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Article impact statement: Waterbird communities do not adjustment to climate warming when natural habitat conversion is >5% over 15 years.

Abstract

While the impacts of climate and land use changes on biodiversity have been widely documented, their joint effects remain poorly understood. We evaluated how non-breeding waterbird communities adjust to climate warming along a gradient of land use change. Using mid-winter waterbird counts (132 species) at 164 major non-breeding sites in 22 Mediterranean countries, we assessed the changes in species composition during 1991-2010, regarding thermal niche position and breadth, in response to regional and local winter temperature anomalies and to natural habitat conversion. We showed that in response to the temperature increase, communities became relatively richer in warm-dwelling species, but less where natural habitat conversion occurred. At the sites affected by natural habitat conversion, the overall species richness decreased with time, while the abundance relatively increased for the species with a broader thermal niche, independently of their thermal affinities. The strong negative relationship between natural habitat conversion and community adjustment to temperature increases suggests an antagonistic interaction between climate warming and habitat change. Indeed, we found no evidence of community adjustment to climate warming when natural habitat conversion was higher than 5% over 15 years. These results underline the importance of habitat conservation in community adjustment to climate warming.

Introduction

Climate warming and land use change are among the strongest drivers of biodiversity changes, and their combination has major consequences for its conservation (Pereira et al. 2010). A temperature increase is likely to increase the relative abundance of warm-dwelling species (Devictor et al. 2008), while land use change decreases the relative abundance of habitat-specialized species (Clavel et al. 2011). An increasing body of literature reports interacting effects between climate warming and land use change on species abundance as being either synergistic or antagonistic (Brook et al. 2008; Oliver and Morecraft 2014; and Côté et al. 2016). A synergetic interaction between climate warming and land use changes should result in an increase in warm-dwelling and habitat generalist species, while an antagonistic one could result in the apparent lack of species response to one driver. As an example, climate warming and the conversion of tropical forest to farmland lead to an increase in abundance of warm-dwelling birds, adapted to warmer and drier conditions (synergic, Frishkoff et al. 2016), while major land use changes in Europe likely prevent the increase of warm-dwelling bird despite climate warming (antagonistic, Kerbiriou et al. 2009; Galewski and Devictor 2016). Yet, the

detection of the interaction effect depends on the magnitude of the biological changes, which is influenced by the intensity of the driver (Côté et al. 2016). To date, few empirical studies have explored species thermal tolerance (Jiguet et al. 2006) in relation to a gradient of land use change interacting with climate warming (Oliver and Morecraft 2014; Pearce-Higgins and Green 2014; Sirami et al. 2016).
Species tolerance and persistence facing one or more drivers of change are related to the breadth of their ecological niche (Hutchinson 1957) and to the position where these changes occur within the niche along suitable environmental gradients (Grenouillet and Comte 2014). Generalist species, with larger niche dimensions, have a higher tolerance to environmental variations (Clavel et al. 2011) or extreme events (Jiguet et al. 2006). Conversely, specialists have smaller niche dimensions, but they show a higher performance in exploiting their environmental niche when conditions are favourable (Poisot et al. 2011). Since niche breadth is correlated between the different dimensions of the niche (Brown 1984), i.e. specialist species are usually specialists in more than one niche dimension (Barnagaud et al. 2012; Carboni et al. 2016), specialist species are presumed to be more vulnerable to the joint effects of several drivers of biodiversity changes (Slatyer et al. 2013). In case of interaction between climate warming and land use change, one would then expect land use change would reduce the abundance of specialist species more than that of generalist species (Clavel et al. 2011), which are probably both thermal and habitat generalists due to the correlations between niche dimensions (Barnagaud et al. 2012).

To assess these responses, the community weighted mean trait indices (Lavorel et al. 2008) are useful approaches based on species niche position and breadth, commonly used to investigate community adjustment to climate warming and land use change (Devictor et al. 2008; Clavel et al. 2011). Due to climate warming, the average thermal affinity of the community (hereafter, community temperature index, CTI) assessed with the species thermal niche positions (hereafter, species temperature index STI) is expected to increase (Devictor et al. 2008). Similarly, due to additional land use change (Clavel et al. 2011) or high temperature variation (Jiguet et al. 2006) the average thermal range of community (hereafter, community temperature range, CTR) assessed with the species thermal niche range (hereafter, species temperature range STR) is expected to increase. While the CTI increase with temperature is largely described, notably for breeding (e.g. Devictor et al. 2008; Gaüzère et al. 2016) and non-breeding birds (Godet et al. 2011; Gaget et al. 2018), the CTR should provide additional insights on why alternative CTI changes can be observed in case of significant land use change (e.g. Kerbiriou et al. 2009; Galewski and Devictor 2016).

