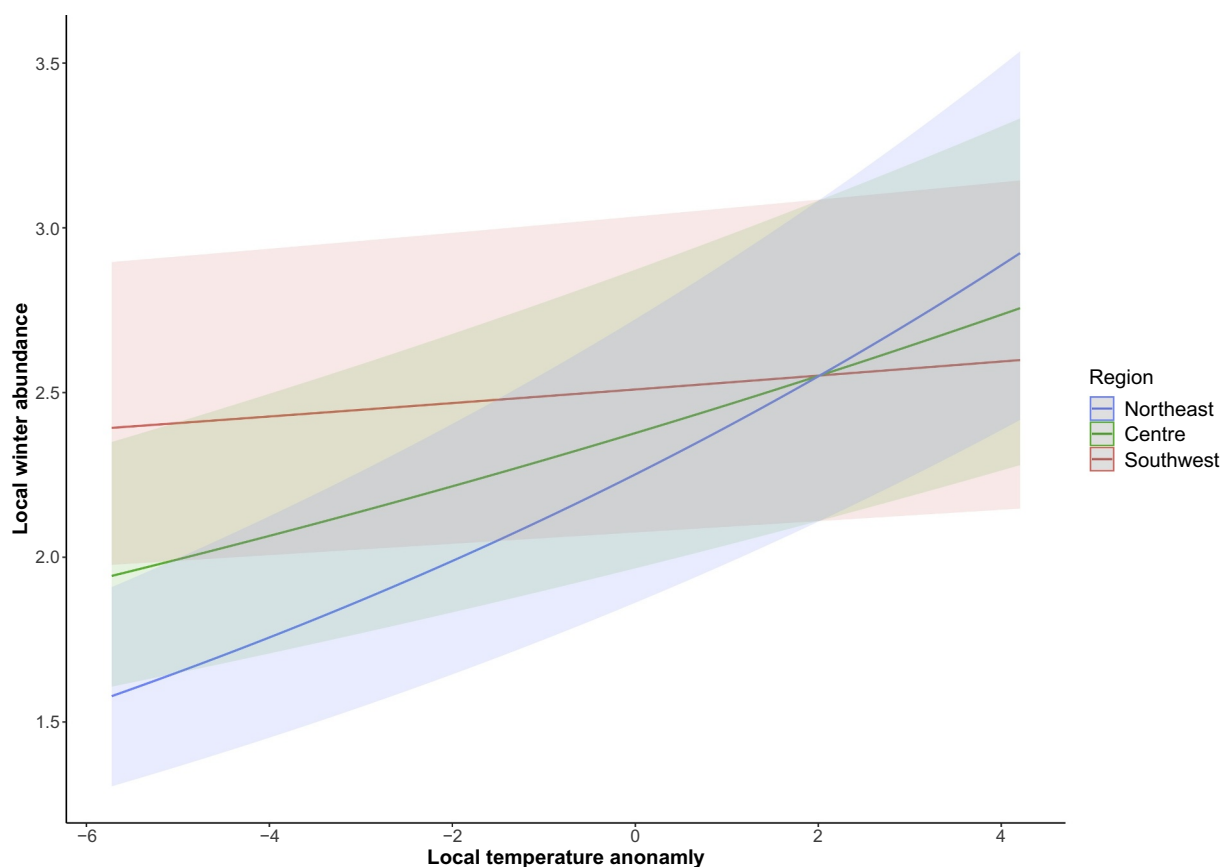


Fig. 2. Link between the local abundance (y-axis) and the local temperature anomaly (x-axis) at the 0.5×0.5 degrees grid cells where the wetland is located. Lines represent the predicted local abundance of waterbirds calculated from the back-transformed model estimates at northeasterliness values of -1 (red), 0 (green), $+1$ (blue), corresponding to the southwestern areas, the centre, and the northeastern parts of the study region (see also matching colours in Fig. 2).

increased most rapidly with increasing temperature anomaly. At the other extreme, the abundance of wintering waterbirds on wetlands situated in the SW were least influenced by temperature anomalies.

