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Interactions between climate warming and management actions determining bird community change in protected areas

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ABSTRACT

Biodiversity is increasingly negatively affected by climate warming, making this issue a major conservation concern. Many bird species respond to warming temperatures by shifting distribution ranges, but these shifts often lag behind temperature changes. Protected areas (PAs) can facilitate such shifts, but a growing body of literature suggests that not all PAs facilitate climate warming responses equally, as realized management actions can differ. Here, we study waterbird community change as a response to climate warming in relation to targets of conservation projects implemented in Natura 2000 protected areas across the EU. We combine long-term waterbird survey data (i.e. International Waterbird Census) with data on conservation funded by the EU LIFE program, the main EU instrument for conservation. We used the community temperature index to measure thermal community changes over 28 years. We found community adjustment to climate warming lagged behind temperature. However, community change was twice as fast in sites were conservation was targeting wetland habitats compared with sites without habitat conservation. Targeting waterbirds directly did not lead to variation in community change compared with other types of species conservation. Our results imply that on the management level conservation targeting a community's habitat (rather than targeting the species group directly) is more likely to provide benefits for community adjustment to climate warming. This study demonstrates that management actions currently not targeting climate warming impacts on biodiversity, have the potential to support species responding to climate warming. However, conservation strategies need to be adapted to the challenges arising with climate warming.

1. Introduction

Current and projected climate warming will have increasing negative impacts on biodiversity (Bellard et al., 2012; IPCC, 2022). Many species, including birds, respond to changes in climate in various ways (McLaughlin et al., 2002; Parmesan, 2006; Pearce-Higgins et al., 2015; Stephens et al., 2016). One such response is a shift in distribution range towards the poles or higher elevations, which allows species to track their climatic niche and thereby cope with climatic changes such as warming temperatures (Devictor et al., 2008; Freeman et al., 2018; Tombre et al., 2019).

Such distribution shifts become easily visible in waterbirds (Maclean et al., 2008). Most waterbird species migrate between breeding and non-breeding grounds. This mobility assures they can quickly react to changes in temperature by adjusting where they overwinter (Maclean et al., 2008; Lehikoinen et al., 2013; Lehikoinen et al., 2021).

However, not only in waterbirds, are the observed distribution shifts often too slow to track temperature changes accordingly (Devictor et al., 2008; Lindström et al., 2013; Gaget et al., 2021), leading to climatic debt, a lag of biodiversity responses behind climatic changes (Devictor et al., 2012; Lenoir et al., 2020). Increasing mismatches between species niches and environmental conditions are therefore one major challenge for conservation. Developing conservation strategies that help species cope with climate warming, often called climate change adaptation strategies for biodiversity, will become increasingly important (Mawdsley et al., 2009; Bonebrake et al., 2018; Schuurman et al., 2022).

One main conservation tool in Europe is protected areas (PAs) (Godet and Devictor, 2018). They can act as buffers to climate warming or other negative pressures that interact with climate warming (Virkkala et al., 2014; Lehikoinen et al., 2019) and facilitate range shifts by providing suitable habitat for faster colonization and population growth (Thomas et al., 2012; Gillingham et al., 2015).

While protected areas are historically not managed to improve biodiversity responses to climate change, there has been substantial previous work suggesting their positive effects on the responses of bird communities to climate warming. PAs have been found to reduce disturbances and human exploitation, thereby improving conditions inside the protected area and reducing habitat loss and degradation (Andam et al., 2008; Gaston et al., 2008; Nelson and Chomitz, 2011).

Colonization of wetland bird species was observed to be greater inside than outside protected areas, likely due to higher habitat suitability inside protected areas (Hiley et al., 2013). PAs were also found to facilitate adjustment of bird community composition to temperature changes (Gaüzère et al., 2016; Hintsanen et al., 2023). Nevertheless, protection of an area per se is not yet enough to support species population responses to climate warming, as outcomes can be dependent on management (Visconti et al., 2019). A study by Wauchope et al. (2022) found that sites designated for waterbirds are more likely to benefit population increase than protected areas without management for waterbirds. For instance, Gaget et al. (2022) found the observed climate-warming driven community shifts of waterbirds in the European Unions (EU) Natura 2000 PA network to be faster in PAs designated for waterbirds and having a management plan.