Here, we investigated changes in the thermal niche position and breadth of non-breeding waterbird communities according to changes in temperature and to natural habitat conversion (NHC). We considered the changes in species abundance (n = 132) at 164 sites across the Mediterranean basin (n = 22 countries) during 20 years. We described community changes in terms of species thermal affinity by using the CTI and species thermal range by using the CTR. By determining species contributions to changes in these two community indices (Princé and Zuckerberg 2015), we evaluated which species relatively increased in abundance with increasing temperature or with the interaction between increasing temperature and NHC. We thus hypothesized that 1) the relative abundance of the warm-dwelling species will increase (CTI increase) with increasing temperature, and 2) the relative abundance of thermal generalists will increase (CTR increase) with the interaction between NHC and increasing temperature.

Material and methods

Study sites: temperature changes and NHC

We focused on the Mediterranean region (22 countries, Fig. 1). This region faces rapid land conversion (Newbold et al. 2015) and climate warming (+0.25°C per decade in winter, Mariotti et al. 2015, Appendix S1). Using the HadCRUT4 dataset (Morice et al. 2012), we calculated local (Tanom

Local, 0.5° grid resolution and based on the geographic coordinates of the monitored site) and regional (Tanom Regional, Mediterranean region, 30°N-45°N and 10°W-40°E) winter temperature anomalies as the average of the mean temperature of November, December and January per year minus the average temperature of these months over the 1991-2010 period (Pearson correlation: rTanom Local-Tanom Regional = 0.45, rTanom Regional-Year = 0.32, and rTanom Local-Year = 0.37).

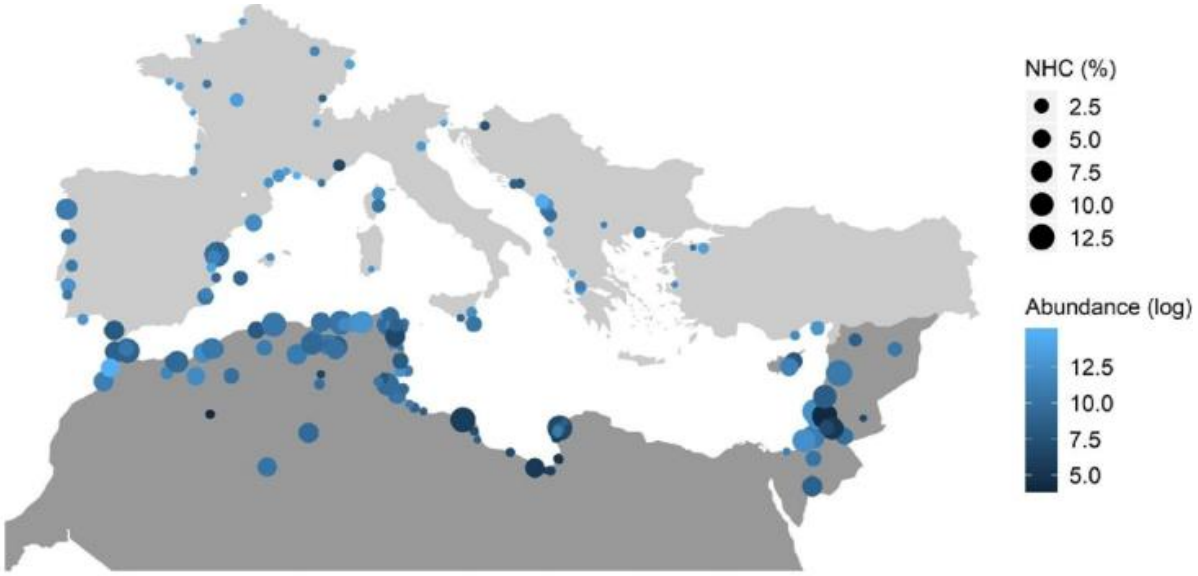

Figure 1:Distribution of the monitored sites in the Mediterranean Basin (n=164). Point size is proportional to the natural habitat conversion (NHC) and point colour corresponds to the non¬breeding waterbird average abundance (log), light blue for the more numerous. Light and dark grey colours correspond to the northern and the southern shore, respectively

To document the NHC at 164 bird-surveyed sites, we used the GlobWetland-II database (http://www.globwetland.org). Land cover data in 1990 and 2005 were derived from Landsat satellite images (see Beltrame et al. (2015); Perennou et al. (2018) for methods, resolution of 30m). From the classification provided by Perennou et al. (2018) we defined as “natural habitats”, habitats with reduced anthropogenic impacts (e.g., marshes, rivers, lagoons, reedbeds, or grasslands) and “man-made habitats” as habitats intensively impacted by anthropogenic activities (e.g., urban area, agricultural lands, dams, salines or reservoirs). We measured the proportion of NHC at each site between 1990 and 2005 (reported error rate across natural and man-made habitats: 4.42%).