Such a spatial pattern could be partly related to the larger variability in winter weather conditions in NE Europe, compared to southern Europe and North Africa. For example, during severe winters, northern and eastern regions in Europe are almost inhospitable to wintering waterbirds, when all wetlands are frozen (Guillemain and Hearn, 2017; Musilová et al., 2018a). During such severe winters, birds completely desert these regions to relocate where climatic conditions are more favourable farther south, and those individuals attempting to winter at higher latitudes likely suffer high mortality (Ridgill and Fox, 1990). In contrast, during mild winters, greater numbers of ice-free wetlands are available towards NE Europe, and Russia, allowing short-stopping (*sensu* Elmberg et al., 2014) individuals to overwinter closer to their breeding grounds (Clausen et al., 2018; A. Lehtikoinen et al., 2013; Podhrázký et al., 2017). These mild conditions can boost local waterbird abundance in NE Europe (Pavón-Jordán et al., 2019). This reported pattern might also partly reflect changes in mortality rates, with decreased survival in severe winters happening prior to the counts in January (Pavón-Jordán et al., 2017).

This finding carries important implications for conservation: increasing winter temperatures in northern and eastern Europe may drive increasing waterbird abundances there (either by shifting individuals or reduced mortality). These regions, and the wetlands therein, will thus require greater attention from the monitoring schemes (Fox et al., 2019) and the community of conservation practitioners and decision makers to create effective and cohesive site safeguard network (see also Guillemain and Hearn, 2017).

4.2. Spatio-temporal variation in waterbird abundance across four types of wetlands

We found that IBA-PA (i.e. those IBAs that are also partially or fully covered by protected areas) and IBA-only (i.e. those IBAs that are not covered by protected areas) wetlands supported the greatest number of wintering waterbirds throughout Europe and North Africa in the past 26 years, especially in C and NE Europe. This finding was expected given that the IBA criteria include thresholds based on the abundance of aggregative species such as waterbirds (Donald et al., 2018), and many PAs may have been designated on the basis of the waterbird populations that they support (Gleason et al., 2011; Green and Elmberg, 2014; Stroud et al., 2004). Unlisted wetlands (not identified as IBA nor formally designated as PA) hosted the lowest abundance of wintering waterbirds in the early-1990s throughout the study region. However, at the end of the study period, these unlisted sites accommodated higher abundance than PA-only and similar to IBA-only wetlands in the SW region.

The spatio-temporal analysis of changes in waterbird abundance across Europe and North Africa revealed important differences between the four types of wetlands considered in our study. In general, we found non-linear (quadratic) trends in waterbird winter abundance across the study region in all wetlands but in PA-only, where there was no significant trend during 1990–2015. The lack of a trend in wintering numbers in PA-only wetlands was unexpected and could be related to the fact that many of these wetlands might have reached their carrying capacity, while other sites have recovered from adverse effects of past pressures (Marion and Bergerot, 2018; Méndez et al., 2018). This finding suggests that PA-only wetland sites have remained important for waterbirds for the past three decades irrespective of ongoing

