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## **Anticipating the effects of climate warming and natural habitat conversion on waterbird communities to address protection gaps**

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## **ABSTRACT**

Thermal adjustment of waterbird communities to climate warming is crucial but hampered by natural habitat conversion, increasing their climatic debt. As it is, in contrast, facilitated in protected areas, assessing the adequacy of the current protected areas network with respect to future climate and land-use changes and identifying priority sites to protect is of major importance. In this study, we assess the thermal adjustment limitations that non-breeding waterbird communities might experience by the end of the 21<sup>st</sup> century in the Mediterranean region to highlight priorities for wetland protection. Priorities were set by combining the exposure of waterbird communities to natural habitat conversion and climate warming with their thermal specialization. The latter was calculated using winter abundance data of 151 species from 2932 sites of the International Waterbird Census in 21 Mediterranean countries. Exposure was assessed using future projections of temperature and land-use under four CMIP6 scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5). We found that strictly protected areas are located in wetlands whose waterbird communities, without protection, would likely experience high limitations in thermal adjustment in the coming decades. This highlights that the location of existing protected areas may effectively support the thermal adjustment of waterbird communities to future climate warming. However, 490 sites considered at risk lack protection, including 32 sites of international importance for waterbirds, stressing the need to strengthen the protected areas network in these sites in priority. Our study provides important guidance for conservation planning in the Mediterranean region to support waterbird responses to climate change.

## **KEYWORDS**

Community thermal adjustment, Conservation planning, International Waterbird Census, Mediterranean region, Ramsar convention, Wetlands

## INTRODUCTION

Many studies have documented how recent climate change, and especially temperature increases, has affected biodiversity in the past decades: alteration of phenologies, shifts of distributions and abundances toward poles and higher elevations, disruption of interactions and modifications of structure and composition of communities (Kappelle et al., 1999; Parmesan, 2006; Root et al., 2003). Developing future scenarios of biodiversity under climate change has also become a central issue in the last decades. However, in many studies with this aim, the future impact of land-use changes on biodiversity through habitat loss and degradation has been overlooked (Santos et al., 2021; Titeux et al., 2016; but see Asamoah et al., 2022 and Newbold, 2018 for instance), although it was the main driver of species declines and extinctions during the past decades and is expected to remain so in the coming years (Caro et al., 2022; IPBES, 2019; Newbold et al., 2015). Therefore, it is crucial to include these two anthropogenic pressures when assessing the future effects of global changes on biodiversity, especially as their effects may interact (Mantyka-pringle et al., 2012).

Protected areas (PAs) can mitigate the effects of climate change, land-use changes and their interaction on biodiversity. Previous studies demonstrated that PAs can facilitate the colonization of new areas by species shifting their distribution poleward (Thomas et al., 2012) and reduce the extinction risk of species at their trailing distribution edge (Lehikoinen et al., 2019; Peach et al., 2019). The effectiveness of PAs in mitigating the effects of climate change on biodiversity is partly attributable to their ability to provide high-quality habitats and reduce other anthropogenic pressures (Thomas and Gillingham, 2015), such as habitat loss and degradation (Geldmann et al., 2013; Leberger et al., 2020). Therefore, it is imperative – although rarely done (but see Verniest et al. [2022]) – to explicitly consider these two anthropogenic pressures by anticipating their future intensity and distribution when

identifying potential new PAs (Heller and Zavaleta, 2009; Pörtner et al., 2021), especially since we will need to designate many new PAs to meet ambitious targets of protecting 30% of land by 2030 within the Kunming-Montreal global biodiversity framework (CBD, 2022).

The conservation of natural wetlands in the Mediterranean region is of major importance as these ecosystems are key to many species and highly threatened by climate and land-use changes (Galewski et al., 2021; MWO-2, 2018; Perennou et al., 2020). Wetlands are among the most threatened ecosystems on the planet, with a loss of 90% of them since 1700 as result of human activities (Convention on Wetlands, 2021; WWF, 2020). In the Mediterranean region, almost half of these ecosystems have been lost since 1970 (MWO-2, 2018) because of anthropogenic pressures such as climate and land-use changes. As these changes are heterogeneously distributed (MWO-2, 2018; Leberger et al., 2020) and expected to remain so and to increase in the coming decades in this region (Drobinski et al., 2020; Malek et al., 2018; MedECC, 2020; Taylor et al., 2021), anticipating future climate and land-use changes is a major issue for spatial conservation planning of Mediterranean wetlands (Taylor et al., 2021). This is especially true given that Mediterranean biodiversity is very sensitive to both these pressures (Newbold et al., 2020), is of exceptional value and highly dependent on wetlands (MWO-2, 2018; Geijzenborffer et al., 2018; Myers et al., 2000), and Mediterranean PAs network suffers important gaps in wetland conservation (Geijzenborffer et al. 2019; Leberger et al., 2020; Popoff et al., 2021).

Identifying waterbird communities that might experience limitations in thermal adjustment to future climate warming can contribute to effective designation of additional PAs in wetlands. Waterbirds are species that are ecologically dependent on wetlands (Ramsar Convention) for at least part of their annual cycle and of which they are a good indicator of the conservation status. Conservation measures, such as protected areas and management measures, contribute to the conservation of waterbird populations at global scale (Amano et

al., 2018; Wauchope et al., 2022) and in the Mediterranean region (Gaget et al., 2020b; Kleijn et al., 2014) by mitigating the impacts of the anthropogenic pressures they face, such as climate change (Gaget et al., 2018; 2020b). Waterbirds have been extensively monitored for decades through the International Waterbird Census (IWC) (Delany, 2005) to inform many international conservation policies (*e.g.*, Ramsar Convention, Convention on Migratory Species, Barcelona Convention, and European Union Directives, such as Birds, Water Framework and Marine Strategy Directives). The IWC data also provided invaluable knowledge to conservation biology (*e.g.*, Amano et al., 2018; Johnston et al., 2013; Wauchope et al., 2022). Using IWC data, Gaget et al. (2020a) found that thermal adjustment of wintering waterbird communities in a climate warming context, *i.e.*, changes in community composition in response to climate warming, is mainly driven by thermal specialists, but is prevented by natural habitat conversion. However, PAs were also found to improve communities adjustment to climate warming (Gaget et al., 2021; Pavón-Jordán et al., 2015). Despite the potential importance of these results for conservation planning, they have not yet been used to project the potential adjustment of waterbirds to future temperatures.