Such protected area management can include a wide variety of conservation actions (such as improvement of breeding opportunities, predator control or restoration of previously exploited habitat types (such as peatlands or wet meadows)), that do not target climate warming adaptation per se. By altering habitat conditions or influencing species population dynamics, such management actions have the potential to facilitate bird responses to climate warming (Mawdsley et al., 2009; Bowgen et al., 2022) but it is unlikely that all management actions are affecting waterbird communities equally. Impacts can differ between particular management actions, but also species characteristics and local habitat characteristics. Interactions with other biotic or abiotic drivers (Parmesan, 2006), might also influence species responses to climate warming (Williams and Newbold, 2020). By classifying conservation interventions for climate change adaptation according to their specific species or habitat targets, Bowgen et al. (2022) found that actions targeting a species' habitats were the most successful in reducing negative impacts of climate change on these species. Species-specific interventions have often been found to be effective mostly for the targeted species (Bowgen et al., 2022), but conservation targeting specific species can also provide benefits for not directly targeted community members, for example through overall improvement of habitat conditions (Rhinehart et al., 2024) or by addressing a more extensive range of threats (Olivares-Rojas et al., 2024). Information on conservation targets is often more readily available than detailed information on implemented actions and using species or habitat targets to classify conservation projects reduces the risk of subjective interpretation of detailed conservation actions.

However, as biodiversity responses to warming temperatures also include dynamics that might not be desirable under traditional conservation strategies, such as population declines at the warm distribution edge during distribution range shifts, conservation benefits for species responses to climate warming might differ from benefits for more traditional conservation goals (Bonebrake et al., 2018). Therefore, the potential of conservation to facilitate species responses to warming temperatures, including actions not directly designed for climate change adaptation, needs to be evaluated in order to create successful future conservation strategies.

With this study, we aim to further investigate the impacts of conservation on waterbird community responses to warming temperatures by examining how the targets of conservation projects impact waterbird community responses. We intentionally include conservation projects not directly designed to target climate change adaptation for biodiversity to evaluate their potential to facilitate waterbird responses to warming temperatures. We specifically focus on conservation projects with different targets (species and habitat targets) funded by the EU LIFE program and implemented in protected areas within the European Union. The LIFE program, particularly the Nature and Biodiversity subprogram, is one of the main funding instruments to enforce management actions within the Natura 2000 protected area network in the EU. Projects can be characterized by their species or habitat targets. Despite LIFE funding being part of the EU strategy for biodiversity conservation, projects were often not specifically targeting threats caused by climate change and the LIFE programs role in improving species responses to climate warming needs further evidence. Indeed, the effects of LIFE funding on waterbird community adjustment to climate warming have been identified as inconsistent (Gaget et al., 2022). Although transition is underway (e.g. LIFE Natur'Adapt), the majority of conservation funding under the LIFE program was developed to target traditional conservation needs not considering climate warming (Lung et al., 2014). Nevertheless, actions not originally aiming at climate warming adaptation could have positive effects on waterbird responses to climate warming, which so far have not been consistently estimated or captured in any pan-European analyses. With this study we aim at investigating the potential of all types of conservation projects (different habitat and species targets) under the LIFE program, and include projects regardless of whether actions were originally designed for climate warming adaptation for biodiversity or not.

Several methods exist to assess climate warming impacts on biodiversity (Pacifici et al., 2015). Here we use the Community Temperature Index (CTI, Devictor et al., 2008), which is frequently used to track community shifts with regard to thermal niches. The CTI is a community weighted mean index based on climate niches of all species in a community (Devictor et al., 2008). CTI temporal trends reflect community reshuffling, as species track temperature changes by shifting their distribution range, i.e. the CTI increases with the relative increase of warm-dwelling species in a community. We consider a faster CTI increase as a positive community response to climate warming, as it indicates average species ability to track temperatures (Gaget et al., 2021).