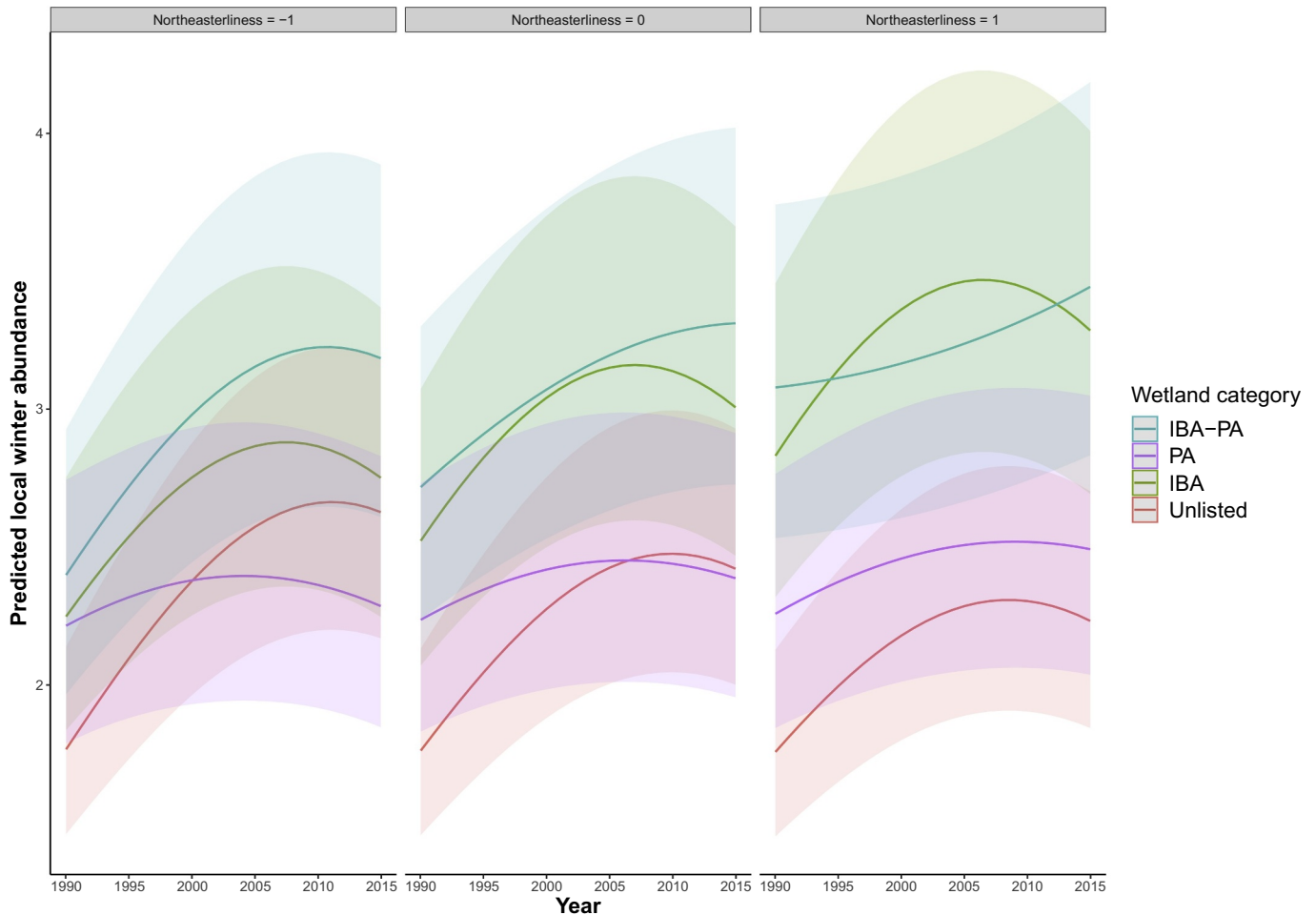


Fig. 3. Predicted winter local waterbird abundance in each wetland category from the model at northeasterness values of -1 , 0 , and $+1$, corresponding to the south and western region (left panel), the centre (central panel), and the north and eastern region (right panel), respectively (see also Fig. 1). The four wetland categories (x-axis) are: *Unlisted* (IWC sites that do not overlap with a PA or an Important Bird and Biodiversity Area (IBA)), *IBA* (IWC sites that fall inside wetlands identified by Birdlife International as IBA) that are not formally designated as a protected area), *PA* (IWC sites that fall inside a legally protected wetland, which are not identified as IBAs), and *IBAPA* (IWC sites that fall in a wetland that is both listed as IBA and designated as protected area). The 95% Confidence Interval (CI) of each trend estimate is represented by the shaded areas.

environmental and climate change, and across the whole study region considered. In addition, it is worth noting that Unlisted wetlands hosted, on average, higher abundance of waterbirds than PA-only wetlands at the end of the study period at the SW region. Possible explanations for this could be that such PAs (i) have reached carrying capacity and ‘spill-over’ effects explain the increasing trends in Unlisted wetlands (Méndez et al., 2018), (ii) are located in landscapes/habitats that are currently sub-optimal for some waterbird species in terms of food, shelter, and competition for resources, compared to newly available wintering areas (Guillemain and Hearn, 2017; Pavón-Jordán et al., 2015; Ramo et al., 2013), and/or (iii) are designated for taxa other than waterbirds, or for reasons other than waterbirds (e.g. for aesthetic or recreational values).

We found that trends inside Unlisted wetlands, IBAs, and IBA-PAs were predominantly non-linear across the entire region, increasing from 1990 to the mid-2000s and levelling-off thereafter. IBAs, and especially IBA-PAs, hosted higher abundances of wintering waterbirds compared to PA-only and Unlisted Wetlands. This outstanding performance of IBAs and IBA-PAs in comparison to PA-only and Unlisted Wetlands is especially prominent in the C and NE regions. These findings suggest that the ecological value of wetlands identified as IBAs has remained high throughout the past 26 years. From a conservation perspective, this finding also highlights the urgency to monitor and

eventually legally protect currently identified IBAs, as they are vulnerable to human-driven development.