In this study, we highlight priorities for wetland protection to improve waterbird responses to climate warming in the Mediterranean region. To this end, we assessed the thermal adjustment limitations that non-breeding waterbird communities (151 species) at 2932 IWC sites in 21 Mediterranean countries might experience by the end of the 21<sup>st</sup> century because of the interacting effect of climate warming and land-use changes. Assuming that waterbird communities can adjust their community composition to climate warming, but that this adjustment is not fast enough to cope with the velocity of the temperature increase (Gaget et al., 2021), and that natural habitat conversion is an additional limit to waterbird community adjustment to climate warming (Gaget et al., 2020a), we investigated whether communities that might experience the greatest thermal adjustment limitations to future climate warming

are protected, with a particular focus on wetlands of international importance for waterbirds. To this end, we applied a trait-based Climate Change Vulnerability Assessment framework (CCVA) (Pacifci et al., 2015), which can be used to prioritize the implementation of spatial conservation measures (Foden et al., 2019), to combine: i) the thermal specialization of waterbird communities derived from species thermal ranges; ii) the exposure of waterbird communities to climate warming; and iii) their exposure to natural habitat conversion. To ensure the robustness of this prioritization, exposure metrics were computed using late 21<sup>st</sup> century (2081 – 2100) projections under four recent scenarios (O’Neill et al., 2016) that have very different spatial patterns of land-use in the Mediterranean region (Verniest et al., 2022). In a context of adaptation to climate change, this study provides spatial prioritization that highlights wetlands of importance for waterbird communities that might be protected to help mitigate the negative impacts of climate warming on waterbirds and expand the Mediterranean protected areas network.

## MATERIAL AND METHODS

### *Waterbirds monitoring*

We used winter abundance data collected from the International Waterbird Census (Delany, 2005) in Mediterranean countries from 2008 to 2017. IWC surveys were conducted once a year in mid-January by professional and skilled volunteers following a standardized survey protocol and coordinated by Wetlands International (<http://www.wetlands.org>). Sites with fewer than 3 surveys during the study period or without climate data were deleted, and species that do not overwinter in Mediterranean countries were excluded to avoid vagrant species (see Appendix S1 for more information on species and site selection). The above-mentioned criteria resulted in a dataset of 151 waterbird species monitored at 2932 sites (average number of surveys per site: 6.0) in 21 countries (Appendix S2). Countries were assigned to four subregions: Balkans, Maghreb, Middle-East and Western Europe (Appendix S2).

We used the most up-to-date spatial database of PAs for Mediterranean countries, *i.e.*, the Mediterranean Wetlands Observatory database, that combines national inventories with multiple international data sources, such as the World Database of Protected Areas (<https://www.protectedplanet.net>), the Common Database on Designated Areas (<https://www.eea.europa.eu>) and Natura 2000 (<https://www.eea.europa.eu>). Half of the sites were considered protected (n = 1526, 52.0%), *i.e.*, their geographical features (point, line or polygon) partially or entirely overlapped a PA. One third of protected sites had an IUCN management category from I to IV (n = 534, 18.2%, hereafter referred to as ‘strictly protected sites’). Protected sites with other IUCN management category (*i.e.*, V or VI) or no IUCN management category were referred to as ‘other protected sites’ (n = 992, 33.8%). Sites that did not overlap a PA were referred to as ‘non-protected sites’ (n = 1406, 48.0%).

We considered 233 sites (7.9%) as of international importance for waterbirds according to the definition of the Ramsar convention (*i.e.*, sites that regularly support one threatened waterbird species, 20,000 waterbirds, or 1% of a population) and based on the results of Popoff et al. (2021).

### *Thermal specialization of waterbird communities*

We evaluated the thermal specialization of waterbirds at the community level (hereafter referred to as ‘Spec<sub>T°</sub>’) from species thermal ranges. For each species, we computed the Species Temperature Range (STR) as the difference between the maximum (90% upper) and the minimum (10% lower) temperatures of its wintering thermal range, which was assessed following Galet et al. (2020a), *i.e.*, using long-term (1950 – 2000) January temperatures across its non-breeding distribution (BirdLife International & HBW, 2017). Therefore, high STR species experience a wide range of winter temperatures while low STR species experience a narrow range of winter temperatures.

For each site survey, we then calculated the Community Temperature Range (CTR), a weighted mean index that informs the average thermal range of species occurring in a community. For a community defined in time and space, the CTR corresponds to the average STR of species within the community weighted by their  $\log(x + 1)$ -transformed abundance (Godet et al., 2011). We computed its inverse to describe the thermal specialization of waterbird communities, *i.e.*, Spec<sub>T°</sub>. Therefore, high Spec<sub>T°</sub> values indicate that the community has a high thermal specialization and that the average thermal range of a community is low. Finally, we calculated site Spec<sub>T°</sub> averaged from site surveys Spec<sub>T°</sub> values.

### *Environmental data*

For both climate and land-use data, we used future projections under four CMIP6 scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) (Eyring et al., 2016) to ensure that the identification of sites for priority protection considers different future pathways. These scenarios combine future socio-economic conditions with radiative forcing levels in 2100 (O'Neill et al., 2016).