Waterbird monitoring

Waterbirds were monitored under the framework of the International Waterbird Census programme (see Delany (2005) for the protocol). A single annual count in January was performed to monitor the waterbird populations during the non-breeding season, by both professional and volunteering ornithologists under the coordination of Wetlands International (www.wetlands.org). Bird species abundance data were used for the 164 sites covered by the GlobWetland-II database. In order to study the long-term changes in community composition, these sites met the following criteria: (1) at least two counts between 1991 and 2010 and (2) more than five wetland species recorded during each count. We considered the 132 species of the Western Palearctic region that were listed in the African-Eurasian Migratory Waterbird Agreement (AEWA, http://www.unep-aewa.org; Appendix S2), corresponding to species for which the Mediterranean Basin is an important region during the non-breeding season (97% of full migratory species). The dataset included 1,797 count events and 36.8 million counted birds, with on average 11.0 (SD 5.2) count events per site across the two decades, and 90 (SD 17) surveyed sites per year, without temporal trend during the study period (linear model, $p > 0.5$).

Species temperature metrics and species trait originalities

To calculate the CTI and CTR, we first determined the winter STI and the winter STR. The winter STI was assessed following Gaget et al. (2018) adapted from the breeding STI (Devictor et al. 2008), as the average of the mean temperature of January (WorldClim database, http://worldclim.org/, resolution 0.05 decimal degree, from 1950-2000) across the non-breeding species range in the African-Eurasian region covered by the AEWA (extracted from www.birdlife.org 2015). The STR was assessed as the interval between the average temperatures of the thermal minimum (5% lower) and maximum (95% upper) of the non-breeding species thermal range (see Gregory et al. (2009)). STI and STR refer to the thermal niche position and the thermal niche breadth of the species, respectively, and were not correlated (rPearson = -0.11, p = 0.2).

To determine whether species were cold- vs. warm-dwelling and thermal specialists vs. generalists, we computed „species trait originalities". The species trait originality is a measure of the extent to which the species temperature metric value differs from those of the other species in the community. We computed the species trait originality as the difference between the species temperature metric value and the average community weighted mean of the presence/absence data in the study area (Mediterranean Basin). Cold-dwelling (or, conversely, warm-dwelling) species have an STI below (above) the average CTI, and thermal specialist (or, conversely, generalist) species have an STR below (above) the average CTR.

Data analysis

Community weighted mean indices

We computed the CTI and CTR to evaluate changes in the thermal average and thermal range composition in communities. The CTI was calculated by weighting the STI value of each species inside a community by the log(x+1) of its abundance divided by the log of total species abundance, following Godet et al. (2011). We calculated similarly the CTR, using the STR instead of the STI (Appendix S3).

We evaluated how the CTI and CTR varied with NHC, with the proxies of climate warming (Tanom Local, Tanom Regional and year as a global warming proxy) and their interaction. We performed three different generalized linear mixed models (GLMMs, Gaussian error distributions, package nlme, Pinheiro et al. 2014) using one of the climate proxies per model. The response variable was the CTI or the CTR. The explanatory terms were the fixed effects and interactions between NHC and the climate proxy. The sites nested within a country were used as random effects to deal with the heterogeneity in national monitoring schemes (Gaget et al. 2018). The variables were standardized per site to focus on inter-annual variations. We added an exponential structure based on the geographical coordinates and verified the absence of spatial autocorrelation in the model residuals via autocorrelation plot checking (Zuur et al. 2009).

We performed complementary analyses to investigate potential bias. First, we verified that the site size, used as a covariable did not affect the results. Second, as the NHC was lower in the north of the Mediterranean Basin (Appendix S4, Fig. 1), we checked whether the CTI and CTR trends differed among the northern and southern Mediterranean shores. We used the same methodology as previously described (with the year, NHC and their interaction as fixed effects) and ran two individual GLMMs of the northern (Portugal to Turkey, n = 61 sites) and southern (Morocco to Syria, n = 103 sites) shores of the Mediterranean region. Third, we assessed whether the CTI and CTR trends were driven by a few abundant species by calculating them from the presence/absence data only. Species contributions.

We assessed species-specific contributions to the CTI and CTR trends. We used a jack-knife approach, in which species were removed one by one from the dataset to compute CTI and CTR values without the effect of the removed species (Princé and Zuckerberg 2015). The difference between the CTI (or

CTR) trend based on all species and the CTI (or CTR) trend based on all species minus species i corresponded to the contribution of species i. A species resulting in a CTI increase (or, conversely, decrease) with time had a positive (or, conversely, negative) contribution; the same applies for the CTR (Gaget et al. 2018).

Relative species trend

We inferred the relative species abundance trend from the species contributions to the CTI and CTR trends. Species contribution depended on the relative species trait originality and relative species population trend (Gaget et al. 2018). A species was relatively decreasing when 1) it had either a positive contribution and a positive trait originality or 2) a negative contribution and a negative trait originality. Conversely, a species was relatively increasing when 1) it had either a negative contribution and a positive trait originality or 2) a positive contribution and a negative trait originality. We mapped the distribution of the species that relatively increased and decreased (CTI contribution > 1%) using species distribution maps extracted from www.birdlife.org (2015), which were weighted by the species contribution to the CTI trend.

Trends in overall abundance and species richness

We estimated the temporal trends in abundance and species richness using GLMMs, with negative binomial distribution for the abundance, and Poisson error distribution for the species richness (package glmmTMB, Magnusson et al. 2017). We used the fixed effects and interactions between NHC and year and the random effect of the sites nested within the corresponding country. We controlled for spatial autocorrelation as in previous models.