Interestingly, we also found that the trend inside IBA-PAs in the NE region did not level-off in the mid-2000s but continued increasing throughout the entire study period. This finding has important relevance for future conservation planning because we also found the highest correlation between wintering waterbird abundance and winter temperature anomaly in the NE region, where winter temperature anomaly is increasing most rapidly, compared to the rest of the continent (Osborn and Jones, 2014). Our findings show that wetlands identified as IBAs that are also classified as PAs (IBA-PAs), not only host a greater abundance of wintering waterbirds, but also have the capacity to accommodate increasing wintering numbers, compared to other type of wetlands. We assume that number of wetlands included in each category to be constant over our study period (we do not include e.g. date of designation in the models). We therefore believe that the steady increase in wintering numbers inside IBA-PA in the NE, compared to the levelling off observed in the other wetland categories reflects genuine ecological processes (increased over-winter survival and abundance shift of wintering waterbirds, both possibly associated with consecutive winters with positive temperature anomaly since the 1990s) facilitated by targeted conservation interventions (e.g. designation of IBAs as protected areas).

Conversely, in the SW part of the study region, results indicate that IBA-PAs accommodate the highest abundance of wintering waterbirds among all wetland types. This suggests that waterbirds benefit from the legal protection of these sites potentially because this contributes to conserving their ecological value and reduces disturbance (e.g. from hunting). The increasing overall numbers of wintering waterbirds in unprotected wetlands in the SW is encouraging but it also means that a growing proportion of waterbirds wintering here are exposed to threats (e.g. hunting, low-quality feeding sites, human disturbance, higher predation) without a site-scale mechanism for their mitigation. As we do not investigate species-specific trends, we do not know which species are driving these (see Ramo et al., 2013). Hence, it is vital that periodic monitoring of wetlands outside the network of protected areas and IBAs, such as occurs under the IWC, track trends in these populations to understand which species are involved to anticipate potential future population changes.

Our findings align with previous studies showing that taxa such as birds, butterflies, and other invertebrates use protected areas at their 'cold' edge more often than expected by chance as they colonize new areas (Hiley et al., 2013; P. Lehtikoinen et al., 2019; Thomas et al., 2012). They also highlight that large numbers of waterbirds winter in unprotected IBAs in NE Europe (see also Fox et al., 2015; Pavón-Jordán et al., 2015). Moreover, these studies used data from breeding/summer season, where the variability in habitat availability at the 'cold' margins is lower than during the non-breeding/winter season, partly because site designation has not always kept up with new patterns of mid-winter waterbird distributions. Therefore, our findings add new insights and strengthen the evidence of distribution shifts of species under rapid climate change.

Interestingly, despite the progressive increase in available wetland habitats during winter in northern and eastern Europe as a consequence of a long-term increase in winter temperature (Adam et al., 2015; Fox et al., 2015; Fox et al., 2016; Pavón-Jordán et al., 2019) our findings suggest that waterbirds wintered more often within IBA-PA and IBA wetlands. This is probably due to the higher quality and suitability of IBAs and IBA-PAs for waterbirds compared to Unlisted and PA-only wetlands, although we cannot exclude the fact that this is due to the highly aggregative behaviour of most of these species during the non-breeding season. Moreover, some of these newly accessible wetlands might have been identified as IBAs or designated as PAs due to their importance for other groups and/or in other seasons.

It is worth noting the steep increase in abundance at Unlisted wetlands, especially in the SW region. Due to changes in general winter weather conditions (Hanna et al., 2015; Hurrell and Deser, 2010), some wetlands may have become important for wintering waterbird species in recent years, which were not included in the network of PAs and IBAs (Guillemain and Hearn, 2017; Musilová et al., 2018b). Since we found more similar trends in IBA-PA and IBAs than in Unlisted wetlands, it seems unlikely that the increase in wintering abundance might result from a saturation of some of the already existing IBA-PAs causing spill-over to Unlisted wetlands (Marion and Bergerot, 2018; Méndez et al., 2018). Nevertheless, the increase in the abundance outside protected areas has direct conservation implications. One of the criteria for designation of sites as protected areas under the Ramsar Convention and the EU Birds Directive is the presence of 1% of the biogeographical population of a species of conservation concern (Méndez et al., 2018; Stroud et al., 2004). Hence, some wetlands may gain conservation importance (and qualify for a legally protected area) if the numbers of such species increase due to the shifts while others might no longer qualify as IBA, typically at the SW edge of the distribution (Guillemain and Hearn, 2017; Johnston et al., 2013; Méndez et al., 2018). These wetlands, however, still remain important 'refuges', which are critical in those years with harsh winter weather conditions (Alagador et al., 2014; Mawdsley, 2011; Musilová et al., 2015; Pavón-Jordán et al., 2019).