Past (2008 – 2017) and future (2081 – 2100) mean temperature in January were extracted from the WorldClim 2.1 dataset (Fick and Hijmans, 2017; past temperature originally from CRU-TS 4.03, Harris et al., 2014). Temperature data was mean-aggregated from a 2.5 arc-minutes resolution to a 15 arc-minutes resolution (approx. 28 x 28 km at the equator) to match land-use data spatial resolution (see below). Following Foden et al. (2019), we used for each scenario the future projections from the eight General Circulation Models (GCMs) available to date in WorldClim 2.1 (Appendix S3), and replicated all processing steps described in the following sections eight times (once per GCM) to assess the potential limitations of waterbird communities in adjusting their composition to future climate warming for each scenario and each GCM.

We extracted past (2012 – 2013, median years of 2008 – 2017) and future (2090, median of 2081 – 2100) proportions of land-use categories from the Land Use Harmonization 2 dataset (Hurt et al., 2020). This dataset provides yearly estimates of the proportion of 12 land-use categories at a 15 arc-minutes spatial resolution.

#### *Exposure of sites to climate warming and natural habitat conversion*

To assess the exposure of surveyed sites to climate warming (hereafter ‘Expo<sub>T</sub>’), we contrasted past temperatures experienced by communities to future temperatures, weighted by past temperature variations. First, we computed the 2008 – 2017 average and standard deviation from the yearly mean temperature in January. Second, we then quantified for each

scenario the differences between past and future temperatures using the Standardized Euclidian Distance as in Williams et al. (2007):

$$ExpOT_i = \sqrt{\frac{(a_i - b_i)^2}{S_i^2}} \quad (1)$$

where  $a_i$  and  $b_i$  are the past and future mean temperatures in January at cell  $i$ , and  $S_i$  is the past standard deviation.

To assess the exposure to natural habitat conversion (hereafter ‘Exp<sub>ONHC</sub>’), we contrasted past and future land-use. We computed the proportion of anthropized habitats by summing the proportion of seven land-use categories: urban land, C3 annual crops, C3 perennial crops, C4 annual crops, C4 perennial crops, C3 nitrogen-fixing crops and managed pasture. Conversely, primary land (forested and non-forested), secondary land (forested and non-forested) and rangeland were considered as natural habitats. The past proportion of anthropized habitats was assessed as the average of years 2012 and 2013, while the future proportion of anthropized habitats was 2090. We then calculated for each scenario Exp<sub>ONHC</sub> as dissimilarities between the two periods at cell  $i$  by subtracting the past to the future proportion of anthropized habitats.

#### *Index of future thermal adjustment limitations*

To assess future thermal adjustment limitations of waterbird communities, we combined their thermal specialization (Spec<sub>T°</sub>) with the two exposure metrics (Exp<sub>OT°</sub> and Exp<sub>ONHC</sub>) using a trait-based vulnerability assessment framework (Pacifci et al., 2015).

Following Huntley et al. (2016), we first converted Exp<sub>ONHC</sub>, Exp<sub>OT°</sub>, and Spec<sub>T°</sub> into three-level ordinal variables (Low, Moderate, High). Because 5% of natural habitat conversion has been shown to prevent community adjustment to climate warming of non-breeding waterbirds in a Mediterranean context (Gaget et al., 2020a), we used a 5% threshold

to convert  $Exp_{ONHC}$  into an ordinal variable: Low: inferior to 0%, Moderate: between 0% and 5%, High: superior to 5%.  $Exp_{T^\circ}$  was converted into an ordinal variable using two quantiles as thresholds (provided in Appendix S4). To account for differences in exposure intensity between scenarios, the two quantiles were calculated from the values of all scenarios. Similarly to  $Exp_{T^\circ}$ , we converted  $Spec_{T^\circ}$  into a three-level ordinal variable using the two quantiles method (Appendix S4).

We then computed an index of future thermal adjustment limitations (hereafter ‘ $Lim_{T^\circ}$  index’) by combining the three ordinal variables using a rule-based logic framework (Table 1). This approach allowed us to account for interactions between the two exposure metrics and  $Spec_{T^\circ}$  (Huntley et al. 2016). Through the combinations used to compute the  $Lim_{T^\circ}$  index, we assumed that natural habitat conversion was the main factor that could limit community adjustment to climate warming (Gaget et al., 2020a), *i.e.*, that  $Exp_{ONHC}$  was the main driver of the  $Lim_{T^\circ}$  index. As the temperature increase can be too fast for the adjustment of waterbird communities to climate warming (Gaget et al. 2021), we also considered that higher  $Exp_{T^\circ}$  values would exacerbate limitations caused by natural habitat conversion in community adjustment to climate warming. Finally, community adjustment to climate warming is mainly driven by thermal specialist species under low natural habitat conversion rates, through the colonization of warm-dwelling specialists and the extirpation of cold-dwelling specialists (Gaget et al., 2020a). Therefore, under low  $Exp_{ONHC}$  conditions, we assumed that communities with high  $Spec_{T^\circ}$  values, *i.e.*, with a higher representation of species with a narrow thermal range than species with a wide thermal range, would adjust to future temperature increase more easily than communities with low  $Spec_{T^\circ}$ . In contrast, thermal specialists and generalists both contribute to the non-significant community adjustment to climate warming in high rates of natural habitat conversion conditions, with the extirpation of thermal specialists and the colonization of thermal generalists regardless of their thermal

affinities (Gaget et al., 2020a). Therefore, under high  $Exp_{NHC}$  conditions, we considered that communities with high  $Spec_{T^{\circ}}$  would not have a more positive thermal adjustment than communities with low  $Spec_{T^{\circ}}$ .

Following Huntley et al. (2016), we assessed the robustness of our findings to variations in the rule-based logic framework presented below (Table 1) by performing all analyses with slightly different combinations of levels (Low, Moderate, High). This sensitivity analysis resulted in very similar results to those presented in the main body of this article and are provided in Appendix S5.