Statistical analyses were performed with R 3.3.0 (R 2015), and the model residuals were graphically inspected to verify the model validity (Zuur et al. 2009). Graphical representations of the CTI and CTR interaction trends were generated with the visreg R package (Breheny et al. 2013) by combining 2D surface plots and segmented plots for 0%, 5%, and 10% NHC.

Results

Natural habitat conversion

For these study sites, the natural habitats covered in average 65% (SD 27) of the site surface in 2005, which represented a decrease of 0-13% since 1990 (on average 2.95 (3.40 SD), Appendix S4, S5). Approximately 60% of the NHC was due to conversion to man-made wetlands, A0% to agriculture and 10% to urbanisation.

CTI and CTR changes

The CTI increased during the twenty years of monitoring ($p < 0.001$, Table 1).

	Variables	Estimate	SE	DF	*t*	*p*	R^2
CTI	NHC	0.00	0.02	162	0.06	0.953	R_m^2=0.025
	Year	0.18	0.02	1631	8.17	<0.001	R_c^2=0.740
	NHC:Year	-0.09	0.02	1631	-4.06	<0.001	
	NHC	0.04	0.03	162	1.43	0.155	R_m^2=0.011
	Tanom Regional	0.13	0.05	1631	2.69	0.007	R_c^2=0.739
	NHC:Tanom Regional	-0.16	0.05	1631	-3.25	0.001	
	NHC	0.00	0.02	162	-0.10	0.923	R_m^2=0.010
	Tanom Local	0.01	0.02	1631	0.78	0.433	R_c^2=0.737
	NHC:Tanom Local	-0.04	0.02	1631	-2.30	0.020	
CTR	NHC	0.00	0.12	162	0.03	0.974	R_m^2=0.021
	Year	-0.26	0.03	1631	-8.45	<0.001	R_c^2=0.631
	NHC:Year	0.12	0.03	1631	3.69	<0.001	
	NHC	0.00	0.13	162	0.01	0.996	R_m^2=0.002
	Tanom Regional	-0.18	0.07	1631	-2.80	0.005	R_c^2=0.624
	NHC:Tanom Regional	0.11	0.07	1631	1.63	0.104	
	NHC	0.03	0.12	162	0.20	0.844	R_m^2=0.010
	Tanom Local	-0.02	0.02	1631	-0.88	0.380	R_c^2=0.620
	NHC:Tanom Local	0.01	0.02	1631	0.40	0.692	
Ab.	NHC	-0.40	0.14	162	-2.88	0.004	R_m^2=0.040
	Year	0.01	0.02	1631	0.47	0.636	R_c^2=0.887
	NHC:Year	0.02	0.02	1631	0.95	0.341	
S.R.	NHC	-0.14	0.04	162	-3.34	0.001	R_m^2=0.046
	Year	0.10	0.01	1631	17.99	<0.001	R_c^2=0.879
	NHC:Year	-0.03	0.01	1631	-5.24	<0.001	

Tableau 1: Effects of natural habitat conversion (NHC) on the community temperature index (CTI) and community temperature range (CTR) using three proxies of climate warming: the year, Tanom Regional for regional temperature anomalies and Tanom Local for local tem. $_a$ *Both* R_{m2} *(marginal and fixed effect only) and* R_{c2} *(conditional and full model) values were reported (Nakagawa and Schielzeth, 2013).*

The CTI also increased, more moderately, with $T_{anom\ Regional}$ but not with $T_{anom\ Local}$ (Table 1, Fig. 2a). However, the interaction was negative between NHC and years ($P = -0.09$, $p < 0.001$, Fig. 2a), $T_{anom\ Regional}$ ($P = -0.16$, $p = 0.001$) or $T_{anom\ Local}$ ($P = -0.04$, $p = 0.02$) (Table 1). In other words, the higher the habitat conversion was, the lower the CTI increase during the study period or the lower the CTI increase as a function of T_{anom} Regional or $T_{anom\ Local}$. Note that the apparent CTI decrease as a function of $T_{anom\ Regional}$ and $T_{anom\ Local}$ when NHC>10% was not significant (Appendix S7). On both sides of the Mediterranean, we found a similar CTI increase ($P_{Northern} = 0.25$, $p < 0.001$; $P_{Southern} = 0.27$, $p < 0.001$) and a similar negative interaction ($P_{Northern} = -0.16$, $p < 0.01$; $P_{Southern} = -0.13$, $p < 0.02$).

