Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Combined climatic and anthropogenic stress threaten resilience of important wetland sites in an arid region

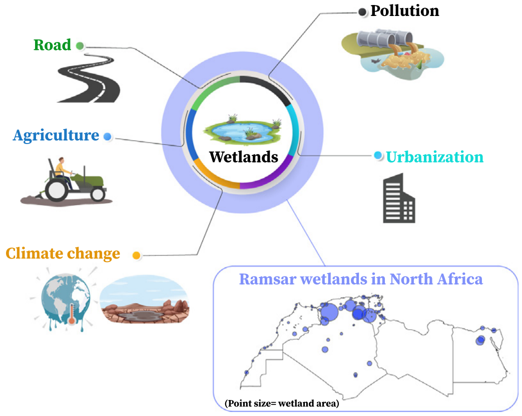
Rassim Khelifa [a,b,*], Hayat Mahdjoub [c], Michael J. Samways [d]

[a] Zoology Department, University of British Columbia, Vancouver, Canada
[b] Biodiversity Research Centre, University of British Columbia, Vancouver, Canada
[c] Department of Evolutionary Biology and Environmental Science, University of Zurich, Zurich, Switzerland
[d] Department of Conservation Ecology and Entomology, Stellenbosch University, South Africa

HIGHLIGHTS

- Protected wetlands are heavily affected by climate change and anthropogenic perturbation
- These changes are detrimental in regions where the climate is already extreme and variable
- North African Ramsar sites witnessed alarming changes in climate and human influence
- Climate change is projected to be severe in areas with high conservation value

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 4 July 2021
Received in revised form 22 September 2021
Accepted 1 October 2021
Available online xxxx

Editor: Sergi Sabater

Keywords:
North Africa
Ramsar sites
Drought
Warming
Human footprint index
Wetlands

ABSTRACT

Climate change and anthropogenic perturbation threaten resilience of wetlands globally, particularly in regions where environmental conditions are already hot and dry, and human impacts are rapidly intensifying and expanding. Here we assess the vulnerability of Ramsar wetlands of six North African countries (Western Sahara, Morocco, Algeria, Tunisia, Libya, and Egypt) by asking three questions: (1) what are the recent anthropogenic changes that the wetlands experienced? (2) what are the projected future climatic changes? (3) how wetlands with different conservation priorities and globally threatened species are impacted by anthropogenic pressures? We used climatic data (historical and future projections) from WorldClim 2, drought index (SPEI), and human footprint index (HFI for 2000 and 2019) to estimate anthropogenic pressures, as well as waterbird conservation value (WCV: a metric indicating conservation priority of sites) and the breeding distribution of three threatened waterbird species (*Aythya nyroca*, *Marmaronetta angustirostris*, and *Oxyura leucocephala*) to understand how biodiversity is impacted by anthropogenic pressure. We found that temperature, precipitation, drought, and human footprint index (HFI) increased during earlier decades. Interestingly, areas with high HFI are projected to encounter lower warming but more severe drought. We also found that WCV was positively correlated with the magnitude of current HFI, indicating that sites of high conservation value for waterbirds encounter higher levels of anthropogenic pressure. The breeding range of the three threatened species of waterbirds showed a marked increase in HFI and is projected to experience a severe increase in temperature by 2081–2100, especially under the

---

* Corresponding author.
E-mail address: rassimkhelifa@gmail.com (R. Khelifa).

https://doi.org/10.1016/j.scitotenv.2021.150806

Please cite this article as: R. Khelifa, H. Mahdjoub and M.J. Samways, Combined climatic and anthropogenic stress threaten resilience of important wetland sites in an arid..., Science of the Total Environment, https://doi.org/10.1016/j.scitotenv.2021.150806

high emission scenario (SSP8.5) where environmental temperature becomes closer to the species critical maximum. Our results highlight the importance of integrating new conservation measures that increase the resilience of North African protected wetlands to reduce extinction risk to biodiversity.

1. Introduction

Wetlands are highly productive systems, with rich and diverse biodiversity, and providing various important ecosystem services while contributing to human well-being (Davidson et al., 2019; Gardner et al., 2015; Mitsch and Gosselink, 2015). Due to their disproportionate higher biodiversity compared to other ecosystems (Gopal, 2009), protecting major global wetlands is a strategic tool for maintaining global biodiversity (McInnes et al., 2020). However, their conservation has been historically challenging due to high anthropogenic pressure (Chen et al., 2018; Davidson et al., 2018; Sievers et al., 2018), which is expected to increase globally in the future due to human population growth (Wittemyer et al., 2008). Climate change is a significant threat to wetlands, affecting the ecological integrity of the ecosystems through changes in hydrological regimes, physio-chemical properties, and biological communities (Davidson, 2014; Mor et al., 2019; Xi et al., 2021). Worryingly, future projections for climate predict major alteration of various abiotic conditions (Xi et al., 2021), which could exceed the ecological tolerance of biological communities. These climatic and anthropogenic perturbations threaten the resilience and functioning of these sensitive ecosystems (Finlayson et al., 2005; Gardner and Finlayson, 2018), warranting a clear understanding and predictions of these impacts for their effective management (Taylor et al., 2021).

Many wetlands are globally protected for their remarkable biological, physical, cultural, and socioeconomic importance (Finlayson et al., 2018). Ramsar sites for instance, are among the most important protected areas in the world, involving 171 countries that use standardized criteria based on biological diversity and habitat uniqueness (Bridgewater and Kim, 2021; Gardner and Davidson, 2011). There are over 2400 Ramsar sites globally, covering 2.5 million km^2. Populations of taxa like waterbirds increase more rapidly in protected than unprotected wetlands (Kleijn et al., 2014), suggesting that protected areas confer the best ecological conditions for population growth and persistence (Pavón-Jordán et al., 2020). In addition, Ramsar wetlands vary greatly in size and other habitat characteristics, and consequently in their resilience to climate change and anthropogenic perturbations (Cherkaoui et al., 2015). For instance, larger compared to smaller wetlands might be less vulnerable to drought induced by climate change or water extraction for irrigation and human consumption. While Ramsar sites are well protected by local authorities, some sites experience increasing perturbations, including intense land use, excessive hunting and fishing, water abstraction, and pollution (Gaget et al., 2020). Together with the rapidly changing climate, the resilience of these valuable protected areas, which are refuges to considerable biodiversity and are hotspots for waterbird wintering, breeding and migration, are at great risk, and their management is becoming increasingly difficult.

Globally, some areas are more at risk than others in terms of climatic and anthropogenic pressure (Pekel et al., 2016; Xi et al., 2021). Across North Africa, wetlands are typically shallow and occur in hot, dry, and unpredictable climates (Faramarzi et al., 2013). In recent years, these wetlands have experienced increased frequency of extreme climatic events, projected to fluctuate greatly during the current century (Ahmadalipour and Moradkhani, 2018; Bucchignani et al., 2018; Khelifa et al., 2021a). These changes are exacerbated by the human population being concentrated in cooler areas where most wetlands occur (Khelifa et al., 2021c). Hence, these wetlands commonly encounter high human perturbation, including irrigation, fishing and hunting (Ramdani et al., 2001). Although local biodiversity is adapted to the hot, dry, and fluctuating environmental conditions, it is the combination of climate change and anthropogenic pressure that could be detrimental to species persistence in the area (Newbold et al., 2020). In addition, due to the high climate velocity and predominance of geographic barriers (deserts in North Africa to the south, and Mediterranean Sea to the north) (Loarie et al., 2009), many species will encounter dispersal limitations, and consequently will not be able to escape the extreme adverse conditions induced by the human-climate interaction (Cuttelod et al., 2009). Our current knowledge of the climatic and anthropogenic impacts on aquatic ecosystems in the region is still limited for managing biodiversity and maintaining ecosystem services. To manage for the future necessitates firstly understanding the past, as well as current and future dynamics of climatic and anthropogenic factors to determine possible biodiversity responses, dispersal opportunities, and extinction risk.

The objective of this study is to understand the historical climatic and anthropogenic stress that North African protected wetlands have experienced, and evaluate how future climatic changes will impact these aquatic ecosystems. We specifically select the North African Ramsar sites of six North African countries (Morocco, Western Sahara, Algeria, Tunisia, Libya, and Egypt), then we analyze the average, minimum, and maximum annual temperatures, annual precipitation, and Standardized Precipitation-Evapotranspiration Index (SPEI), between 1980 and 2018, at all Ramsar sites. We also quantify future projected changes in temperature and precipitation for 2081–2100 using CMIP6 future climate projections to determine future dynamics of environmental conditions in local protected wetlands. We also evaluate the change in human influence by comparing estimates for the most updated Human Footprint Index (HFI) estimated for 2000 and 2019. In addition, we investigate the association between waterbird conservation value (WCV: a metric indicating conservation priority of a site based on abundance and species composition of waterbirds), climate change, and HFI. We then assess the vulnerability to climate warming of key threatened waterbirds to climate warming by estimating the thermal safety margin. We finally provide recommendations for effective management and conservation of North African protected wetlands.

2. Materials and methods

2.1. Study area

Our analysis was restricted to North African protected wetlands (Ramsar), particularly those occurring in six countries: Western Sahara, Morocco, Algeria, Tunisia, Libya, and Egypt. The climate of the region is one of the warmest and driest in the world, typically Mediterranean in the north and mainly arid (desert) in the south (Köppen climate classification). The study area is crossed by two major global flyways of bird migration (East Atlantic and Black Sea/Mediterranean), and includes hundreds of wetlands that host wintering, breeding, and stopover populations of many bird species. The site locations of Ramsar sites were obtained from the Ramsar Site Information Service (https://rsis.ramsar.org/). We were interested in the area of the site, total number of criteria (reflecting the ecological importance of the site), total number of threats (indicating the environmental perturbation), and total number of ecosystem services (reflecting the socioeconomic importance of the site) (Tables S1–S3).