### *Data Analysis*

For each future scenario, we built a multi-model of the  $Lim_{T^{\circ}}$  index by assigning to each site the most frequent  $Lim_{T^{\circ}}$  value (*i.e.*, the mode) across the eight GCMs. In case of a tie, the highest level was assigned. This multi-model was used for the statistical analyses detailed below.

We identified protection priorities by comparing  $Lim_{T^{\circ}}$  index values between site protection statuses (strictly protected, other protected, non-protected), statuses of international importance for waterbirds (internationally important, or not internationally important) and future scenarios. The effect of each variable was assessed separately and in combination with a subregion effect and their interaction to assess differences between subregions. To this end, we used on each individual variable Proportional Odds Logistic Regression models (POLRs) that can be applied to ordinal response variables such as the  $Lim_{T^{\circ}}$  index (Guisan & Harrell, 2000).

Similarly, we compared  $Exp_{OT^{\circ}}$ ,  $Exp_{NHC}$  and  $Spec_{T^{\circ}}$  values between protection statuses, statuses of international importance and future scenarios (only for  $Exp_{OT^{\circ}}$  and  $Exp_{NHC}$ ) using linear models (LMs) in order to explore the potential drivers of differences of the  $Lim_{T^{\circ}}$  index. In addition, to evaluate similarities in spatial patterns of exposure between

scenarios, we assessed the correlation between scenarios for  $\text{Exp}_{\text{OT}^\circ}$  and  $\text{Exp}_{\text{NHC}}$  with a Kendall's rank correlation tests (Kendall, 1948). Finally, we assessed the correlation between  $\text{Exp}_{\text{OT}^\circ}$ ,  $\text{Exp}_{\text{NHC}}$  and  $\text{Spec}_{\text{T}^\circ}$  for each scenario to evaluate similarities in spatial patterns between the three components of the  $\text{Lim}_{\text{T}^\circ}$  index. These analyses were carried out using an average multi-model across the eight GCMs for  $\text{Exp}_{\text{OT}^\circ}$ .

Statistical significance was assessed using 95% confidence intervals for POLR and LMs and was set at  $P < 0.05$  for correlation tests. POLRs were fitted with the *MASS* package (Venables & Ripley, 2002). Statistical analyses were performed using R 4.1.0 (R Core Team, 2021). Geoprocessing operations were performed using QGIS 3.4.15 (QGIS Development Team, 2020) and R 4.1.0 (R Core Team, 2021), mainly with the *sf* (Pebesma, 2018) and *raster* (Hijmans, 2021) packages.

## RESULTS

### *Future thermal adjustment limitations of waterbird communities*

The  $\text{Lim}_{T^{\circ}}$  index was ‘High’ in at least one scenario for more than a third of sites (39.5%,  $n = 1158$ ) and in all scenarios for only 14 sites (0.5%, Figure 1). Values of the  $\text{Lim}_{T^{\circ}}$  index increased with the radiative forcing level of scenarios in Western Europe and the Balkans, except for the SSP3-7.0 scenario for which the index took lower values than in SSP2-4.5 and SSP5-8.5 (Appendices S6 and S7). However, we found very different results for other subregions (Appendices S6 and S7), with, for instance, the lowest values of the  $\text{Lim}_{T^{\circ}}$  index for the Maghreb sites obtained for the SSP5-8.5 scenario. The number of sites with a high  $\text{Lim}_{T^{\circ}}$  index was lowest for SSP5-8.5 (6.6%,  $n = 193$ , Appendices S6 and S8). The variability in  $\text{Lim}_{T^{\circ}}$  index between GCMs was very low in all scenarios (Appendix S9).

### *Future thermal adjustment limitations of waterbird communities at sites of international importance*

The sites of international importance for waterbirds in all subregions had higher values of  $\text{Lim}_{T^{\circ}}$  index than other sites in two scenarios (Appendices S10 and S11). More than half of the sites of international importance ( $n = 131$ , 56.2%) had a ‘High’  $\text{Lim}_{T^{\circ}}$  index in at least one scenario, and most of them were protected (75.6%,  $n = 99$ , Figures 1 and 2). Those that were not protected ( $n = 32$ ) were mostly located in Turkey, the south of the Iberian Peninsula, and the coast of North-West Africa (Figure 2). Only two sites of international importance (0.9%) had a ‘High’  $\text{Lim}_{T^{\circ}}$  index in all scenarios and both were protected (Figure 1): ‘Laghi Como: Garlate: Olginate’ (Italy) and ‘Lago Maggiore’ (Italy).

### *Future thermal adjustment limitations of waterbird communities in protected areas*

The  $\text{Lim}_{\text{T}^{\circ}}$  index was higher for strictly protected sites than non-protected sites in at least three scenarios for all subregions (Appendices S10 and S12). Other protected sites also had also higher values of  $\text{Lim}_{\text{T}^{\circ}}$  index than non-protected sites in at least two scenarios for the Maghreb, the Middle-East and Western Europe (Appendices S10 and S12). Almost half of protected sites (*i.e.*, strictly protected and other protected sites) had a 'High'  $\text{Lim}_{\text{T}^{\circ}}$  index in at least one scenario ( $n = 668$ , 43.8%, Figures 1 and 2). On the other hand, 490 sites whose communities had a high  $\text{Lim}_{\text{T}^{\circ}}$  index in at least one scenario were not protected (42.3%, Figures 1 and 2). A list of these sites is provided as Supplementary Material. More than a third of these sites (40.6%,  $n = 199$ ) were located in the Maghreb and the Middle-East (Figure 2).