First, we assess non-breeding waterbird community changes over 28 years in Natura 2000 (N2K) protected areas. Second, we then contrast CTI temporal trends between sites having received funding from the LIFE program for projects with different levels of waterbird specific habitat or species targets, to compare their potential to facilitate waterbird community changes. We compare CTI temporal change in sites associated with wetland or waterbird conservation to sites associated with conservation targeting other habitats or species or receiving funding for conservation projects not specifically targeting any species or habitat. We expect interactions between the species and habitat targeted projects carried out at the same site, and investigate these interaction effects. Finally, we compare community changes to temperature shifts to estimate climatic debts, and assess the lag of thermal community adjustment to climate warming.

2. Methods

2.1. Data

2.1.1. EU LIFE projects

To study the effects of LIFE funded conservation on non-breeding waterbird community responses to climate warming, we extracted information on conservation projects from the EU LIFE Program website (https://webgate.ec.europa.eu/life/publicWebsite/search/advanced, European Comission, EU LIFE Programme, July 2022). From here on we refer to this data as the LIFE database. The extracted and curated database was made available online (Jonas et al., 2025). The database provides for each project (among other): the project reference number; associated N2K areas (if available); country, region and location where the project was implemented; start and end year of the project; total budget; the EU directive or regulation that supports the project and the species and habitats that were targeted by the project. Targeted species are listed by their scientific name, while habitats are listed under the corresponding Habitats Directive Annex I code. Projects can target only specific species or only specific habitats or target both, specific species and habitats, as one project can include a wide range of conservation actions. Projects can also have no species and no habitat targets. Such actions are for example related to educational or planning purposes. While these projects might not have direct effects on biodiversity, we included these projects as we are assessing the effects of targets of conservation projects and the indirect effects of funding on community responses. If the project description in the LIFE database clearly stated N2K area names in which the project was implemented but no site codes were provided, N2K area codes were manually added by searching for the N2K area name in the EUNIS database for protected areas in Europe (https://eunis.eea.europa.eu/sites.jsp). If this produced a N2K code according to the site name we included this site as being associated with the respective LIFE project in the LIFE database. From the entire LIFE database, we retained only projects that were associated with at least one N2K area, as this information was needed to connect LIFE conservation data with waterbird count data (see below).

2.1.2. International Waterbird Census

To assess non-breeding waterbird community changes we used waterbird abundance data collected under the International Waterbird Census (IWC). The census is coordinated by Wetlands International (www.wetlands.org) and conducted in 143 countries worldwide (Delany, 2010). Counts are organized by professional national coordinators and carried out by experienced volunteers. Each censused site is visited once per year and counts follow a standardized protocol. All observed species as well as their abundance are reported. The data we use here was collected in January from 1993 to 2020 at over 18,000 sites covering all 27 EU countries. For each site information on the spatial location is available, either in the form of centre coordinates or additionally including information on the extend of the censused area (site polygon). All birds observed at one census site are considered a waterbird community in this study.

To avoid anecdotical effects due to rare species, we removed species with low abundance (<500 individuals in total over entire study period or low occurrence (<10 occurrences over all surveys) based on arbitrary thresholds (Tayleur et al., 2016). In addition, to ensure the reliability of the CTI temporal trends, we omitted sites with <5 IWC surveys and surveys with <2 species. Due to this removal of sites and surveys, the abundance of one species fell slightly below 500 (see Appendix A.1), but the species was kept in the data due to the arbitrary nature of the threshold.

2.1.3. Natura 2000 (N2K) protected areas

LIFE conservation projects and IWC data were linked through N2K areas they were associated with (see description of the matching process below and Fig. 1). The N2K protected area site network is the largest protected area network in the EU. We acquired data on N2K areas from www.eea.europa.eu. This dataset includes all 27,031 N2K areas in Europe, with their unique site code and spatial location information in the form of polygon data.