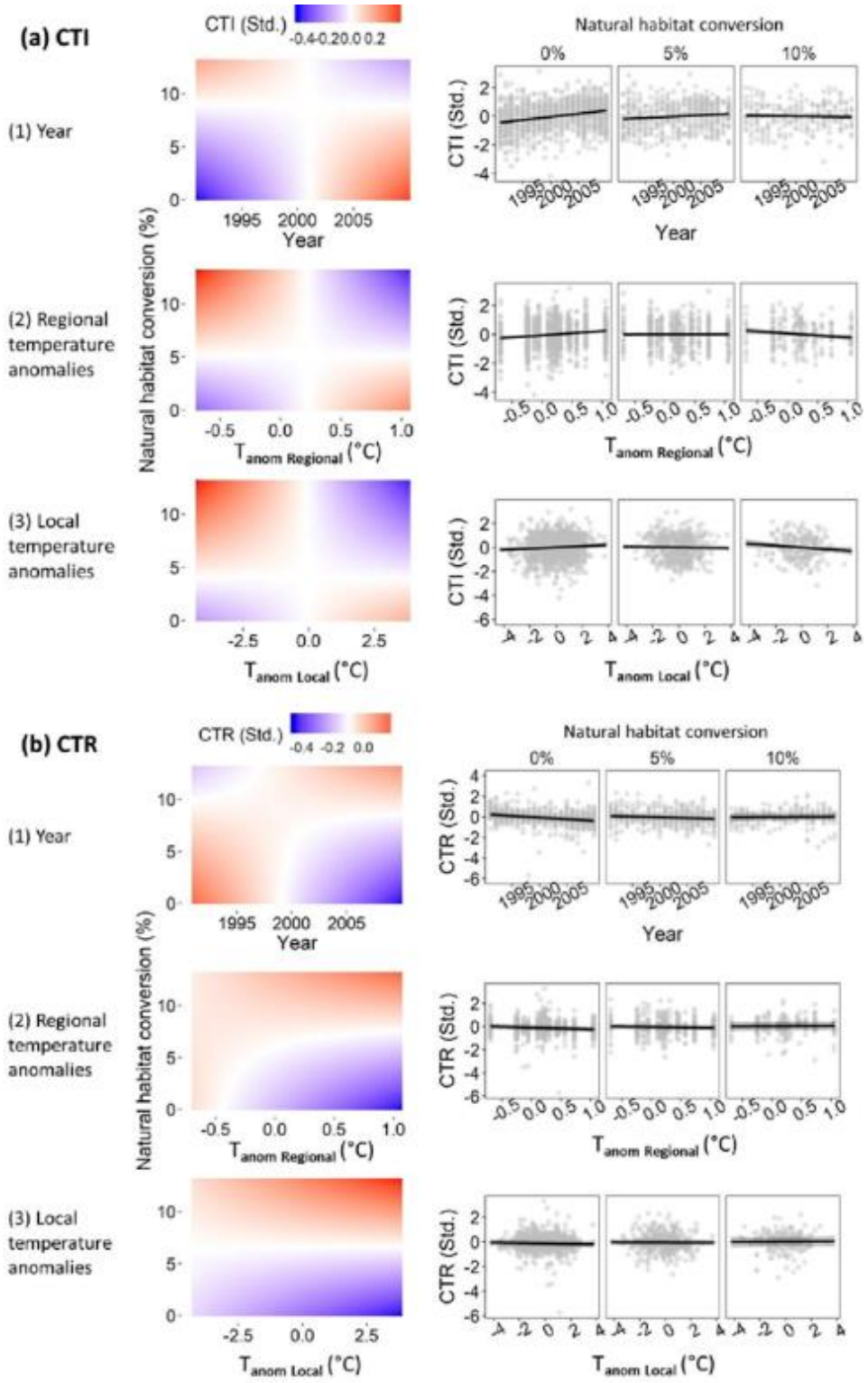

Figure 2: Community temperature index (CTI, standardized) (a) and community temperature range (CTR, standardized) (b) over three proxies of climate warming: (1) year, (2) regional ($T_{anom\ Regional}$) and (3) local temperature anomalies ($T_{anom\ Local}$), and over natural habitat conversion (%) by 2D surface plots with colour gradients depending on the CTI or CTR

The CTR decreased with time (P = -0.14, p < 0.001, Table 1, Fig. 2b) but decreased less with time when the NHC increased (P = 0.06, p < 0.001, Fig. 1, Table 1, Fig. 2b). $T_{anom\ Regional}$ had a significant negative effect on CTR (P = -0.10, p = 0.005) but not $T_{anom\ Local}$ (Table 1, Fig. 2b). Similar trends were found for CTI and CTR based on species abundance (Table 1) and species

presence/absence (Appendix S6; one exception was a change in significance for the CTR trend as a function of $T_{anom\ Regional}$), suggesting that the trends were not driven solely by the most abundant species.

Species contributions

Twenty-four species among the 132 (18%) were highly contributing to the CTI trend, with a contribution higher than 1% (Fig. 3, Appendix S2). Among these 24 species, 71% were relatively increasing, and 82% were warm-dwelling specialists (STR originality < 0 and STI originality > 0), mainly spending the non-breeding season on the southern Mediterranean shore (Fig. 4). Conversely, seven cold-dwelling species, i.e., species with a northern distribution (Fig. 4), were relatively decreasing (contribution higher than 1%).