### *Exposure of sites to climate warming and natural habitat conversion*

The values of  $\text{Exp}_{\text{OT}^{\circ}}$  were higher (lower) at sites of international importance than at other sites in the Balkans and the Middle-East (Maghreb and Western Europe) in all scenarios (Appendix S13). Sites of international importance had higher  $\text{Exp}_{\text{ONHC}}$  than other sites in three scenarios for Western Europe, but the differences for other subregions were less clear (Appendix S14).  $\text{Exp}_{\text{OT}^{\circ}}$  was overall higher at other protected sites than at non-protected sites except for Maghreb countries (Appendix S15). Strictly protected and other protected sites had overall higher  $\text{Exp}_{\text{ONHC}}$  values than non-protected sites (Appendix S16).

$\text{Exp}_{\text{OT}^{\circ}}$  values increased with the radiative forcing level of scenarios in all subregions and were highest for Maghreb sites (Appendix S17). Surveyed sites had overall lower  $\text{Exp}_{\text{ONHC}}$  values in SSP3-7.0 than in other scenarios and had overall highest values in the Middle-East (Appendix S17). Sites had similar  $\text{Exp}_{\text{OT}^{\circ}}$  spatial patterns between scenarios ( $0.52 < \tau < 0.91$ ,  $P < 0.01$ , Appendix S18) but different  $\text{Exp}_{\text{ONHC}}$  spatial patterns between scenarios ( $0.04 < \tau < 0.25$ ,  $P < 0.01$ , Appendix S18).

$\text{Exp}_{\text{OT}^\circ}$  and  $\text{Exp}_{\text{NHC}}$  were weakly correlated in SSP1-2.6, SSP2-4.5 and SSP3-7.0 (Mean absolute  $\tau = 0.09$ ,  $P < 0.001$ , Appendix S19). In contrast, in SSP5-8.5,  $\text{Exp}_{\text{OT}^\circ}$  and  $\text{Exp}_{\text{NHC}}$  were strongly and negatively correlated ( $\tau = -0.36$ ,  $P < 0.001$ , Appendix S19), suggesting that sites with high  $\text{Exp}_{\text{OT}^\circ}$  have low  $\text{Exp}_{\text{NHC}}$ .

#### *Thermal specialization of waterbird communities*

$\text{Spec}_{\text{OT}^\circ}$  was higher at sites of international importance for waterbirds than at other sites except for Maghreb countries (Appendix S19).  $\text{Spec}_{\text{OT}^\circ}$  was higher at strictly protected sites than at other protected sites and non-protected sites in all subregions (Appendix S20).  $\text{Spec}_{\text{OT}^\circ}$  was higher for Balkans and Maghreb communities than for Western Europe and Middle-East communities (Appendices S21 and S22).

$\text{Spec}_{\text{OT}^\circ}$  and  $\text{Exp}_{\text{OT}^\circ}$  were very weakly correlated in SSP1-2.6 and SSP2-4.5 ( $-0.04 < \tau < -0.03$ ,  $P < 0.01$ , Appendix S19) and were not correlated in SSP3-7.0 and SSP5-8.5.  $\text{Spec}_{\text{OT}^\circ}$  and  $\text{Exp}_{\text{NHC}}$  were very weakly correlated in SSP1-2.6 and SSP5-8.5 ( $-0.06 < \tau < -0.04$ ,  $P < 0.01$ , Appendix S19) and were not correlated in SSP2-4.5 and SSP3-7.0.

## DISCUSSION

In this study, we identified for the first time the wintering waterbird communities that might experience the greatest limitations to adjust to climate warming by the end of the century, and demonstrated that current Mediterranean PAs, and especially strictly PAs, were overall well located to support their thermal adjustment. However, we identified 490 entirely non-protected sites whose communities may experience high limitations in thermal adjustment, including 32 sites of international importance (*sensu* Ramsar Convention). Building on the importance of PAs for future biodiversity conservation in response to both climate warming and natural habitat conversion, our results reinforce the need for PAs designation and acknowledge that decades of wetland conservation efforts are expected to help waterbird responses to climate warming.

### *Thermal adjustment and vulnerability to climate warming*

Our approach presumes that waterbird communities with a better thermal adjustment are less vulnerable to climate warming. Vulnerability to climate change is defined as “the extent to which biodiversity is susceptible to or unable to cope with the adverse effects of climate change” (IPCC, 2007; Foden et al., 2019). As a limited thermal adjustment to warmer conditions could lead to increased climatic debt (Gaget et al., 2021; Soultan et al., 2022), it may be considered as a factor of vulnerability to climate change. Wintering waterbird communities adjust to climate warming by species composition changes mainly through thermal specialist species (*i.e.*, high  $\text{Spec}_T^\circ$  species), with the colonization of communities by warm-dwelling specialists and the extirpation of cold-dwelling specialists from waterbird communities (Gaget et al., 2020a). Therefore, communities with a high proportion of thermal

specialists should adjust better to climate warming, and thus should be less vulnerable, than communities with a high proportion of thermal generalists (*i.e.*, low  $\text{Spec}_{T^\circ}$  species).

However, considering future limitations in community thermal adjustment (*i.e.*,  $\text{Lim}_{T^\circ}$  index) as a proxy of vulnerability to climate warming must be done with great caution as its interpretation and estimation raise questions. Thermal generalist species may not adjust to temperature increases because they may be less sensitive and may have a greater adaptive capacity than thermal specialists, and consequently be less vulnerable to climate warming despite their higher climatic debt. Furthermore, changes in  $\text{Spec}_{T^\circ}$ , a community weighted-mean index, only reflect changes in the relative proportion of specialists and generalists, not their presence, and other mechanisms such as interspecific competition and anthropogenic disturbance can also influence thermal adjustment (Liang et al., 2017). Finally, the spatial resolution (approx. 28 x 28 km at the equator) of the land-use data is very coarse and its very low thematic resolution (12 categories) does not include a definition of wetlands. This results in a large uncertainty on the relationship between natural habitat conversion and the monitored wetlands, as well as in a potential overestimation of the exposure to climate warming ( $\text{Expo}_{T^\circ}$ ) (Heikkinen et al., 2020). Improved future projections of land-use are required to accurately quantify waterbird exposure to natural habitat conversion.