2.1.4. Temperature data

We used average yearly winter temperature from 1993 to 2020 to quantify the increase in temperature at each IWC site. To calculate average yearly winter temperatures, we averaged monthly mean temperature for November, December and January, as early winter

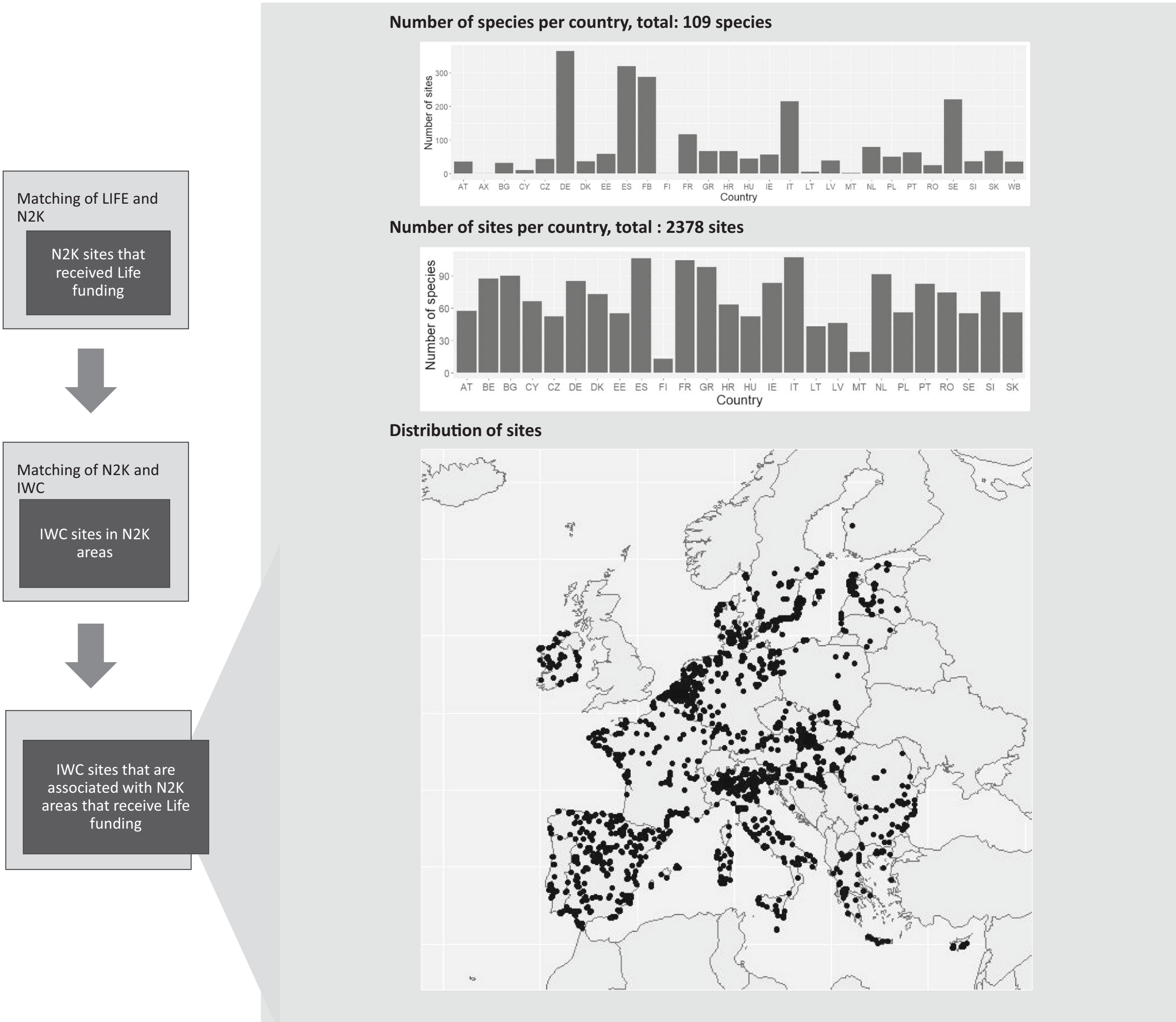

Fig. 1. Process of linking IWC count data to LIFE projects. First, data on LIFE projects in N2K areas was collected, then IWC data was matched with N2K areas. Subsequently, LIFE projects were associated with IWC data. The map shows the distribution of all IWC sites included in the study. Additionally, background information about the number of monitored species per country and the number of IWC sites per country within the subset of IWC sites included in the study is shown.

temperatures are considered likely to influence waterbird non-breeding grounds (Lehikoinen et al., 2013; Pavón-Jordán et al., 2019). We used temperature data from the CRU TS v.4.03 dataset with a resolution of 0.5°, downloaded from https://cds.climate.copernicus.eu (Harris et al., 2020). By using a spatial resolution of 0.5° we aimed at capturing general patterns in temperature change (not at the micro-scale). Mean monthly temperatures for November, December and January at the centre coordinates for each IWC site were extracted and averaged per winter.