2.2. Climatic data

We obtained climate data (2.5-minute spatial resolution) from WorldClim v2 for 1980–2018 (Fick and Hijmans, 2017). We specifically used monthly minimum (Tmin) and maximum (Tmax) temperatures to calculate monthly and annual average temperature ($Tm = [Tmin + Tmax] / 2$). Similarly, monthly precipitation was used to calculate total annual precipitation. These four climatic variables were used to assess the temporal pattern of climate during 1980–2018. To check whether the WorldClim data accurately reflected the observed climatic data in the region, we performed a regression of the observed values (response variable) against the predicted values (explanatory variable) across 131 weather stations (with times series >10 years), and we found a good representation for both annual average temperature ($R^2 = 0.94$) and annual precipitation ($R^2 = 0.87$). To determine the temporal pattern of drought, we used one-month values of the Standardized Precipitation Evapotranspiration Index (SPEI) for 1980–2018 obtained from the global SPEI database (Vicente-Serrano and Staff, 2015). Future projections of temperature and precipitation were obtained from WorldClim 2 for 2081–2100 using three scenarios corresponding to the shared socio-economic pathways (SSP) 126 (low emission scenario; SSP2.6), 245 (moderate emission scenario; SSP4.5), and 585 (high emission scenario; SSP8.5) of the CMIP6 future climate projections (based on all nine models: BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, GFDL-ESM4, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0) (Fick and Hijmans, 2017). Because data of all nine models were highly correlated ($r \geq 0.98$) (Fig. S1), we used a single model (BCC-CSM2-MR) to determine spatial correlation of future climate data with other covariates (e.g. time, site area). We further used the present and future Köppen-Geiger climate classification (1 km^2 resolution) (Beck et al., 2018) to determine the shift in climate type of Ramsar sites between the present-day (1980–2016) and projected future conditions (2071–2100) under the scenario SSP8.5.

2.3. Human influence data

We used the machine learning-based Human Footprint Index (HFI), developed by Keys et al. (2021), as a metric for human influence on natural habitats. This index, based originally on Williams et al. (2020), is the most up-to-date human footprint index available, providing estimates for 2000 and 2019. HFI is based on eight human pressures affecting terrestrial habitats of the Earth, including (a) extent of the built environment, (b) population density, (c) electric infrastructure, (d) agricultural lands, (e) pasture lands, (f) roadways, (g) railways, and (h) navigable waterways. HFI values range from 0 to 1 where 0 indicates low human pressure and 1 indicates very high human influence. The resolution of HFI is 0.00989273° latitude and 0.00989273° longitude. For each Ramsar site, we calculate the average HFI across a buffer of 5 km around the wetland. To estimate temporal changes in human influence, we calculated the difference in HFI between 2000 and 2019 ($\Delta HFI = HFI_{2019} - HFI_{2000}$).

2.4. Conservation priority and environmental stress

We assessed the correlation between wetland importance for biodiversity and climatic and anthropogenic perturbation to determine whether biodiversity of high conservation priority is associated with higher risk of environmental stress. To test this, we used the Waterbird Conservation Value (WCV) for the studied Ramsar sites (Sayoud et al., 2017). The WCV is the sum of the proportion of each species' count relative to the global 1% threshold level for each species (Harebottle and Underhill, 2016). As WCV takes into account both diversity and abundance, high WCV values indicate more diverse and abundant waterbird assemblage, and so reflect a priority index for the conservation of wetlands.

2.5. Thermal safety margin

To determine whether threatened species are at risk of extinction, we first selected locally breeding threatened waterbird species that are commonly used to classify Ramsar sites in North Africa (*Aythya nyroca*, *Marmaronetta angustirostris*, and *Oxyura leucocephala*), then we calculated past environmental thermal safety margin (TSM) of each species and its projected temporal change in the future using this equation: $TSM = CTmax - Tenv$, where CTmax is the critical maximum temperature of the species estimated using the maximum value of Tm (historical average: 1970-2000) within the breeding grounds of the species geographic range obtained from global distribution maps (polygons) of species of the IUCN Red List of Threatened Species, and Tenv is the past (1970-2000) or future (2081-2100) average ambient Tm within the breeding grounds of the species geographic distribution in North Africa. We estimated the future change in TSM using all nine models of the future projections under three scenarios (SSP2.6, SSP4.5, and SSP8.5).

2.6. Statistical analyses

Our analyses were performed with R 4.0.2 software (R Development Core Team, 2021). We used the raster (Hijmans et al., 2015), sf (Pebesma, 2018), and sp (Pebesma et al., 2012) packages to handle geographic data and statistics. To analyze the temporal pattern of climatic variables (Tm, Tmin, Tmax, P, and SPEI), we used the nlme package (Pinheiro et al., 2020) to perform linear mixed effects model (LME) with the climate variable as a response, year as an explanatory variable, and site as a random effect. We also tested for the potential correlation of area, total number of criteria, and total number of ecosystem services with the climate variables, as well as potential interaction with year, to highlight potential differences in the temporal pattern of climatic changes. Prior to computing any LME, we first tested for the potential occurrence of spatial autocorrelation using the Moran I test from the ape package (Paradis et al., 2004). We accounted for spatial autocorrelation in all models using the autoregressive structure of order 1. To analyze future climate change, we first calculated the change in average temperature between 2081-2100 and the baseline period 2000–2018, then we used similar LMEs as those used for the historical change in climate. To assess the temporal change in human influence, we conducted an LME including HFI as a response variable, year (factor with two levels: 2000 and 2019) and site-specific covariates as explanatory variables, and site as a random effect. Whether testing for climatic or anthropogenic changes, the interaction of year and site characteristics reveals, for instance, whether larger, more biodiverse, or more socioeconomically valuable sites have witnessed different magnitudes of environmental changes compared to other sites. To test whether conservation value of the waterbird assemblage is associated with the magnitude of future climate change and current anthropogenic pressure, we carried out linear regressions with WCV as an independent variable, and future projection of temperature and precipitation change for 2081–2100, and the recent estimate of HFI (2019) at each site as response variables.

3. Results

Most (92.6%) of the 136 Ramsar sites were located in Algeria, Tunisia, and Morocco. Only four Ramsar sites were located in Egypt, four in Western Sahara, and two in Libya. These North African Ramsar sites were classified based on one to seven of nine criteria. The most frequent number of criteria was three (46 sites) and the most frequent criteria were criterion 1 (70.6%), 2 (63.2%), 3 (69.1%), and 4 (64.7%) (Fig. S2), which reflect the uniqueness of wetland type and the importance of species and ecological communities. There was a positive correlation between total number of criteria and total number of threats ($r = 0.31$, $p = 0.0002$), and between total number of ecosystem services provided by the site and total number of threats ($r = 0.31$, $p < 0.0001$) (Fig. S3), indicating that sites of highest conservation and socioeconomic value are exposed to wider spectrum of disturbances. The area of the Ramsar site was not correlated to either the total number of criteria, threats, or ecosystem services ($p > 0.05$).

3.1. Historical climatic change

North African wetlands have one of the warmest and driest conditions in the world (Fig. 1A, D). The average annual temperature across North African Ramsar sites falls in the 66th percentile of all global Ramsar sites, whereas the warmest site represents the 83rd percentile (Fig. 1B). The average and minimum annual precipitation are the 13th and ~0th percentile of that of all global Ramsar sites (Fig. 1E). Larger Ramsar sites were on average warmer ($r = 0.29$, $p = 0.0004$) and drier ($r = -0.52$, $p < 0.0001$) than smaller Ramsar sites (Fig. 1C, F).

Our analysis of the temporal pattern of annual average temperature (Tm) during 1980–2018 showed a significant increase ($p < 0.0001$) with an average ± SD warming of 0.029 ± 0.006 $°\mathrm{C} \cdot \mathrm{yr}^{-1}$ (0.017–0.055 $°\mathrm{C} \cdot \mathrm{yr}^{-1}$) (Fig. S4). This warming showed a longitudinal spatial pattern with higher magnitudes in the west in Morocco and in the east in Egypt, and lower magnitudes in between (mostly Algeria and Libya). The analysis of temperature extremes showed discrepancy in the magnitude of warming between Tmin (0.027 ± 0.012 $°\mathrm{C} \cdot \mathrm{yr}^{-1}$) and Tmax ($0.030 \pm 0.005$ $°\mathrm{C} \cdot \mathrm{yr}^{-1}$), indicating that the annual amplitude of temperature increased. Interestingly, all Ramsar sites experienced a slight increase in average annual precipitation (P) ($p < 0.001$), with an average slope of 0.43 ± 1.20 $\mathrm{mm} \cdot \mathrm{yr}^{-1}$ (0.43–1.20) (Fig. S4). SPEI showed an overall decline (-0.008 ± 0.006 yr^{-1}; range: -0.03–0.002 yr^{-1}) ($p < 0.0001$), but the change in SPEI was not correlated with wetland size ($t = -0.78$, $p = 0.43$).

We tested for the potential correlation between the temporal changes in Tm and P with the number of criteria and number of ecosystem services of sites. We found that the magnitude of historical warming was stronger in sites with higher number of ecosystem services ($t = 3.22$, $p = 0.001$), number of threats ($t = 2.46$, $p = 0.01$), but weaker in sites with higher number of criteria ($t = -4.42$, $p < 0.0001$). These results reveal that sites with different levels of environmental threat and socioeconomic importance witnessed stronger warming, but those with higher ecological values experienced slightly weaker warming during the past four decades.

The change in P was not correlated with the number threats ($t = -0.31$, $p = 0.75$) and the number of ecosystem services ($t = 0.21$, $p = 0.82$), revealing that sites with different levels of environmental threat and socioeconomic importance did not show a pattern in the magnitudes of change in precipitation. The increase in P was higher in sites with higher number of criteria, indicating that the larger (and hotter) sites benefitted from an increase in precipitation during the past four decades. The decline in SPEI (increased drought intensity) was weaker in sites with higher number of threats ($t = 2.29$, $p = 0.02$), higher number of criteria ($t = 3.39$, $p = 0.0007$), but similar across sites with various numbers of ecosystem services ($t = 1.07$, $p = 0.28$).