Nevertheless, these limitations do not diminish the significance of our study because they do not undermine our assumption that communities impacted by high rates of natural habitat conversion are less able to adjust to climate warming (Gaget et al., 2020a). Given the rule-based logic framework used to compute the  $\text{Lim}_{T^\circ}$  index, the limitations based on the thermal specialization of the community also do not invalidate the higher vulnerability of communities exposed to high rates of natural habitat conversion compared to communities not exposed to natural habitat conversion. Finally, the combinations of this framework were

somewhat arbitrarily decided, but very similar findings were found with different combinations in the sensitivity analysis (Appendix S5).

#### *Future scenarios of thermal adjustment*

Although one might anticipate greater limitations in community thermal adjustment to climate warming at high radiative forcing, this pattern was only partially observed and not even across all subregions. This is because the exposure to land-use changes does not necessarily increase with the radiative forcing level of the scenarios and has very different spatial patterns between CMIP6 scenarios in the Mediterranean region (Verniest et al., 2022). Therefore, the lower values of  $\text{Lim}_{T^{\circ}}$  index in SSP3-7.0 in Western Europe and the Balkans can be explained by the low values of its main driver, *i.e.*,  $\text{Exp}_{\text{ONHC}}$ , taken in this scenario. The lowest values of the  $\text{Lim}_{T^{\circ}}$  index in the Maghreb under SSP5-8.5 are due to the strongly negative  $\text{Exp}_{\text{ONHC}}$  values on the coast of Morocco, Algeria, and Tunisia because of the extensive conversion of crops into secondary natural land.

Although it might be appealing to infer that high radiative forcing scenarios are not that problematic, such conclusion must be tempered. Indeed, other CMIP6 scenarios combining the same high radiative forcing levels (*i.e.*,  $7.0 \text{ W.m}^{-2}$  and  $8.5 \text{ W.m}^{-2}$ ) with other socio-economic conditions (*e.g.*, SSP2), for which data are not yet available, could result in a very different future land-use and thus potentially in higher values of the  $\text{Lim}_{T^{\circ}}$  index, as  $\text{Exp}_{\text{ONHC}}$  is its main driver. Furthermore, waterbird community thermal adjustment is far to be perfect and results in a climatic debt even at lower rates of temperature increase (Gaget et al., 2021). Our research reinforces the importance of considering future projections of habitat loss and degradation, whose results against scenarios are far less straightforward than for climate projections.

### *Addressing gaps in the protected areas network*

Using a trait-based CCVA framework, we highlighted that waterbird communities of wetlands overlapped by strictly PAs (IUCN category from I to IV) would experience greater limitations to adjust to climate warming than non-protected waterbird communities, certainly due to the higher exposure of strictly PAs to natural habitat conversion. We also found that many of the communities that may experience the greatest limitations are protected: among the 14 sites whose waterbird communities had a high  $\text{Lim}_{T^{\circ}}$  index in all scenarios, 10 located in western Europe (France, Italy, Spain), including the two sites of international importance for waterbirds, are partially or entirely protected. We believe these findings to be encouraging in two respects. First, it implies that PAs are generally located in wetlands where the need to help waterbird communities adjust to new thermal conditions will be most critical. Second, future projections of land-use might overestimate  $\text{Exp}_{\text{ONHC}}$  in PAs, since Integrated Assessment Models (IAMs) (Harfoot et al., 2014) used to produce these projections do not explicitly account for PAs and have a very coarse spatial resolution. This is especially the case for strictly PAs that have more restrictive management than other PAs (Dudley et al., 2008), and thus, we assume, have a better ability to reduce anthropogenic pressures. Nevertheless, we assume that many sites that were considered as protected in this study are only partially overlapped by PAs (Popoff et al., 2021), although this could not be verified throughout the entire study area because the exact delineation of the IWC monitored sites is not available in many cases (Gaget et al. 2021). Therefore, we advocate that the delineation of each IWC site be completed and made available. This would enable the expansion of strictly PAs in wetlands hosting waterbird communities that might experience limitations to adjust to climate warming and that are only partially covered by a strict protection status (*i.e.*, strict nature reserve, wilderness area, national park, natural monument or feature, and habitat/species management area, Dudley et al., 2008). In addition, a decline in the

effectiveness of PAs to reduce anthropogenic pressures such as natural habitat conversion, which was observed in some regions (Geldmann et al., 2019), might threaten the ability of PAs to facilitate the thermal adjustment of waterbird communities to climate warming. We thus recommend the implementation of effective management plans in current PAs to ensure their ability to support waterbird responses to climate change (Gaget et al., 2022) and positive waterbird population trends (Wauchope et al., 2022).

Despite the above-mentioned result, we identified 490 waterbird communities that might experience significant thermal adjustment limitations in at least one scenario and that are not included in the current PAs network (Supplementary Material). Maghreb and Middle-East countries account for 199 of these communities (40.6%), including 22 at sites of international importance for waterbirds, notwithstanding the low number of selected sites in these countries ( $n = 586$ , 20.0%). Our results are coherent with Breiner et al. (2022) in which authors found that African and Middle-East Critical Sites for waterbirds are key to support waterbird responses to climate change. Such sites are also important to protect to ensure the connectivity of the wetlands along the Eurasian-African migration flyway (Deboelpaep et al. 2022). Our results urge Mediterranean countries to quickly designate new PAs to protect the 490 communities we identified, with priority given to the 32 wetlands of international importance for waterbirds (Popoff et al., 2021). Protecting these wetlands will help waterbird communities adjust to climate warming (Gaget et al., 2021) but might also benefit these ecosystems as a whole, which are among the most threatened on Earth and the least targeted by conservation measures (Abell & Harrison, 2020), as well as human populations (MWO-2, 2018). The designation of new PAs in wetlands whose waterbird communities might experience high thermal adjustment limitations to future climate warming should be facilitated by the new protection targets of the Kunming-Montreal global biodiversity framework (CBD, 2022).