2.2. *Linking IWC count data to LIFE project conservation targets*

We considered waterbird communities to benefit from LIFE conservation projects implemented at the same spatial location. As spatial information was not available for LIFE conservation projects, we matched waterbird count data with conservation projects through associated N2K areas (Fig. 1). All included LIFE projects report N2K sites they are implemented in, and therefore can easily be linked to N2K areas. To connect IWC data with N2K protected areas we used the spatial location of the IWC census sites. We considered IWC sites to be associated with a N2K area, if both areas intersect. For IWC sites without available polygon area we created a 500 m buffer around the centre coordinate to estimate IWC area.

All LIFE projects that were implemented at the N2K area a waterbird census site was located in, where considered as associated with that IWC site and having a potential impact on the respective waterbird community. We retained only those IWC sites associated with a N2K area that had received at least one LIFE project (Fig. 1). This resulted in 2378 IWC sites, associated with at least one LIFE project, distributed across EU countries (Appendix A.2). IWC sites were distributed across 26 countries with a total of 109 recorded bird species and over 38,000 surveys.

LIFE project conservation targets were categorized according to the species and habitat types they are targeting. Species and habitat targets were summarized in 3 categories each. For the species target these 3 categories are: waterbird (at least one waterbird species is targeted), other-species (at least one specific species is targeted but none of them is a waterbird) and no-species (no specific species are targeted). For the habitat target the 3 categories are: wetland (at least one type of wetland habitat is targeted), other-habitat (at least one specific habitat type is targeted but none of them is a wetland habitat) and no-habitat (no specific habitat types are targeted). We considered as wetland habitat any type of coastal, marine, freshwater or wetland habitat. Other habitat types included grassland, forest, heathland and sparsely vegetated habitats.

The conservation targets of all LIFE projects one IWC site was associated with, were summarized and considered as the conservation targets this waterbird community was potentially affected by. Conservation targets of several LIFE projects were summarized following the same categories as described above. This resulted in the assignment of one species and one habitat target category for each IWC site.

We note that the extent of IWC sites does not necessarily match exactly with the extent of the corresponding N2K area boundaries. It is possible, that the monitoring was partly conducted outside of N2K areas, so that not all of the monitored area is under protection or is receiving conservation funds or management actions. However, as waterbirds can easily move between nearby areas, we assume conservation actions to affect bird communities, even if part of the monitored IWC site falls outside the PA (but see Discussion).

Management actions implemented earlier might have stronger effects on waterbird community responses. Therefore, for each IWC site included in the analysis, the year of implementation of the first LIFE project was extracted from the LIFE database.

To account for effects of wetland area on CTI, we extracted wetland surface area at each IWC site using European Union's Copernicus Land Monitoring Service information (CORINE Land Cover 2006, doi: https://doi.org/10.2909/93eede6e-c196-40e3-9253-7f2237b49de1). We used landcover data from 2006, to reflect wetland surface area at the central year of the study period. Wetland surface area did not change substantially between 2000 and 2018 (Appendix A.12), therefore we used static landcover data from the year 2006, as this is the closest year with available data to the central year of our study period. As information on the polygon area of all IWC sites was not available, we used wetland surface area within the N2K area an IWC site was matched with, as an estimate of IWC site wetland surface area. If one IWC site was matched with several N2K areas, the wetland surface area within all corresponding N2K areas was summed for the respective IWC site (Appendix A.11). The types of habitats reported in the Corine Land Cover data we included as wetlands were: Beaches, Inland marshes, Peat bogs, Salt marshes, Salines, Intertidal flats, Water courses, Water bodies, Coastal lagoons, Estuaries, Sea and Ocean (CLC-Codes: 331, 411, 412, 421, 422, 423, 511, 512, 521, 522, 523).