3.2. Future climate projections

The three scenarios of future projection for 2081–2100 based on nine climate models for temperature showed that annual average temperature will continue to increase at Ramsar sites ($p < 0.001$) (Fig. 2A). The average warming across sites and climate models is projected to be 1.16 ± 0.45 °C, 2.44 ± 0.65 °C, and 5.05 ± 1.23 °C for SSP2.6, SSP4.5, and SSP8.5, respectively. However, this increase in mean temperature will be higher at sites with larger areas in SSP4.5 and SSP8.5, revealed by the three way interaction between period, scenario and wetland area ($p < 0.002$). The warming did not show correlation with the number of criteria ($t = 0.12$, $p = 0.90$), number of ecosystem services ($t = 0.82$, $p = 0.41$), or number of threats ($t = 0.43$, $p = 0.66$).

The three scenarios of future projection for 2081–2100 for annual precipitation showed an overall decrease in all climate models ($p < 0.001$) (Fig. 2B). On average across all sites and climate models, P will decline by 22.8 ± 30.7 mm, 32.0 ± 37.6 mm, and 66.4 ± 64.5 mm by the end

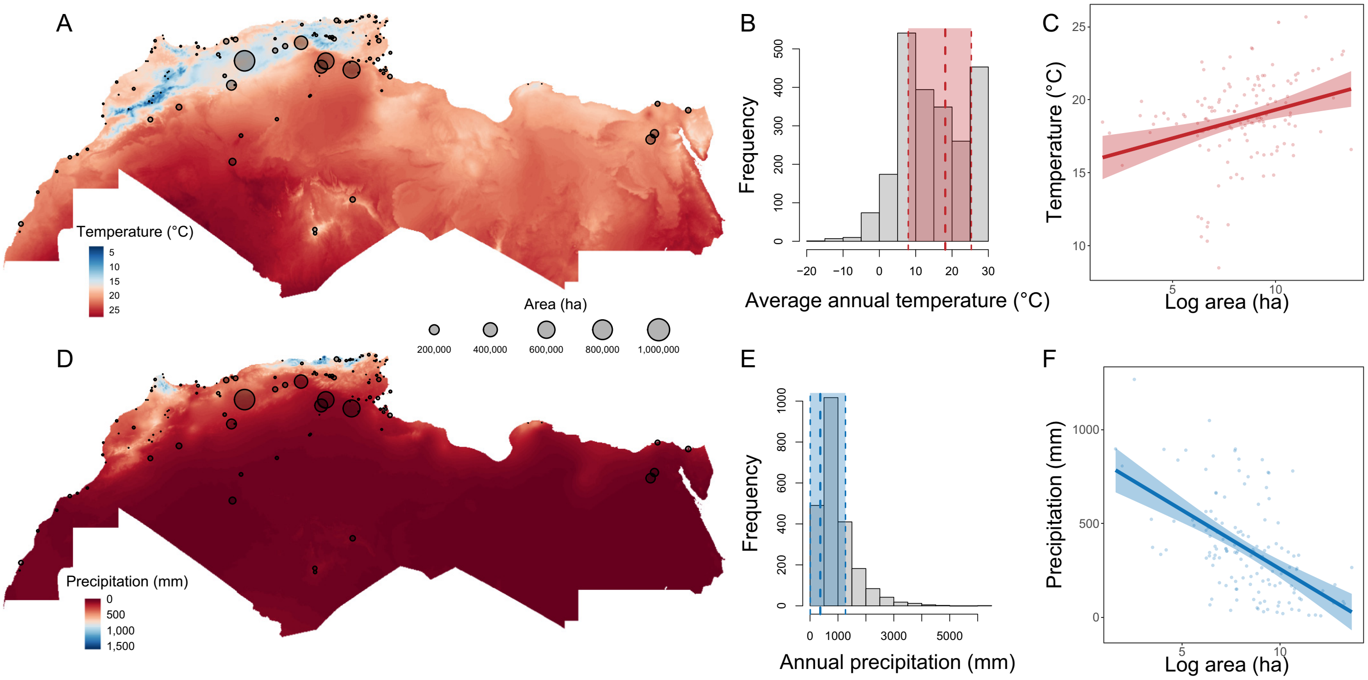


Fig. 1. a. Climatic conditions in North African Ramsar wetlands. (A) Annual average temperature. (B) Frequency distribution of the annual average temperature of global protected wetlands, highlighting the minimum, mean, and maximum values of North African protected areas (red vertical dashed lines). (C) Correlation between annual average temperature and the area of the Ramsar site. (D) Annual precipitation. (E) Frequency distribution of the annual precipitation of global protected wetlands highlighting the minimum, mean, and maximum values of North African protected areas (blue vertical dashed lines). (F) Correlation between annual precipitation and the area of the Ramsar site. Lines in C and F are linear regressions and ribbons are standard errors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

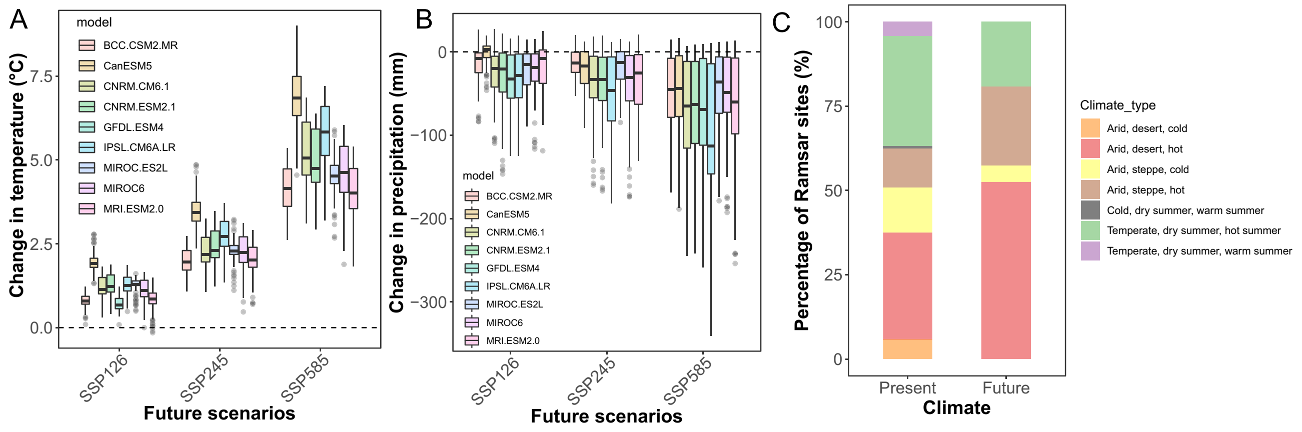


Fig. 2. Future projected change in climate of North African Ramsar sites. (A) Change in annual average temperature by 2081–2100 based on nine climate models and three scenarios. (B) Change in annual precipitation by 2081–2100 based on nine climate models and three scenarios. (C) Frequency of climate type from present-day (1980–2016) to future conditions (2071–2100) based on the scenario SSP8.5 and the Köppen-Geiger classification (Beck et al., 2018).

of the century for SSP2.6, SSP4.5, and SSP8.5, respectively. Our models testing for the correlation of site covariates with the magnitude of change in precipitation showed that the larger sites will undergo the most severe decline in precipitation, particularly in SSP4.5 and SSP8.5 ($p < 0.002$). The change in precipitation was not different across sites with different number of ecosystem services or different number of threats (except for the SSP8.5 where the decline in precipitation is expected to be stronger in sites with higher number of threats ($t = -2.32$, $p = 0.02$)). The decline in precipitation is projected to be more severe in sites with higher number of criteria in all scenarios ($t = -2.45$, $p = 0.01$).

Climate types of North African Ramsar sites are projected to change to more hot and arid climates ($\chi^2 = 32.5$, $df = 6$, $p < 0.0001$) (Fig. 2C). The total number of climates is expected to decline from seven currently (1980–2016) to four for projected future conditions (2071–2100) under SSP8.5. Specifically, while only 31.7% of sites currently have an arid-desert-hot climate, this percentage may increase to 52.5% by the end of the century. The frequency of arid-steppe-cold and temperate-dry summer-hot summer decreased from 13.3% and 32.5% to 5% and 19.2%, respectively. Overall, the climate of North African Ramsar sites is projected to become more homogenous.