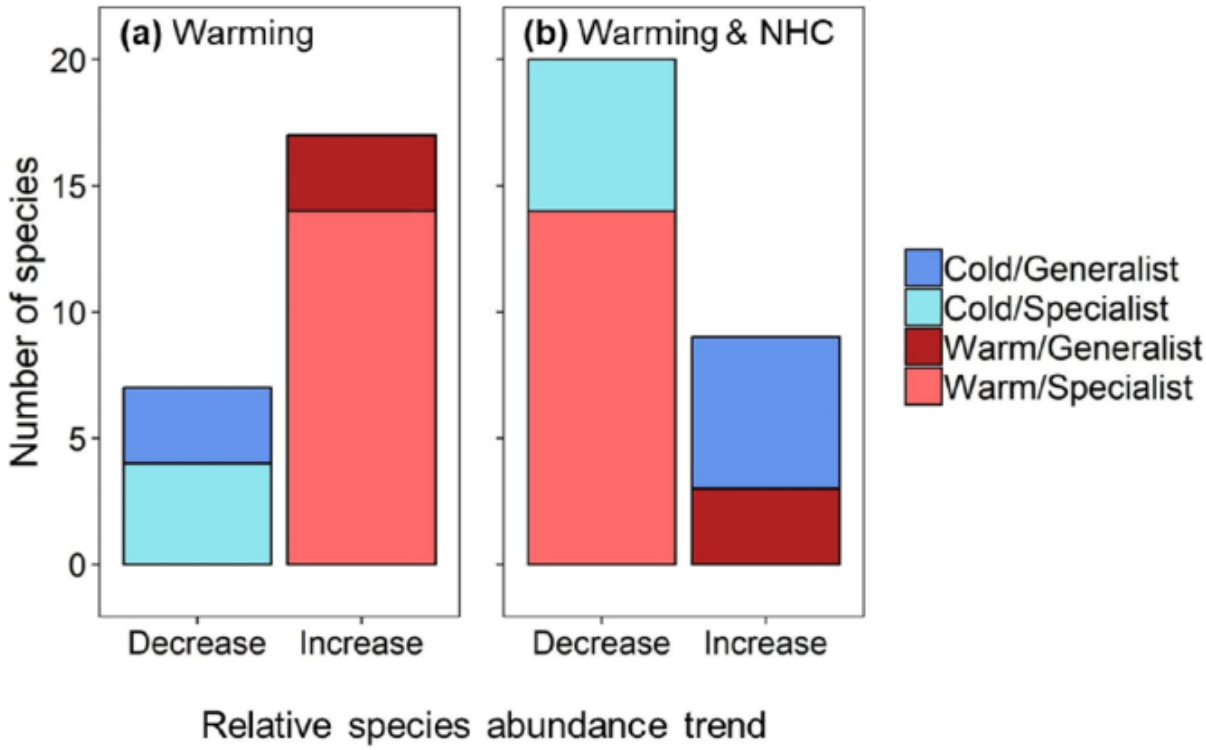

Figure 3 : Number of species with relative increasing or decreasing abundances, according to their contributions to CTI values over the years (a) and to CTR values over the years, considering the interactions with natural habitat conversion (NHC) (b). The species trends of cold- vs. warm-dwelling species and thermal specialist vs. generalist species (1991-2010) are relative to the overall species trends.

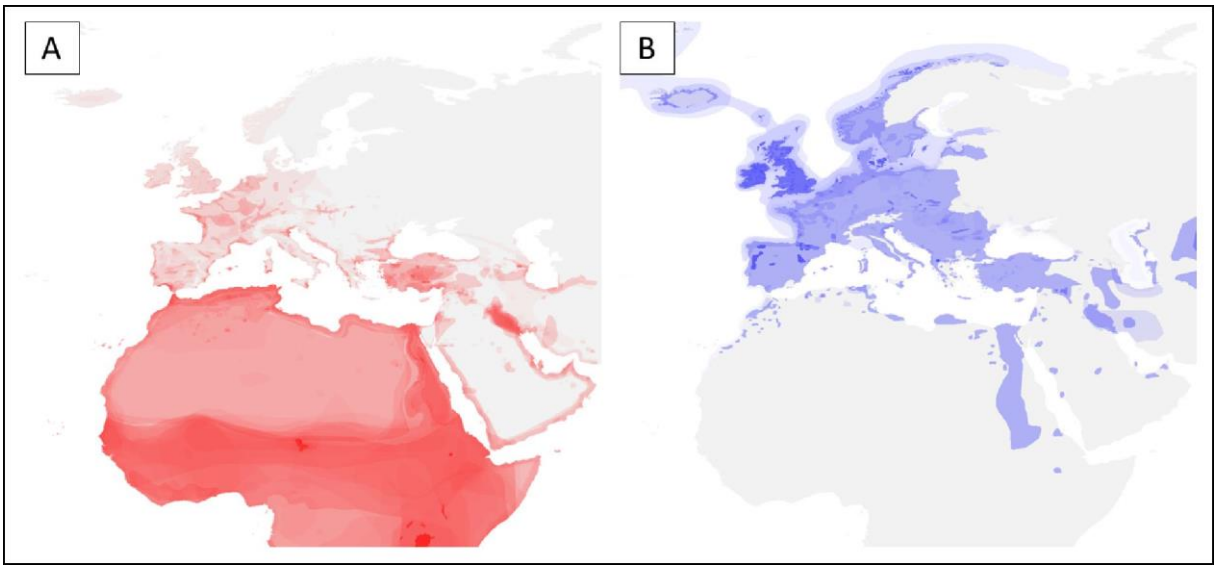

Figure 4: Non-breeding distribution of the species relatively increasing (A, n = 17) and decreasing (B, n = 7) in abundance over the years (CTI contribution > 1%). The light to dark colour contrast corresponds to the superposition of species distributions (distribution maps extracted from www.birdlife.org 2015) weighted by the species contributions to the CTI trend (Appendix S1).