2.3. CTI calculation

To assess changes in waterbird communities the community temperature index (CTI) (Devictor et al., 2008) was used. The CTI represents the average species temperature indices (STI) of all species present in the community, weighted by species abundance (Godet et al., 2011). An increase in CTI from one year to the next can therefore result from a relative decrease in cold-dwelling individuals or a relative increase in warm-dwelling individuals or both.

We calculated species' STI as the average winter (November, December, January) temperature across a species distribution range within the geographical area defined by AEWA during the non-breeding period following Gaget et al. (2021) and Gaget et al. (2018). We downloaded distribution ranges from BirdLIFE Datazone (www.datazone.birdlife.org). We used temperature data from WorldClim, which are monthly average temperatures for the period from 1970 to 2000 with a spatial resolution of 10 min (www.worldclim.org, Fick and Hijmans, 2017). As the distribution ranges for some species can include subspecies living in sub-saharan areas which can influence the STI, these areas were excluded from distribution ranges of the respective species for STI calculation (*Botaurus stellaris*, *Porphyrio porphyrio*, *Gallinula chloropus*, *Tachybaptus ruficollis*, *Podiceps cristatus*, *Podiceps nigricollis*, *Phalacrocorax carbo*, *Ardea cinerea*, *Ardea alba*). STI values ranged from STI −15.78 °C to 24.15 °C (mean (SD) = 12.23 °C (8.77 °C), Appendix A.1). CTI for each IWC site and censused year was calculated as:

$$CTI = \frac{\sum_{s=1}^{n} (\log(\text{abundance}_s + 1)^* STI_s)}{\sum_{s=1}^{n} (\log(\text{abundance}_s + 1))}$$

where n = number of species in the community, s = each species present in the community, *abundance* = number of individuals reported from the survey and STI = the species temperature index (see above).

2.4. Statistical analysis

To address our first question and assess how waterbird CTI changed over time at each IWC site, we used linear mixed-effect models. We used CTI as the response variable (Gaussian distribution) and year as fixed effect. To study the effects of conservation targets on CTI change, we included the type of habitat targeted by LIFE projects (categorical variable with three levels: no-habitat, other-habitat and wetland-habitat) and the species targeted (categorical variable with three levels: no-species, other-species and waterbird) as fixed effects.

The surface area of protected wetlands has been found to be positively correlated with CTI increase (Gaget et al., 2021), indicating that habitat size might influence CTI. Earlier implementation of conservation actions might lead to stronger effects as impacts of conservation efforts often lag behind implementation (Watts et al., 2020). To control for the possible effect of larger wetland surface area or earlier implementation of conservation projects, we included wetland surface area (continuous, log-transformed) and the year of implementation of the first LIFE project at a site (continuous) as fixed effects in the model.

As we expected interactions between the above-mentioned variables, we included two-way interactions of habitat target, species target, wetland surface area and year of first implementation with year and a three-way interaction between habitat target, species target and year as fixed effects.

IWC site was added as random effect on the intercept to account for site-specific differences. To control for the initial spatial autocorrelation of residuals, we added a Gaussian random field based on a spatial mesh using a cutoff distance of 0.05 decimal degrees (see Anderson et al., 2022 [preprint]).

Then, to further compare CTI and temperature trends between sites with different conservation targets, both CTI and temperature marginal trends were estimated for the different habitat or species conservation targets, and compared with each other while applying a Bonferroni correction, due to the large number of comparisons.

To asses temperature change over time across IWC sites, we fitted linear mixed-effect models with temperature as the response variable, and the same variables as above as fixed effects, random effect and gaussian random field.

All statistical analysis was performed in R version 4.3.0 (R Core Team, 2023). For model fitting we used the package *sdmTMB*, version 0.4.2 (Anderson et al., 2022 [preprint]). Model validity was checked using the *DHARMa* package, version 0.4.6 (Hartig, 2022). To estimate marginal means of CTI and temperature temporal trends for each of the conservation target categories we used the package *emmeans*, version 1.9.0 (Lenth, 2023).