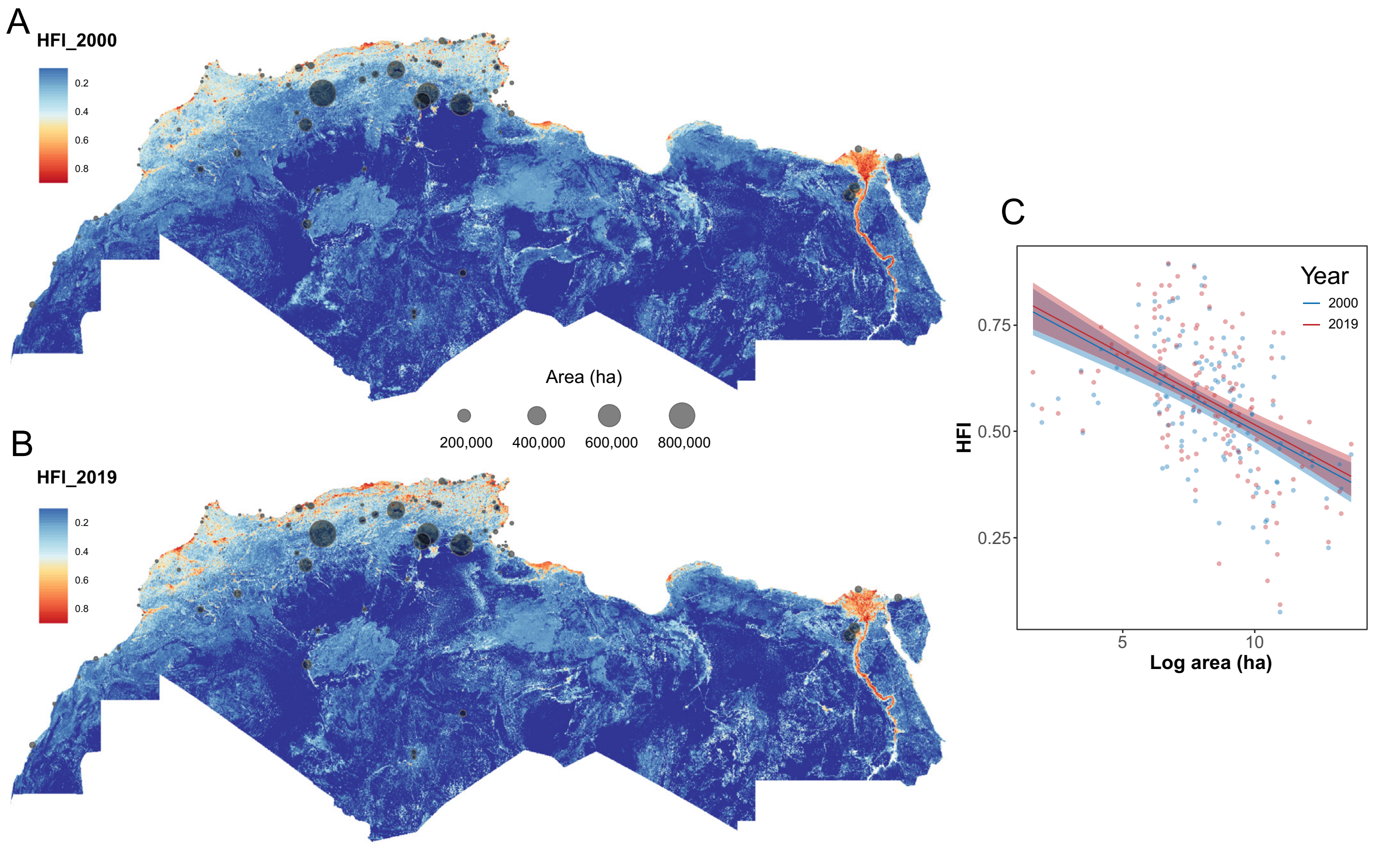


Fig. 3. Temporal change in Human Footprint Index (HFI) between 2000 and 2019 in North Africa. (A) HFI in 2000. (B) HFI in 2019. (C) Correlation between HFI and Ramsar site area in 2000 and 2019. Lines are linear regressions and ribbons are standard errors.

3.3. Human influence

HFI showed a marginal significant increase from 2000 to 2019 ($t = 1.93$, $p = 0.05$). While HFI was higher in smaller Ramsar sites ($t = -5.46$, $p < 0.001$), the increase of HFI was similar across sites with different sizes (Fig. 3). The temporal change in HFI was not correlated with the total number of criteria among the Ramsar sites ($t = -0.54$, $p = 0.58$), number of services ($t = 0.30$, $p = 0.76$), and number of threats ($t = -0.60$, $p = 0.54$). This indicates that sites with various ecological and socioeconomic values experienced similar increase in human influence during the last two decades.

3.4. Relating future climate change and human influence

There was no correlation between Tm and the HFI of recent years at North African Ramsar sites ($t = -0.94$, $p = 0.36$) (Fig. 4a). However, P was positive correlated with HFI ($t = 4.74$, $p < 0.0001$) (Fig. 4b), that is, the wetter the site the higher the human influence. Interestingly, the projected future change in temperature was negatively correlated with HFI, particularly in SSP4.5 and SSP8.5 ($t = -1.91$, $p = 0.05$; $t = -2.03$, $p = 0.04$; respectively), indicating that Ramsar sites with low HFI had stronger warming than Ramsar sites with high HFI (Fig. 4c). Similarly, the projected future change in precipitation was negatively correlated with HFI in all scenarios ($t = -3.62$, $p = 0.0003$; respectively), but the relationship was weak for SSP8.5 due to the high variability in future change in precipitation. These results suggest that sites with low human influence (also the drier sites) will encounter the lowest change in precipitation, whereas sites with high human influence (also the wetter sites) will experience a steeper decline in precipitation (Fig. 4d).

3.5. Relating climatic and anthropogenic pressure to waterbird conservation

The Waterbird Conservation Value score (WCV) for Ramsar sites indicates the conservation priority of sites based on species occurrence

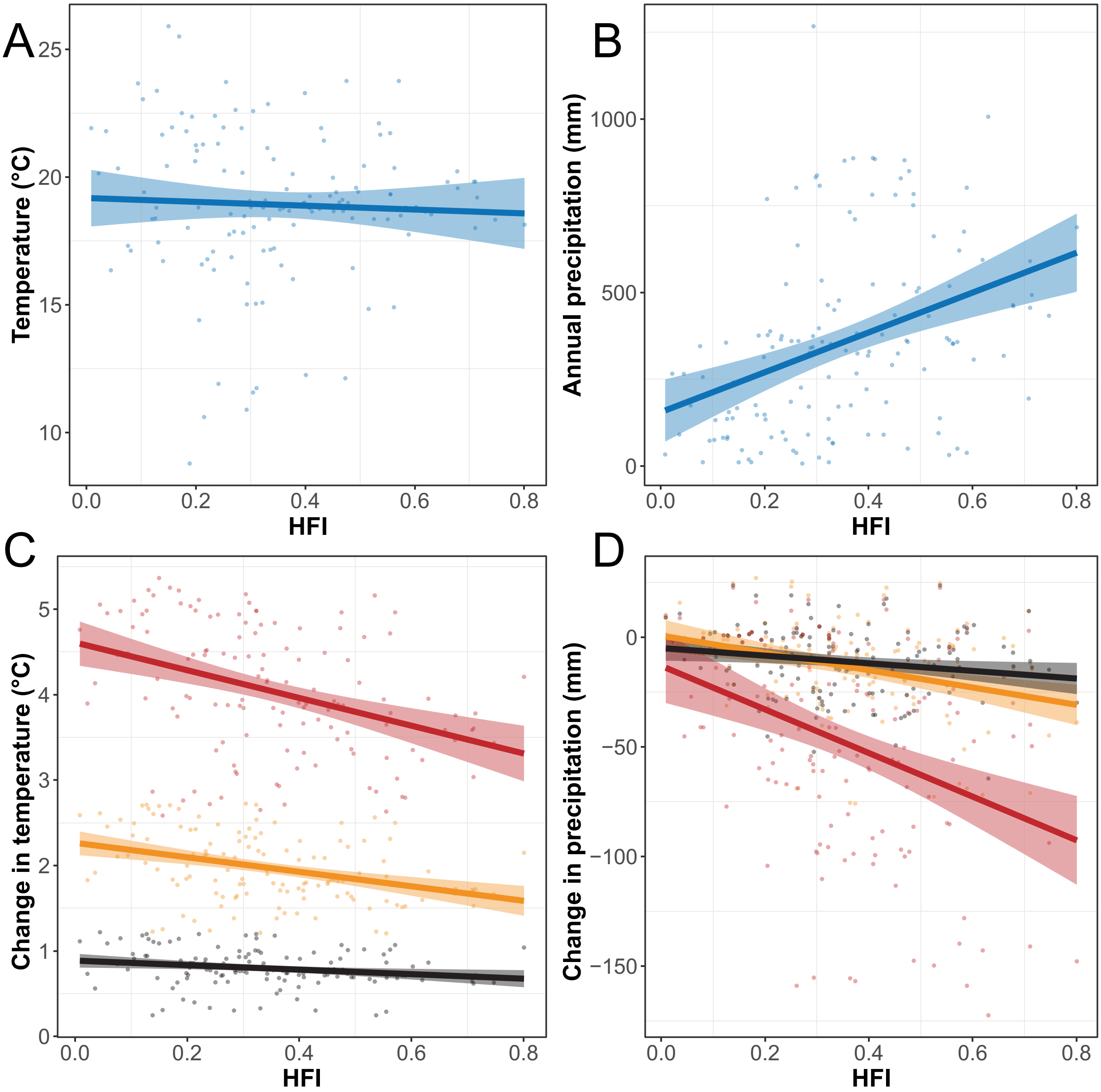


Fig. 4. Relationship between Human Footprint Index (HFI), annual average temperature (A), annual precipitation (B), projected change in annual average temperature by 2081–2100 (C), and projected change in annual precipitation by 2081–2100 (D). Temporal change in climatic variable temperature was calculated using 2000–2018 as baseline period ($\text{Change} = \text{Average}_{2081-2100} - \text{Average}_{2000-2018}$). Lines are linear regressions and ribbons are standard errors. Black, orange, and red indicate SSP2.6, SSP4.5, and SSP8.5, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and abundance. We found that the projected future warming was negatively correlated with WCV of sites, particularly for SSP8.5 ($t = -2.86$, $p = 0.004$) (Fig. 5a). This means that sites with high diversity and abundance will encounter slightly lower magnitude of warming. Furthermore, the projected change in precipitation was marginally negatively correlated with WCV ($t = -1.81$, $p = 0.07$) for SSP2.6 (Fig. 5b). This suggests that there will be increasingly drier conditions in sites with high conservation value. Finally, although the association was weak due to the high variability in HFI and WCV, the HFI_{2019} was positively correlated with WCV of sites ($t = 2.38$, $p = 0.02$) (Fig. 5c), indicating that sites with high diversity and abundance are experiencing the highest anthropogenic pressure.