### *Perspectives*

Prioritizing waterbird conservation should not be based only on wintering, *i.e.*, non-breeding, species distribution but also account for the distribution during the breeding and migration periods (*e.g.*, Deboelpaep et al., 2022). We also recommend assessing the vulnerability of waterbird communities by considering other components of climate change than climate warming, such as precipitation changes and sea-level rise, but also by including as wide a range of relevant anthropogenic pressures as possible, such as hunting, disturbance, and water management. Nevertheless, this study provides important guidance for conservation planning in the Mediterranean region by stressing the need to designate new PAs in 490 sites. Our results also demonstrated that current Mediterranean PAs are in wetlands whose waterbird communities, without protection, would experience high limitations in thermal adjustment by the end of the 21<sup>st</sup> century, and thus that the location of PAs might help to support the thermal adjustment of waterbird communities to future climate warming.

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## **DECLARATION OF INTEREST STATEMENT**

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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## FIGURES

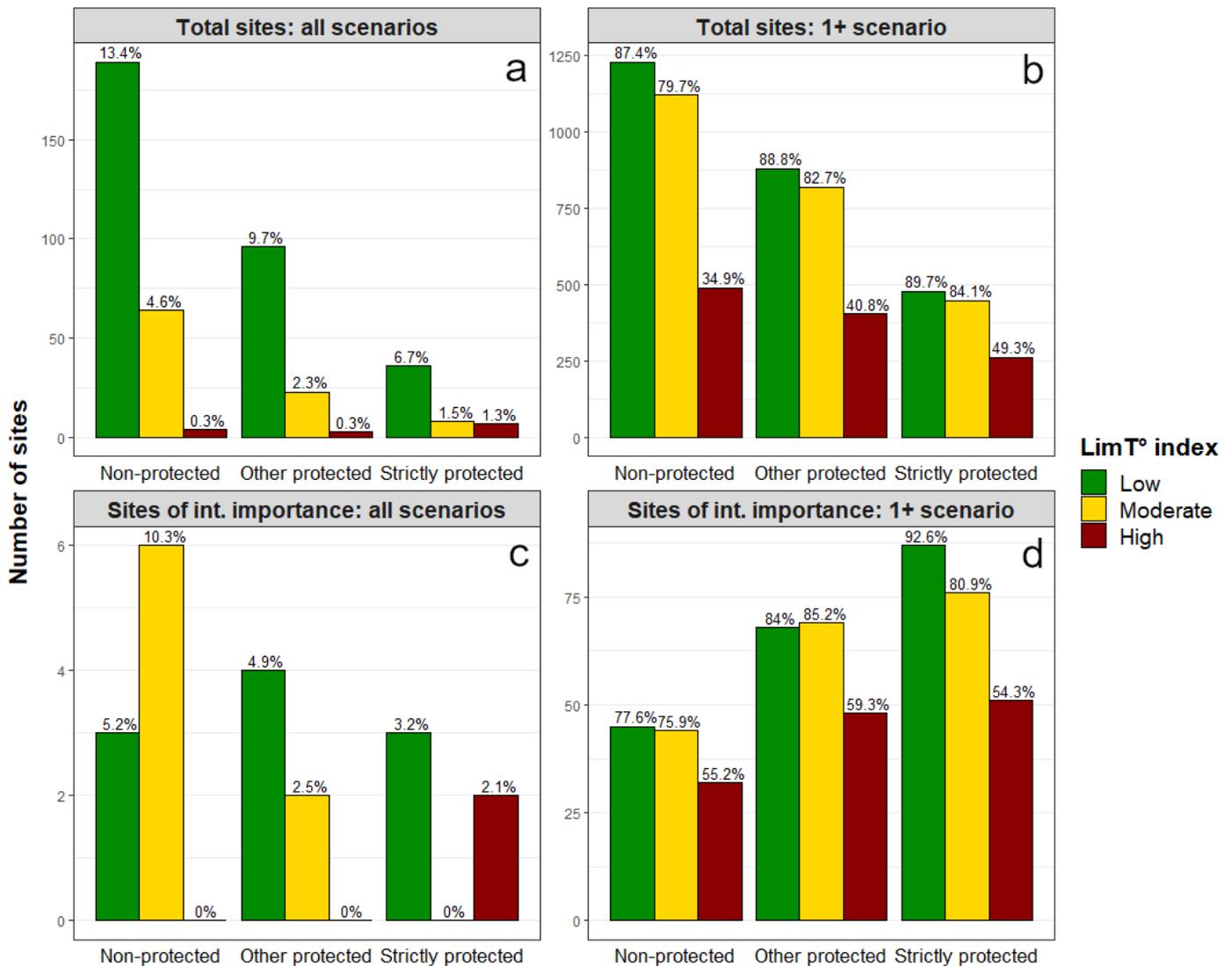
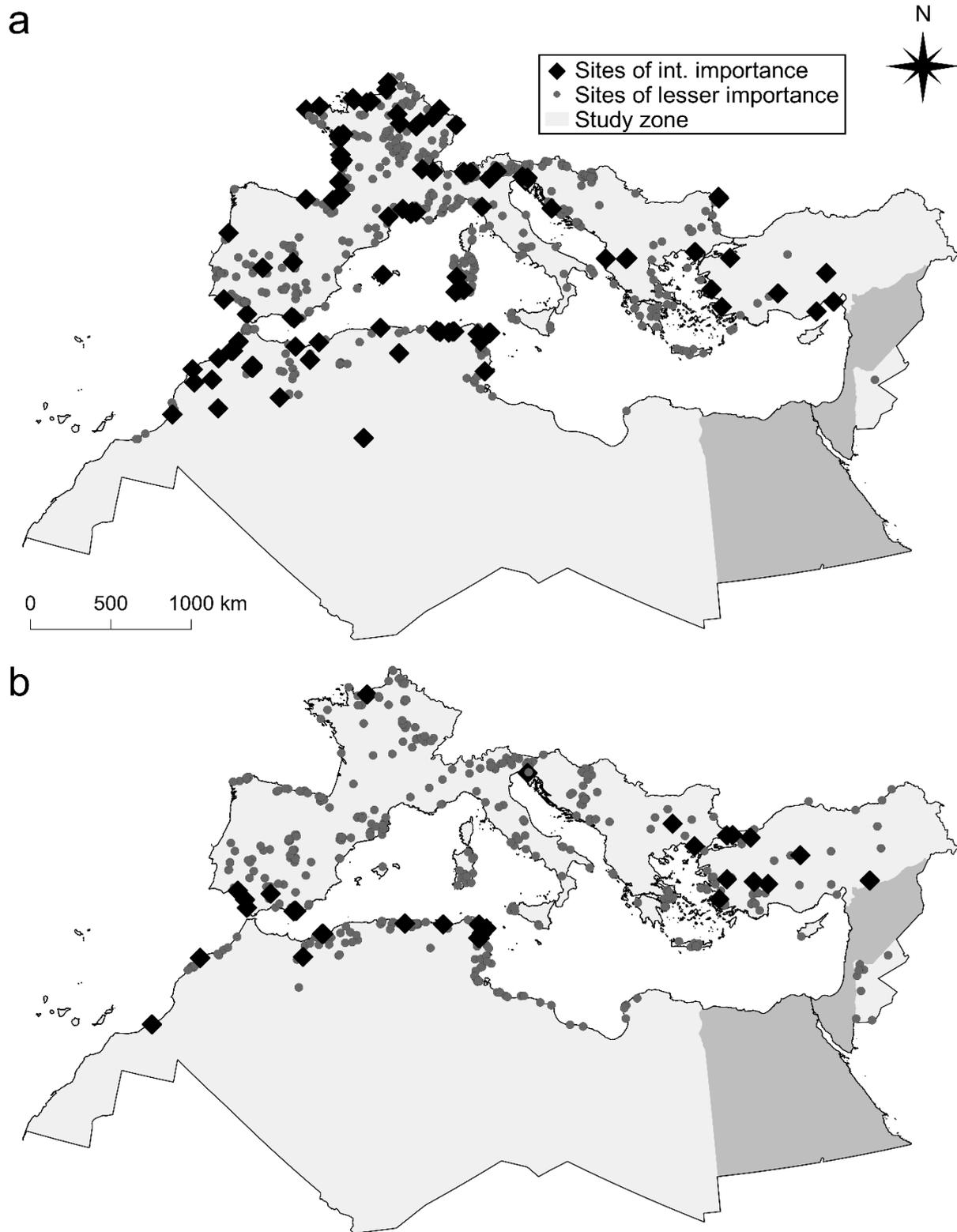