2.5. Climatic debt

To answer our last study question, we estimated the accumulated climatic debt of waterbird communities by transforming CTI and temperature change from a temporal shift (°C/year) to a spatial velocity (km/year), following Devictor et al. (2012). First, we estimated the latitudinal gradient of CTI and temperature change. To do this, we fitted linear models with the average CTI or temperature at a site during the study period as response variable and latitude as fixed effect. To convert this latitudinal gradient from latitude to kilometer, we used the average number of km per decimal degree in the study area (111.128 km per degree). Using this spatial gradient, the temporal shift in CTI and temperature was converted to a spatial shift by calculating the ratio between the temporal shift and the spatial gradient: ((°C/year) / (°C/km) = km/year)). To estimate the climatic debt of waterbird communities, the spatial shift in CTI was subtracted from the spatial shift in temperature for each target category.

3. Results

Across the 2378 IWC sites included in the study, all possible categories of conservation targets were represented (Fig. 2, Table 1). On average one IWC site was matched with 2.73 LIFE projects (SD = 2.74, max = 31). CTI values ranged from −4.93 °C to 22.73 °C with an average of 7.62 °C (SD = 3.16).

Overall, we found a significant increase in CTI over time (year effect in Table 2, Table 3 and Appendix A.4). However, sites with different conservation targets showed differences in CTI change. CTI increase