3.6. Thermal tolerance and conservation concern

We estimated the past (1970-2000) and future (2081–2100) thermal safety margin (TSM) of three threatened species of waterbirds *Aythya nyroca* (Near Threatened), *Marmaronetta angustirostris* (Vulnerable), *Oxyura leucocephala* (Endangered) which have been commonly used to designate Ramsar sites in North Africa. The breeding ranges of *Aythya nyroca*, *Marmaronetta angustirostris*, and *Oxyura leucocephala* in North Africa are presented in Fig. 6a. *A. nyroca* showed an average decline (across models) in TSM of 21.0%, 34.5%, and 62.2% under SSP2.6, SSP4.5, and SSP8.5, respectively. *M. angustirostris* showed an average decline in TSM of 16.3%, 30.3%, and 58.3% under SSP2.6, SSP4.5, and SSP8.5, respectively. *O. leucocephala* showed an average in TSM of 32.1%, 45.5%, and 73.4% under SSP2.6, SSP4.5, and SSP8.5, respectively (Fig. 6b). Additionally, our analysis of the historical change in HFI across Ramsar sites that overlap with their breeding distribution showed a significant increase in HFI in all three species ($t = 5.10$, $p < 0.0001$) (Fig. 6c), indicating increasing anthropogenic stress.

4. Discussion

Our results show that North African Ramsar wetlands, characterized by a warm and dry climate, have encountered severe warming and more intense drought the last few decades. Furthermore, future climate projections predict that both warming and drought will continue to increase in magnitude, while at the same time the diversity of climates will decline. Besides climate, North African wetlands have experienced increased anthropogenic pressure from surrounding land use, including agriculture, urbanization, and other built environments. Wetlands of high conservation value for waterbirds encounter higher levels of anthropogenic stress. The assessment of the effect of climate change on the thermal safety margin of three threatened waterbird species suggests an increased thermal stress and a higher risk of local extinction. Overall, these observed climatic and anthropogenic trends reveal that globally important wetlands in North Africa are imperiled, and require conservation strategies to maintain biodiversity, habitat integrity, and ecosystem services. The results here are important for local conservationists and decision makers, as research on freshwater ecosystem vulnerability to climatic and anthropogenic effects on biodiversity have been little explored in the region.

4.1. Climatic and anthropogenic change

The projected shift in climate types, and the decline in climate diversity at the North African Ramsar sites, is alarming. Community composition and abundance are linked to climatic conditions such that spatial variability in climates sustains a higher beta diversity of biota and more complex community dynamics (Guisan and Zimmermann, 2000; Woodward and Woodward, 1987). A decline in climate diversity will most likely reduce biodiversity and homogenize it, leading to more desert-like assemblages (Pearson and Dawson, 2003). However, while moving towards this critical environmental state, different changes in community interaction will likely happen. Increased temperature could have various ecological implications on wetlands (Xi et al., 2021). Shifts in the phenology of various biological events such as bird migration, insect emergence, or fish spawning could lead to mismatches between predators and prey, and so have major consequences on the food web (Both et al., 2006; Thackeray et al., 2016).

Wetlands in North Africa support many bird species that winter, breed, or stopover (Cherkaoui et al., 2017), and so the change in thermal conditions during different seasons could influence demographic parameters of various populations of different life stages (Schaub et al., 2005). Furthermore, warming typically increases developmental rates of aquatic organisms that ultimately results in a decline in the size of lower trophic levels (Gardner et al., 2011). In turn, these changes reduce the nutritional value of prey to predators (Ohlberger, 2013; Sheridan and Bickford, 2011). The novel climatic conditions will likely be associated with higher frequency of heat waves which will increase the mortality rate of species, particularly in dry conditions (Conradie et al., 2020).

Additionally, precipitation and drought are major determinants of demographic parameters in hot environments (Møller et al., 2010). Many wetlands dry out fast during warmer years, not only restraining the physical space for aquatic species, but also reducing availability of resources such as food and water to successfully thermoregulate (Riddell et al., 2019) or breed (egg deposition, hatching, and survival of offspring), and ultimately promoting emigration or extirpation of local fauna (Albright et al., 2010; Cady et al., 2019). Our results suggest that the increased frequency of drought events will most likely affect

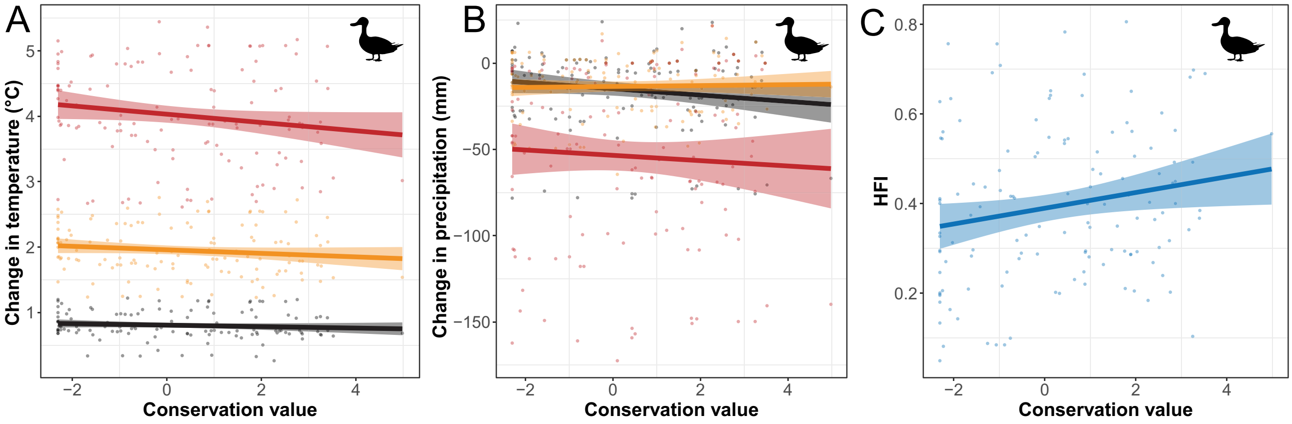


Fig. 5. Relationship between the Waterbird Conservation Value of Ramsar sites based on waterbird species and abundance, projected change in average temperature by 2081–2100 (A), projected change in annual precipitation by 2081–2100 (B), and Human Footprint Index (HFI) (C). Temporal change in climatic variable temperature was calculated using 2000–2018 as baseline period ($Change = Average_{2081-2100} - Average_{2000-2018}$). Lines are linear regressions and ribbons are standard errors.

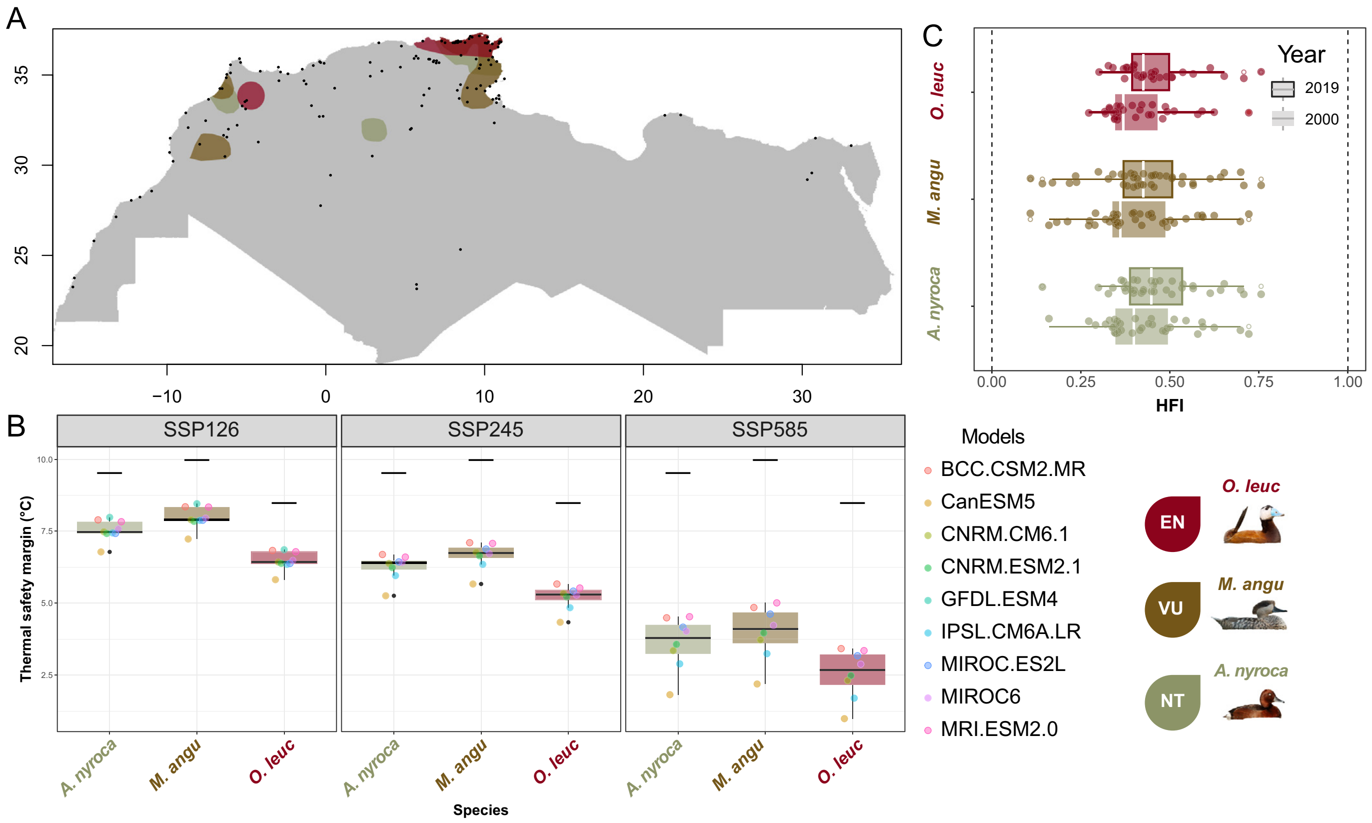


Fig. 6. Temporal change in climatic and anthropogenic stress in three key waterbird species of conservation concern in North Africa (*Aythya nyroca*, *Marmaronetta angustirostris*, and *Oxyura leucocephala*). A. Geographic range of the breeding grounds of three species in North Africa. Black points are Ramsar sites. B. Past (1970-2000; black dash) and future (2081-2100; boxplot) Thermal Safety Margin (TSM) across North African breeding grounds based on nine models of future temperature scenarios (SSP126, SSP245, SSP585). C. Human Footprint Index (HFI) in 2000 and 2019 across Ramsar sites that overlap with the three species range.

species composition and population dynamics of local species. This is especially concerning given that the local protected areas are not exempt from water extraction for irrigation of nearby agricultural lands (Ayache et al., 2009; El Falah et al., 2021; Khelifa et al., 2016). Consequently, these changes threaten the resilience of wetlands to drought, and potentially induce great hydrological changes with profound repercussions on biodiversity.