Twenty-nine species (30%) contributed positively and more than 1% to the interaction effect between the years and NHC on CTR (Fig. 3, Appendix S2). Among these species, 69% were relatively declining, of which 70% were warm-dwelling specialists. The species that were relatively increasing with NHC over time were all thermal generalists (STR originality > 0), either cold- or warm-dwelling (Fig. 3).

Over time, the overall abundance displayed a non-significant trend ($\beta = 0.01$, $p = 0.6$), but species richness increased ($\beta = 0.10$, $p < 0.001$) (Table 1). The abundance and species richness were lower at sites where the NHC was higher ($\beta = -0.4\ 0$, $p < 0.001$; $\beta = -0.14$, $p < 0.001$, Table 1). The species richness decreased with the interaction between time and NHC
($\beta = -0.03$, $p < 0.001$), but the interaction had no significant effect on abundance ($\beta = 0A02$, $p = 0.3$).

Discussion

Our results suggest that non-breeding waterbird communities are changing in response to climate warming, with a relative increase in warm-dwelling species, which are mainly thermal specialists. However, the interaction between natural habitat conversion (NHC) and temperature increases led to a net decrease in species richness and a relative increase in thermal generalists, regardless of their thermal niche position (either cold- or warm-dwelling). We did not observe an increase in CTI where the NHC was higher than 5% over 15 years.

Community temperature changes in response to temperature increases

We have shown that in the Mediterranean region, in response to a 0.5°C increase in winter temperature during the study period (1991-2010) (Mariotti et al. 2015), the CTI for non-breeding waterbirds increased in the absence of NHC. Observing an increasing CTI over time and with increasing regional temperature anomalies, we could expect that climate warming induced a thermal community adjustment according to the thermal affinities of the species (Devictor et al. 2008). Such a level of bird community adjustment to climate warming had already been observed (for review, see Pearce-Higgins and Green 2014), including in non¬breeding waterbirds (Godet et al. 2011, Gaget et al. 2018).

Here, the changes in community thermal composition are more likely explained by the overall increase in temperature, using the year as a proxy, than by the regional (Mediterranean) or local

(site) temperature anomaly increases. The composition and structure of waterbird communities at non-breeding sites seem more dependent on the conditions along the migratory flyway than on the local temperatures, as observed by Sauter et al. (2010). For these migratory birds, year is likely a proxy for the climatic conditions experienced across their overall distribution range and along their breeding, migration and non-breeding areas (Newton 2008). Conversely, the local winter temperature was a poor predictor of non¬breeding waterbird community changes. This finding contrasts with those for breeding bird communities, which were greatly related to local climate variations (Gaüzère et al. 2015). A species range shift could also result in a time lag effect (Princé and Zuckerberg 2015), which occurs when the species shift depends on the temperature experienced during the previous years and not only on the current weather conditions (La Sorte and Jetz 2012). Therefore, the change in relative abundance has probably been smoothed over the years due to the birds' fidelity and longevity at their wintering sites, which may have reduced the response to local inter-annual variations (Maclean et al. 2008). Note that here we focused on the response to temperature increase, but species abundance, community composition and hence the CTI may also be affected by precipitation changes (Gaüzère et al. 2015) which could lead to a multi¬directional species range shift (Tingley et al. 2009). Given that precipitations are predicted to decrease in the Mediterranean region (Mariotti et al. 2015), complementary studies should further investigate the impact of precipitation changes on non-breeding waterbird communities.