Regular and comprehensive assessment of the allocation of scarce

resources are critical to the delivery of effective biodiversity conservation in a changing world (Alagador et al., 2014; Hermoso et al., 2017; Pimm et al., 2014). The main goal of this study was to assess general patterns in the overall response of waterbirds to temperature anomalies and different wetland designations. Analysing all waterbird species collectively was a limitation of our study because not all waterbird species respond to temperature anomalies (Pavón-Jordán et al., 2019) or to conservation measures (Gaget et al., 2020; Méndez et al., 2018) in the same manner. Future studies disentangling species-specific contributions to this pattern will allow us to identify appropriate conservation actions. Nevertheless, our findings underscore the importance of long-term wetland monitoring and the need to designate unprotected IBAs as protected areas, where appropriate (Field et al., 2012). This could improve the potential of the PA network to deliver climate change adaptation, prevent future habitat deterioration and maintain high-quality wetlands that are currently vulnerable to human disturbance (Jones et al., 2018; van Asselen et al., 2013). Such action would benefit not only waterbird populations but also all biodiversity associated with wetland ecosystems (Amano et al., 2018; Green and Elmerberg, 2014; Guillemain and Hearn, 2017; Koschová et al., 2018).

CRedit authorship contribution statement

Diego Pavón-Jordán: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing, Investigation. **Web Abdou:** Writing - review & editing, Investigation. **Hichem Azafzaf:** Writing - review & editing, Investigation. **Michal Balaž:** Writing - review & editing, Investigation. **Taulant Bino:** Writing - review & editing, Investigation. **John J. Borg:** Writing - review & editing, Investigation. **Luca Božič:** Writing - review & editing, Investigation. **Stuart H.M. Butchart:** Writing - review & editing, Investigation. **Preben Clausen:** Writing - review & editing, Investigation. **Laimonas Sniuksta:** Writing - review & editing, Investigation. **Mohamed Dakki:** Writing - review & editing, Investigation. **Koen Devos:** Writing - review & editing, Investigation. **Cristi Domsa:** Writing - review & editing, Investigation. **Vitor Encarnação:** Writing - review & editing, Investigation. **Khaled Etayeb:** Writing - review & editing, Investigation. **Sándor Faragó:** Writing - review & editing, Investigation. **Anthony D. Fox:** Writing - review & editing, Investigation. **Teresa Frost:** Writing - review & editing, Investigation. **Clemence Gaudard:** Writing - review & editing, Investigation. **Valeri Georgiev:** Writing - review & editing, Investigation. **Irakli Goratze:** Writing - review & editing, Investigation. **Menno Hornman:** Writing - review & editing, Investigation. **Verena Keller:** Writing - review & editing, Investigation. **Vasilij Kostushyn:** Writing - review & editing, Investigation. **Tom Langendoen:** Writing - review & editing, Investigation. **Łukasz Ławicki:** Writing - review & editing, Investigation. **Christina Ieronymidou:** Writing - review & editing, Investigation. **Lesley J. Lewis:** Writing - review & editing, Investigation. **Svein-Håkon Lorentsen:** Writing - review & editing, Investigation. **Leho Luigujõe:** Writing - review & editing, Investigation. **Włodzimierz Meissner:** Writing - review & editing, Investigation. **Tibor Mikuska:** Writing - review & editing, Investigation. **Blas Molina:** Writing - review & editing, Investigation. **Petr Musil:** Writing - review & editing, Investigation. **Zuzana Musilova:** Writing - review & editing, Investigation. **Szabolcs Nagy:** Writing - review & editing, Investigation. **Viktor Natykanets:** Writing - review & editing, Investigation. **Leif Nilsson:** Writing - review & editing, Investigation. **Jean-Yves Paquet:** Writing - review & editing, Investigation. **Danae Portolou:** Writing - review & editing, Investigation. **Josef Ridzon:** Writing - review & editing, Investigation. **Andrea Santangeli:** Writing - review & editing,

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108549>.

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