Size of wetlands here correlated with the overall climatic and anthropogenic conditions, as well as with their temporal trend. Wetland size is a critical physical trait, as it usually determines the carrying capacity of sites in terms of species richness and abundance (Bidwell et al., 2014; Sebastián-González and Green, 2014). Hamza and Selmi (2018) found that waterbird distribution and diversity in Tunisian wetlands were mainly determined by size of the wetland. Our results show that larger sites are warmer and drier, and expected to experience more intense warming and drought in the future. Yet, smaller sites encounter higher anthropogenic pressure. The variability in the intensity of warming and drought across sites with different sizes may lead to disproportionate changes in wetland area, where larger wetlands experience a more severe decline in size than smaller wetlands (Davidson, 2014). The increased human influence in smaller wetlands is problematic, as smaller sites are already sensitive to disturbance due to the limited availability of refuges, as well as vulnerable to pollution (Lomnicky et al., 2019; Stevens and Conway, 2020). Our results highlight the importance of integrating wetland size and its related climatic and anthropogenic risks in future management plans to maintain the integrity of these Ramsar ecosystems.

North African wetlands are characterized by the wettest areas being greatly influenced by human activity (Hamza and Selmi, 2018). Yet these areas also have the largest number of Ramsar sites, mostly of a relative smaller size. These are also the sites subject to the most severe decline in precipitation by the end of the century. The projected change in climatic conditions, combined with high anthropogenic pressure, will exert much stress on aquatic biodiversity. These changes will likely threaten the sustainable use of ecosystem services for human well-being (McInnes et al., 2020). Of concern is that even small declines in precipitation can cause hydrological changes with disproportionately large effects on ecosystems, further aggravated by increased warming over the next decades. Overall, these Ramsar sites are in the future likely to face climatic and/or anthropogenic stress far worse than the current ones.

4.2. Species conservation priority

Based on the waterbird conservation value score (WCV), sites of high conservation priority were associated with with lower levels of warming but marginally higher levels of increased drought risk and human perturbation. This means that sites harboring a significant proportion of the global population size of threatened species are expected to experience high climatic and anthropogenic perturbations in the future, which put these populations under high environmental stress and high likelihood of extirpation (Riddell et al., 2021; Riddell et al., 2019). Under such conditions, it is likely that birds will fail to balance heat and water budgets, resulting in a decline in population size (Huey et al., 2012). In addition, the expected future decline in wetland size in the region (Xi et al., 2021) will most likely increase intra- and interspecific competition for space and resources, and aggravate the climatic impacts on demographic parameters. The loss of populations of high WCV in North Africa will exacerbate the current status of various threatened western Palearctic species and push them closer to extinction.

Our results show a consistent pattern revealing that the currently most threatened birds will encounter great thermal challenges to persisting in North Africa. This is because they, like most other species, are western Palearctic species living at the southern limit of their distribution, encountering the warmest conditions of their entire range (Jiguet et al., 2007; Roselaar, 2006). Therefore, as revealed by the analysis of thermal niche, future projection of climate change will be warmer conditions, particularly for species assessed as Endangered, to levels that are near the current estimated critical maximum temperature across the species range (Conradie et al., 2019; Iknayan and Beissinger, 2018). This suggests that in case of a severe climate change, many species, particularly those with restricted distribution, will likely reach the limit of their critical tolerable environmental temperature by the end of the century in North Africa (Riddell et al., 2019). Worryingly, wetlands in North Africa are relatively rare, and so the opportunity of finding potential refuges in the vicinity to escape adverse climatic conditions is limited. This is particularly the case for species with limited dispersal ability like fish, amphibians, and reptiles because of the 'island-like geography' of North African wetlands where the Mediterranean Sea limits species distribution to the North, and the vast Sahara limits species movement to the South. Therefore, the common escape strategies through northward dispersal of trailing edge populations is challenging, and thus a large proportion of the North African aquatic fauna with limited dispersal ability will have to adapt to novel conditions to persist.

Our lack of understanding of how multiple anthropogenic stressors affect biodiversity is problematic. The cumulative impact of thermal stress, drought, pollution, and other stressors might not be only additive, but could also be synergistic, inducing a larger effect than the sum of the single effects of each stressor (Jackson et al., 2016; Jackson et al., 2021; Piggott et al., 2015). Our prediction of the impact of warming on thermal safety margin of waterbirds is thus a simplification because the projected increase in thermal stress will likely be associated with an increase in human disturbance, as human population in North Africa is expected to increase in the near future, producing potential interactive effects that drive rapid population decline (Jarzyna et al., 2016; Northrup et al., 2019).

4.3. Conservation recommendations

Climate change and anthropogenic disturbance at Ramsar sites threaten ecosystem functioning and provision of ecosystem services contributing to human well-being in North Africa. Based on our findings here, we now present some recommendations for implementing strategic plans for the conservation of Ramsar sites in the face of the combined effects of climatic change and anthropogenic stress.

4.3.1. Climate change research

There are few studies on the effect of climate change on biodiversity in North Africa, despite recent severe drought, climate variability, and recorded consequences for aquatic organisms (Khelifa et al., 2021b), sounding the alarm for urgent implementation of long-term monitoring schemes, as well as field and laboratory experiments on thermal adaptation and sensitivity of species to hydrological changes. The use of the available open-source historical climate data and future projections is an asset for understanding species responses to climate change and to predict future impacts on freshwater communities (Khelifa et al., 2021a). Furthermore, anticipation of the consequences of potential severe drought events on the spatial distribution of freshwater biodiversity is crucial to mitigate climate change impacts. For example, use of artificial wetlands such as reservoirs and farm ponds as safe refuges for surviving drought during dry years is one effective way forward (Deacon et al., 2019; Samways et al., 2020).

4.3.2. Anthropogenic pressure

Human demographic growth in North Africa during the last three decades has led to the expansion of urban areas, agriculture, and roads, particularly near the Mediterranean coast where the climate is cooler and the lands most fertile (Khelifa et al., 2021c). Although an area with high anthropogenic disturbance, it hosts the largest number of Ramsar sites and other protected areas. Therefore, future urban development and agricultural expansion needs to be strategic and eco-friendly to limit their direct and indirect impact on wetlands (Pereda et al., 2021). For instance, the construction of national roads needs to take into account the importance of habitat connectivity and low disturbance for the functioning of freshwater ecosystems. This approach however, requires data on species dispersal, habitat requirements, and extent and degree of anthropogenic impact on species demography at national and international levels. Moreover, authorities need to enforce laws to regulate the intensive agricultural practices that use an excessive amount of fertilizers and pesticides near Ramsar sites in particular, and protected areas in general, to limit the toxic runoff into wetlands and to reduce eutrophication risks. However, promoting organic farming at the expense of productivity and financial gain for farmers needs governmental subsidies and awareness raising among the public. In all cases, a collaborative effort among North African researchers and conservation authorities is required to increase the spatial and temporal extent of monitoring of biodiversity to improve our understanding of its vulnerability and ecological requirements for better conservation and management.

4.3.3. Protected-unprotected networks

Increasing the number of Ramsar sites in North Africa is a valuable solution for maintaining aquatic biodiversity, but this requires regular surveys and a multi-taxa monitoring approach of wetlands. Local Ramsar sites are mostly designated using birds because they are easy to identify and quantify. However, the exploration of other taxa in unprotected wetlands could result in the discovery of sensitive fauna that make the site eligible for Ramsar designation, which is highly likely in a hotspot of biodiversity and endemism such as North Africa (Myers et al., 2000). Understanding the role of unprotected areas in the resilience and functioning of Ramsar sites is also crucial. Indeed, nearby unprotected areas are usually used for foraging and reproduction, or as retreat areas for species in the case of environmental perturbation (e.g. drought) (Blanckenberg et al., 2020). It is now strategic to identify the network of wetlands that are essential for the ecological needs of biodiversity in Ramsar sites, incorporating them as a complementary unit, and establish connectivity corridors between the areas. Importantly, the regulation of the pollution levels of tributaries that flow into North African Ramsar sites is very important to maintain a good water quality and effectively manage Ramsar sites.

4.3.4. International collaboration

North African wetlands are used by migratory birds for wintering, breeding, and stopover. Thus, strengthening the link between African and European researchers is advisable for the better management of avian assemblages (Sayoud et al., 2017). Further reasons why North African aquatic biodiversity need an international attention is the potential genetic distinctiveness of local populations of Palearctic species. Prioritizing conservation efforts based on genetic distinctiveness has become a useful tool in conservation biology (Gutiérrez-Ortega et al., 2018; Volkmann et al., 2014), particularly with the decreased costs of next-generation sequencing (Lowry et al., 2017). Genetic analyses reveal a clear signal of genetic differentiation in Palearctic species between North African and European populations (Husemann et al., 2014). This was reported for species with limited dispersal, such as plants (Besnard et al., 2002; Lepais et al., 2013) and reptiles (Guicking et al., 2008), and even in organisms with high dispersal ability such as insects (Ferreira et al., 2016; Froufe et al., 2014; Habel et al., 2009; Habel et al., 2011; Simonsen et al., 2020). This highlights not only the high cryptic diversity in North Africa, but also the limited dispersal between North African and European populations (Hewitt, 2004). Thus, the conservation of North African populations is key for maintaining overall genetic diversity of western Palearctic species.