Species contributions to the CTI increase suggest that more species were experiencing a northern range expansion than a southern range reduction. The increase in CTI was mainly due to a relative increase in warm-dwelling species abundance (n = 17, 15% of the species), combined with decreases in the abundances of a few of cold-dwelling species (n = 7, 5% of the species) (Fig. 3, Appendix S2). The Mediterranean Basin represents the northern (Fig. 4A) and southern (Fig. 4B) distribution edges of those species contributing the most to a CTI increase. A population increase at the leading edge of a species distribution is one of the most common adjustments to climate warming observed in the northern hemisphere (Pearce¬Higgins and Green 2014). This result indicates a likely positive effect of temperature increases on the population dynamics of warm-dwelling species (Gregory et al. 2009). Among these species, for example, the expansion of sedentary populations of the cold-sensitive cattle egret (Bubulcus ibis) was facilitated by milder winters in Europe (Hafner et al. 1992). Additionally, by decreasing their daily energy requirements (Wiersma and Piersma 1994), milder winters promote the northward shift of small shorebird species (Austin and Rehfish 2005). The relative decrease in cold-dwelling species abundance suggests a change at their trailing edge distribution (Thomas and Lennon 1999). As examples, the most abundant European breeding duck, the mallard (Anas platyrhynchos), is a cold-dwelling species with a positive contribution to the CTI increase, which shortened its migration distance at several flyway locations (Sauter et al. 2010, Gunnarsson et al. 2012). Similarly, the greylag goose (Anser anser) shifted its Mediterranean non-breeding range to more northern European countries in the 1990s (Ramo et al. 2015) and at the same time had an overall growing breeding population across Europe (BirdLife 2017). Such changes in non-breeding distributions suggest a reduction in the migratory distances, which may increase bird fitness by allowing them to preserve their fat resources for reproduction and reducing mortality rates during migration (Gilroy 2017). Alternatively, a winter range shift could also diminish the potential risk of an increasing migration distance in the case of a breeding range shift (Zurell et al. 2018). In this study, however, we were unable to identify whether the trailing edge shift corresponded to a range contraction or to a displacement of the entire species distribution area in response to the temperature increase (Pearce-Higgins and Green 2014). Further work should be carried out at the species flyway scale to assess the actual expansion/contraction of the range and its consequences on population dynamics (e.g., Pavón-Jordán et al. 2015).

Interaction between climate warming and NHC

Our results suggest that thermal community adjustment to temperature increase was disrupted towards an adjustment to both NHC and temperature increases, corresponding to an antagonistic interaction between the two drivers. The apparent antagonistic interaction led to a homogenization pattern of non-breeding waterbird communities over time, through a decrease in species richness, a relative decrease in thermal specialists and a relative increase in thermal generalist species. The result was independent of the CTI trend since there was no correlation between thermal niche position (STI) and thermal niche breadth (STR). Here, conversely to previous studies (e.g. Kerbiriou et al. 2009, Galewski and Devictor 2016), the observed decline in species richness over the homogenization process underpin the "losing species" pattern, occurring when species extirpation is higher than species colonization (Clavel et al. 2011). Interestingly, a higher number of specialist species increased when there is a temperature increase alone rather than when the NHC occurred (Fig. 3). This contrasts with other studies on breeding birds which found that the change in temperature induced a relative increase in generalist species (Davey et al. 2013, Gaüzère et al. 2015). In these studies however, the possible confounding interaction between temperature and land use changes was not considered. Antagonistic interactions are not frequently reported in the literature and therefore probably underestimate changes in biodiversity (Côté et al. 2016). Here the observed relative decrease in warm-dwelling specialists was found when the proportion of NHC was larger than 5% over 15 years (Fig. 2a), highlighting the importance of (i) investigating the interaction between land use change and climate warming (Sirami et al. 2016) and (ii) taking into account the magnitude of the changes even if they are relatively low (Oliver and Morecraft 2014).

Such finding provides crucial knowledge to improve future range projections (Pereira et al. 2010) and to prioritize conservation management on factors that can be locally managed, like the NHC (Brook et al. 2008).

Conservation implications

Our results highlight important conservation issues to mitigate the impact of climate change on migratory species. Some of the species that likely increase in abundance with a temperature increase are partial long-distance migrants, e.g., the black-winged stilt (Himantopus himantopus), glossy ibis (Plegadis falcinellus), and ruff (Calidris pugnax), which winter in sub-Saharan Africa, up to Maghreb and sporadically in southern Europe (Fig. 4A). However, in their African non-breeding grounds, these species are greatly impacted by habitat loss and degradation (Vickery et al. 2014), persecution, overexploitation and illegal killing (Bairlein 2016), and temperature and drought increases (Saether and Engen 2010). Thus, as climate warming is predicted to strengthen in the Mediterranean area (Mariotti et al. 2015), Mediterranean and European countries face increasing responsibilities to facilitate species adjustment to temperature increase by reducing the conversion of natural wetlands. Despite that the NHC was considered as a whole due to land cover classification used (Perennou et al. 2018), the diversity of land use threats on wetlands (Beltrame et al. 2015) encourages prioritisation of their impacts, notably by species specific investigations. In a global change context, these results have strong implications for biodiversity conservation and suggest that the adjustments of bird communities to climate warming can be improved by effective protected areas that will prevent NHC (Gaüzère et al. 2016, Lehikoinen et al. 2018, Peach et al. 2018).

A strong negative relationship between NHC and community adjustment to a temperature increase was detected, although the levels of NHC measured at the surveyed sites were lower than the rates reported for wetlands worldwide. The conversion for the 164 studied sites was on average 3% between 1990-2005 (ranging from 0 to 13%), while wetlands, excluding man-made wetlands, declined by an average of 30% between 1970 and 2008 globally (Davidson 2014, Dixon et al. 2016). This would suggest that the waterbird community adjustment to climate warming was greatly reduced at a global scale.

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