Figure 1: Number and percentage (%) of sites according to their index of future thermal adjustment limitations (Lim<sub>T°</sub> index) and their protection status. a: sites with the same value of Lim<sub>T°</sub> index in all scenarios; b: sites with a value of Lim<sub>T°</sub> index in at least one scenario; c: sites of international importance for waterbirds with the same value of Lim<sub>T°</sub> index in all scenarios; d: sites of international importance for waterbirds with a value of Lim<sub>T°</sub> index in at least one scenario. One site can be represented in several bars in panels b and d (*e.g.*, if it has Low, Moderate, and High Lim<sub>T°</sub> value in at least one scenario). Percentages were calculated

relative to sites with the same protection status (top: all sites; bottom: sites of international importance). Details in Appendix S8.



**Figure 2:** Protected (a) and non-protected (b) sites with high future thermal adjustment limitations ( $Lim_{T^{\circ}}$  index) in at least one scenario (protected:  $n = 668$ , non-protected:  $n = 490$ ). Black diamonds: sites of international importance for waterbirds (protected:  $n = 99$ , non-

protected:  $n = 32$ ) according to Popoff et al. (2021), grey circles: sites of lesser importance (protected:  $n = 569$ , non-protected:  $n = 458$ ). Mediterranean countries in which the IWC is carried out but for which no site was selected (Appendix S1) are depicted in dark grey.

## TABLES

Table 1: Rule-based logic framework used to combine the exposure of sites to climate warming ( $Exp_{OT^\circ}$ ), the exposure of sites to natural habitat conversion ( $Exp_{ONHC}$ ) and the thermal specialization of waterbird communities ( $Spec_{T^\circ}$ ) to compute the  $Lim_{T^\circ}$  index for each scenario ( $n = 4$ ) and each GCM ( $n = 8$ ). x = combination of two metrics, L = Low, M = Moderate, H = High. A community with a high thermal specialization ( $Spec_{T^\circ} = H$ ) has a low index of future thermal adjustment limitations ( $Lim_{T^\circ}$  index = L) if exposure to climate warming is high ( $Exp_{OT^\circ} = H$ ) but exposure to natural habitat conversion is low ( $Exp_{ONHC} = L$ ). Under high exposure to natural habitat conversion, the index of future thermal adjustment limitations is always high.

		$Exp_{ONHC} \times Exp_{OT^\circ}$							
$Spec_{T^\circ}$	L x L	L x M	L x H	M x L	M x M	M x H	H x L	H x M	H x H
L	L	L	M	M	M	M	H	H	H
M	L	L	L	M	M	M	H	H	H
H	L	L	L	L	M	M	H	H	H