Data availability statement

All data used in this paper are openly available. Localities of Ramsar sites are available in https://www.ramsar.org/. Temperature and precipitation data were obtained from WorldClim2.1 (Fick and Hijmans, 2017). Data of Human Footprint Index were obtained from (Keys et al., 2021). Data of Waterbird Conservation Value score for Ramsar sites were obtained from the Supplementary material of Sayoud et al. (2017). Species distribution range of birds was obtained from the IUCN redlist website (https://www.iucnredlist.org/).

CRediT authorship contribution statement

RK, HM: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing - original draft

MJS: Supervision; Validation; Writing - review & editing

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.

Acknowledgements

R.K. was funded with a Swiss National Science Foundation (P2ZHP2_175028). We are grateful to two reviewers for their helpful comments. We are thankful to Pierre Defos du Rau for giving permission to use data of Waterbird Conservation Value score for Ramsar sites.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150806.

References

Ahmadalipour, A., Moradkhani, H., 2018. Escalating heat-stress mortality risk due to global warming in the Middle East and North Africa (MENA). Environ. Int. 117, 215–225.

Albright, T.P., Pidgeon, A.M., Rittenhouse, C.D., Clayton, M.K., Flather, C.H., Culbert, P.D., et al., 2010. Effects of drought on avian community structure. Glob. Chang. Biol. 16, 2158–2170.

Ayache, F., Thompson, J., Flower, R., Boujarra, A., Rouatbi, F., Makina, H., 2009. Environmental characteristics, landscape history and pressures on three coastal lagoons in the southern Mediterranean region: merja zerga (Morocco), Ghar El Melh (Tunisia) and Lake manzala (Egypt). Hydrobiologia 622, 15–43.

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data 5, 180214.

Besnard, G., Khadari, B., Baradat, P., Bervillé, A., 2002. Combination of chloroplast and mitochondrial DNA polymorphisms to study cytoplasm genetic differentiation in the olive complex (Olea europaea L.). Theor. Appl. Genet. 105, 139–144.

Bidwell, M.T., Green, A.J., Clark, R.G., 2014. Random placement models predict species–area relationships in duck communities despite species aggregation. Oikos 123, 1499–1508.

Blanckenberg, M., Mlambo, M.C., Parker, D., Motitsoe, S.N., Reed, C., 2020. Protected and un-protected urban wetlands have similar aquatic macroinvertebrate communities: a case study from the cape flats sand fynbos region of southern Africa. PLoS One 15, e0233889.

Both, C., Bouwhuis, S., Lessells, C., Visser, M.E., 2006. Climate change and population declines in a long-distance migratory bird. Nature 441, 81–83.

Bridgewater, P., Kim, R.E., 2021. The Ramsar convention on wetlands at 50. Nat. Ecol. Evol. 5, 268–270.

Bucchignani, E., Mercogliano, P., Panitz, H.-J., Montesarchio, M., 2018. Climate change projections for the Middle East-North Africa domain with COSMO-CLM at different spatial resolutions. Adv. Clim. Chang. Res. 9, 66–80.

Cady, S.M., O'Connell, T.J., Loss, S.R., Jaffe, N.E., Davis, C.A., 2019. Species-specific and temporal scale-dependent responses of birds to drought. Glob. Chang. Biol. 25, 2691–2702.

Chen, H., Zhang, W., Gao, H., Nie, N., 2018. Climate change and anthropogenic impacts on wetland and agriculture in the Songnen and Sanjiang Plain, Northeast China. Remote Sens. 10, 356.

Cherkaoui, S.I., Hanane, S., Magri, N., El Agbani, M.-A., Dakki, M., 2015. Factors influencing species-richness of breeding waterbirds in moroccan IBA and Ramsar wetlands: a macroecological approach. Wetlands 35, 913–922.

Cherkaoui, S.I., Selmi, S., Hanane, S., 2017. Ecological factors affecting wetland occupancy by breeding anatidae in the southwestern Mediterranean. Ecol. Res. 32, 259–269.

Conradie, S.R., Woodborne, S.M., Cunningham, S.J., McKechnie, A.E., 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. Proc. Natl Acad. Sci. USA 116, 14065–14070.

Conradie, S.R., Woodborne, S.M., Wolf, B.O., Pessato, A., Mariette, M.M., McKechnie, A.E., 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. Conserv. Physiol. 8, coaa048.

Cuttelod, A., García, N., Malak, D.A., Temple, H.J., Katariya, V., 2009. The Mediterranean: A Biodiversity Hotspot Under Threat. Wildlife in a Changing World–An Analysis of the 2008 IUCN Red List of Threatened Species, p. 89.

Davidson, N.C., 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar. Freshw. Res. 65, 934–941.

Davidson, N., Fluet-Chouinard, E., Finlayson, C., 2018. Global extent and distribution of wetlands: trends and issues. Mar. Freshw. Res. 69, 620–627.

Davidson, N.C., van Dam, A.A., Finlayson, C.M., McInnes, R.J., 2019. Worth of wetlands: revised global monetary values of coastal and inland wetland ecosystem services. Mar. Freshw. Res. 70, 1189–1194.

Deacon, C., Samways, M.J., Pryke, J.S., 2019. Aquatic insects decline in abundance and occupy low-quality artificial habitats to survive hydrological droughts. Freshw. Biol. 64, 1643–1654.

El Falah, S., Dakki, M., Mansouri, I., 2021. Mapping analysis of the wetland loss in loukkos (Morocco) under agricultural managements. Bulgarian J. Agr. Sci. 27, 186–193.

Faramarzi, M., Abbaspour, K.C., Vaghefi, S.A., Farzaneh, M.R., Zehnder, A.J., Srinivasan, R., et al., 2013. Modeling impacts of climate change on freshwater availability in Africa. J. Hydrol. 480, 85–101.

Ferreira, S., Boudot, J.-P., El Haissoufi, M., Alves, P.C., Thompson, D.J., Brito, J.C., et al., 2016. Genetic distinctiveness of the damselfly Coenagrion puella in North Africa: an overlooked and endangered taxon. Conserv. Genet. 17, 985–991.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.

Finlayson, M., Cruz, R., Davidson, N., Alder, J., Cork, S., de Groot, R., 2005. Millennium Ecosystem Assessment: Ecosystems and Human Well-being: Wetlands and Water Synthesis. Island Press.

Finlayson, C.M., Arthington, A.H., Pittock, J., 2018. Freshwater ecosystems in protected areas. Conservation and Management. Routledge.

Froufe, E., Ferreira, S., Boudot, J.-P., Alves, P.C., Harris, D.J., 2014. Molecular phylogeny of the Western palaearctic cordulegaster taxa (Odonata: anisoptera: Cordulegastridae). Biol. J. Linn. Soc. 111, 49–57.

Gaget, E., Le Viol, I., Pavón-Jordán, D., Cazalis, V., Kerbiriou, C., Jiguet, F., et al., 2020. Assessing the effectiveness of the Ramsar convention in preserving wintering waterbirds in the Mediterranean. Biol. Conserv. 243, 108485.

Gardner, R.C., Davidson, N.C., 2011. The Ramsar Convention. Wetlands. Springer, pp. 189–203.

Gardner, R.C., Finlayson, C., 2018. Global wetland outlook: state of the World's wetlands and their services to people. Ramsar Convention Secretariat.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., Heinsohn, R., 2011. Declining body size: a third universal response to warming? Trends Ecol. Evol. 26, 285–291.

Gardner, R.C., Barchiesi, S., Beltrame, C., Finlayson, C., Galewski, T., Harrison, I., 2015. State of the world's wetlands and their services to people: a compilation of recent analyses. Ramsar Briefing Note No. 7. Ramsar Convention Secretariat, Gland, Switzerland.

Gopal, B., 2009. Biodiversity in wetlands. The Wetlands Handbook. 2, pp. 65–95.

Guicking, D., Joger, U., Wink, M., 2008. Molecular phylogeography of the viperine snake Natrix maura (Serpentes: Colubridae): evidence for strong intraspecific differentiation. Org. Divers. Evol. 8, 130–145.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Gutiérrez-Ortega, J.S., Jiménez-Cedillo, K., Pérez-Farrera, M.A., Vovides, A.P., Martínez, J.F., Molina-Freaner, F., et al., 2018. Considering evolutionary processes in cycad conservation: identification of evolutionarily significant units within Dioon sonorense (Zamiaceae) in northwestern Mexico. Conserv. Genet. 19, 1069–1081.

Habel, J.C., Dieker, P., Schmitt, T., 2009. Biogeographical connections between the Maghreb and the Mediterranean peninsulas of southern Europe. Biol. J. Linn. Soc. 98, 693–703.

Habel, J.C., Lens, L., Rödder, D., Schmitt, T., 2011. From Africa to Europe and back: refugia and range shifts cause high genetic differentiation in the marbled white butterfly melanargia galathea. BMC Evol. Biol. 11, 1–15.

Hamza, F., Selmi, S., 2018. Diversity of waterbirds wintering in Douz wetlands (south Tunisia): factors affecting wetland occupancy and species richness. Ecol. Res. 33, 917–925.

Harebottle, D.M., Underhill, L.G., 2016. Assessing the value of wetlands to waterbirds: exploring a population-based index at flyway and regional levels. Ostrich 87, 7–21.

Hewitt, G.M., 2004. Genetic consequences of climatic oscillations in the quaternary. Philos. Trans. R. Soc. Lond. B Biol. Sci. 359, 183–195.

Hijmans, R.J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Lamigueiro, O.P., Bevan, A., Racine, E.B., Shortridge, A., 2015. Package 'raster'. R package. https://rspatial.org/raster.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A., Jess, M., Williams, S.E., 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos. Trans. R. Soc., B 367, 1665–1679.

Husemann, M., Schmitt, T., Zachos, F.E., Ulrich, W., Habel, J.C., 2014. Palaearctic biogeography revisited: evidence for the existence of a north african refugium for Western palaearctic biota. J. Biogeogr. 41, 81–94.

Iknayan, K.J., Beissinger, S.R., 2018. Collapse of a desert bird community over the past century driven by climate change. Proc. Natl. Acad. Sci. 115, 8597–8602.

Jackson, M.C., Loewen, C.J., Vinebrooke, R.D., Chimimba, C.T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. Glob. Chang. Biol. 22, 180–189.

Jackson, M.C., Pawar, S., Woodward, G., 2021. The temporal dynamics of multiple stressor effects: from individuals to ecosystems. Trends Ecol. Evol. 36, 402–410.

Jarzyna, M.A., Zuckerberg, B., Finley, A.O., Porter, W.F., 2016. Synergistic effects of climate and land cover: grassland birds are more vulnerable to climate change. Landsc. Ecol. 31, 2275–2290.

Jiguet, F., Gadot, A.S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. Glob. Chang. Biol. 13, 1672–1684.

Keys, P.W., Barnes, E.A., Carter, N.H., 2021. A machine-learning approach to human footprint index estimation with applications to sustainable development. Environ. Res. Lett. 16, 044061.

Khelifa, R., Mellal, M.K., Zouaimia, A., Amari, H., Zebsa, R., Bensouilah, S., et al., 2016. On the restoration of the last relict population of a dragonfly urothemis edwardsii selys (Libellulidae: Odonata) in the Mediterranean. J. Insect Conserv. 20, 797–805.

Khelifa, R., Mahdjoub, H., Baaloudj, A., Cannings, R.A., Samways, M.J., 2021b. Effects of both climate change and human water demand on a highly threatened damselfly. Sci. Rep. 11, 7725.

Khelifa, R., Mahdjoub, H., Baaloudj, A., Cannings, R.A., Samways, M.J., 2021c. Remarkable population resilience in a north african endemic damselfly in the face of rapid agricultural transformation. Insects 12, 353.

Khelifa, R., Deacon, C., Mahdjoub, H., Suhling, F., Simaika, J.P., Samways, M.J., 2021a. Dragonfly conservation in the increasingly stressed African Mediterranean-type ecosystems. Front. Environ. Sci. 9.

Kleijn, D., Cherkaoui, I., Goedhart, P.W., van der Hout, J., Lammertsma, D., 2014. Waterbirds increase more rapidly in Ramsar-designated wetlands than in unprotected wetlands. J. Appl. Ecol. 51, 289–298.

Lepais, O., Muller, S.D., Saad-Limam, S.B., Benslama, M., Rhazi, L., Belouahem-Abed, D., et al., 2013. High genetic diversity and distinctiveness of rear-edge climate relicts maintained by ancient tetraploidisation for Alnus glutinosa. PLoS One 8, e75029.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462, 1052–1055.

Lomnicky, G.A., Herlihy, A.T., Kaufmann, P.R., 2019. Quantifying the extent of human disturbance activities and anthropogenic stressors in wetlands across the conterminous United States: results from the National Wetland Condition Assessment. Environ. Monit. Assess. 191, 1–23.

Lowry, D.B., Hoban, S., Kelley, J.L., Lotterhos, K.E., Reed, L.K., Antolin, M.F., 2017. Breaking RAD: An Evaluation of the Utility of Restriction Site-associated DNA Sequencing for Genome Scans of Adaptation. Wiley Online Library.

McInnes, R.J., Davidson, N.C., Rostron, C.P., Simpson, M., Finlayson, C.M., 2020. A citizen science state of the World's wetlands survey. Wetlands 40, 1577–1593.

Mitsch, W.J., Gosselink, J.G., 2015. Wetlands. Wiley.

Møller, A.P., Fiedler, W., Berthold, P., 2010. Effects of Climate Change on Birds. Oxford University Press, Oxford, UK.

Mor, J.-R., Dolédec, S., Acuña, V., Sabater, S., Muñoz, I., 2019. Invertebrate community responses to urban wastewater effluent pollution under different hydro-morphological conditions. Environ. Pollut. 252, 483–492.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Newbold, T., Oppenheimer, P., Etard, A., Williams, J.J., 2020. Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. Nat. Ecol. Evol. 4, 1630–1638.

Northrup, J.M., Rivers, J.W., Yang, Z., Betts, M.G., 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. Glob. Chang. Biol. 25, 1561–1575.

Ohlberger, J., 2013. Climate warming and ectotherm body size–from individual physiology to community ecology. Funct. Ecol. 27, 991–1001.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20 (2), 289–290.

Pavón-Jordán, D., Azafzaf, H., Balaž, M., Bino, T., Borg, J.J., Božič, L., et al., 2020. Positive impacts of important bird and biodiversity areas on wintering waterbirds under changing temperatures throughout Europe and North Africa. Biol. Conserv. 246, 108549.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371.

Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10, 439–446.

Pebesma, E., Bivand, R., Pebesma, M.E., RColorBrewer, S., Collate, A., 2012. Package 'sp'. The Comprehensive R Archive Network.

Pekel, J.-F., Cottam, A., Gorelick, N., Belward, A.S., 2016. High-resolution mapping of global surface water and its long-term changes. Nature 540, 418–422.

Pereda, O., von Schiller, D., García-Baquero, G., Mor, J.-R., Acuña, V., Sabater, S., et al., 2021. Combined effects of urban pollution and hydrological stress on ecosystem functions of Mediterranean streams. Sci. Total Environ. 753, 141971.

Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Reconceptualizing synergism and antagonism among multiple stressors. Ecol. Evol. 5, 1538–1547.

Pinheiro, J., Bates, D., Sarkar, D., DebRoy, S., R Core Team, 2020. nlme: linear and nonlinear mixed effects models. R package version 3.1-151. URL: https://CRAN.R-project.org/package=nlme.

R Development Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramdani, M., Flower, R.J., Elkhiati, N., Kraïem, M.M., Fathi, A.A., Birks, H.H., et al., 2001. North african wetland lakes: characterization of nine sites included in the CASSARINA project. Aquat. Ecol. 35, 281–302.

Riddell, E.A., Iknayan, K.J., Wolf, B.O., Sinervo, B., Beissinger, S.R., 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. Proc. Natl Acad. Sci. USA 116, 21609–21615.

Riddell, E., Iknayan, K., Hargrove, L., Tremor, S., Patton, J., Ramirez, R., et al., 2021. Exposure to climate change drives stability or collapse of desert mammal and bird communities. Science 371, 633–636.

Roselaar, K., 2006. The boundaries of the palearctic region. Br. Birds 99, 602.

Samways, M.J., Deacon, C., Kietzka, G.J., Pryke, J.S., Vorster, C., Simaika, J.P., 2020. Value of artificial ponds for aquatic insects in drought-prone southern Africa: a review. Biodivers. Conserv. 29, 3131–3150.

Sayoud, M.S., Salhi, H., Chalabi, B., Allali, A., Dakki, M., Qninba, A., et al., 2017. The first coordinated trans-north african mid-winter waterbird census: the contribution of the international waterbird census to the conservation of waterbirds and wetlands at a biogeographical level. Biol. Conserv. 206, 11–20.

Schaub, M., Kania, W., Köppen, U., 2005. Variation of primary production during winter induces synchrony in survival rates in migratory white storks Ciconia ciconia. J. Anim. Ecol. 74, 656–666.

Sebastián-González, E., Green, A.J., 2014. Habitat use by waterbirds in relation to pond size, water depth, and isolation: lessons from a restoration in southern Spain. Restor. Ecol. 22, 311–318.

Sheridan, J.A., Bickford, D., 2011. Shrinking body size as an ecological response to climate change. Nat. Clim. Chang. 1, 401–406.

Sievers, M., Hale, R., Parris, K.M., Swearer, S.E., 2018. Impacts of human-induced environmental change in wetlands on aquatic animals. Biol. Rev. 93, 529–554.

Simonsen, T.J., Olsen, K., Djernæs, M., 2020. The african-iberian connection in odonata: mtDNA and ncDNA based phylogeography of Aeshna cyanea (Müller, 1764)(Odonata: Aeshnidae) in Western palaearctic. Arthropod Syst.Phylogeny 78 (309), 320.

Stevens, B.S., Conway, C.J., 2020. Predictive multi-scale occupancy models at range-wide extents: effects of habitat and human disturbance on distributions of wetland birds. Divers. Distrib. 26, 34–48.

Taylor, N.G., Grillas, P., Al Hreisha, H., Balkız, Ö., Borie, M., Boutron, O., et al., 2021. The future for Mediterranean wetlands: 50 key issues and 50 important conservation research questions. Reg. Environ. Chang. 21, 33.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., et al., 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535, 241–245.

Vicente-Serrano, S.M., Staff, M., 2015. The Climate Data Guide: Standardized Precipitation Evapotranspiration Index (SPEI). Retreived from https://climatedataguide.ucar.edu/climate-data/standardized-precipitation-evapotranspiration-index-spei. (Accessed 5 June 2021).

Volkmann, L., Martyn, I., Moulton, V., Spillner, A., Mooers, A.O., 2014. Prioritizing populations for conservation using phylogenetic networks. PLoS One 9, e88945.

Williams, B.A., Venter, O., Allan, J.R., Atkinson, S.C., Rehbein, J.A., Ward, M., Di Marco, M., Grantham, H.S., Ervin, J., Goetz, S.J., 2020. Change in terrestrial human footprint drives continued loss of intact ecosystems. One Earth 3, 371–382.

Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., Brashares, J.S., 2008. Accelerated human population growth at protected area edges. Science 321, 123–126.

Woodward, F.I., Woodward, F., 1987. Climate and Plant Distribution. Cambridge University Press.

Xi, Y., Peng, S., Ciais, P., Chen, Y., 2021. Future impacts of climate change on inland Ramsar wetlands. Nat. Clim. Chang. 11, 45–51.