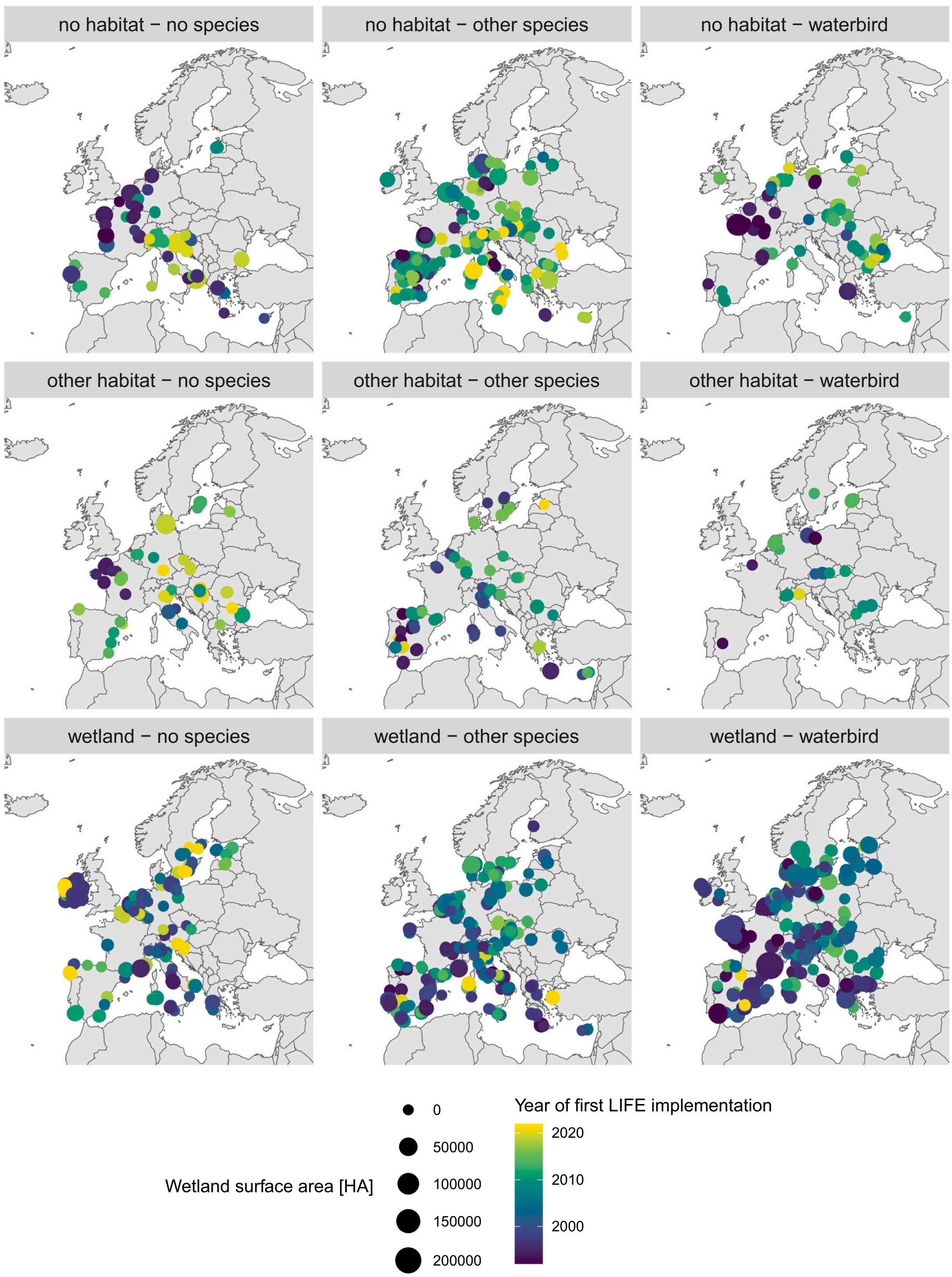

Fig. 2. Distribution of IWC sites according to conservation target category. Sites were categorized by the habitat (wetland, other habitat, no habitat) and species (waterbird, other species, no species) targeted by LIFE projects implemented at each site.

Table 1
Synthetic information relative to the sites monitored for waterbirds (IWC) and the corresponding conservation targets of the LIFE projects. Number of IWC sites for each of the nine combinations of target categories on species and habitat, and average (SD) wetland surface area, abundance, species richness, number of surveys per site and number of LIFE projects per site are reported.

Conservation target categories	Nr of IWC sites included in study	Average (SD) wetland surface area per IWC site [HA]	Average (SD) abundance per survey and site	Average (SD) species richness per survey and site	Average (SD) number of surveys per site	Average (SD) number of Life projects per site
No habitat + No species	105	5852.45 (13,216.60)	15.98 (8.31)	15.72 (11.76)	15.98 (8.31)	1.70 (1.73)
No habitat + Other species	339	3023.43 (8525.15)	15.28 (7.2)	10.05 (7.82)	15.28 (7.2)	1.96 (1.81)
No habitat + Waterbird	215	3331.08 (10,576.30)	14.53 (7.66)	13.11 (10.96)	14.53 (7.66)	1.97 (1.59)
Other habitat + No species	95	4599.79 (8383.16)	16.14 (7.08)	12.58 (10.56)	16.14 (7.08)	1.28 (0.52)
Other habitat + Other species	95	913.02 (3501.52)	15.01 (6.97)	9.76 (6.91)	15.01 (6.97)	2.47 (1.91)
Other habitat + Waterbird	46	3980.94 (3727.54)	16.91 (7.49)	11.87 (7.53)	16.91 (7.49)	2.17 (1.82)
Wetland + No species	245	3238.79 (6715.31)	16.97 (7.21)	14.67 (11.3)	16.97 (7.21)	1.52 (1.05)
Wetland + Other species	443	3604.09 (8153.24)	15.23 (7.56)	12.57 (10.72)	15.23 (7.56)	2.69 (2.46)
Wetland + Waterbird	795	8857.35 (19,112.92)	17.01 (7.06)	12.88 (11.33)	17.01 (7.06)	4.03 (3.56)

Table 2
Temporal trends of CTI values with average value per year across all sites and estimated marginal trends for CTI for the different conservation target categories averaged for the levels of habitat target and species target over the levels of species target and habitat target respectively (see also Appendices A.4 and A.5 for more information on models and results).

	Trend [°C/year]	SE
Average year trend	0.004	0.004
Trends per conservation target category		
Habitat target		
No habitat	0.008	0.002
Other habitat	0.010	0.003
Wetland	0.017	0.001
Species target		
No species	0.007	0.002
Other species	0.014	0.002
Waterbird	0.013	0.002

Table 3
Contrast between average CTI temporal trends for the three levels of habitat target and species target. Only the CTI temporal trends between no-habitat sites and wetland sites differ significantly (see also Appendix A.6 for more information).

Contrast	Estimate	SE	*p*-Value
Habitat target			
No habitat - Other habitat	−0.002	0.004	0.857
No habitat - Wetland	−0.009	0.002	<0.001
Other Habitat - Wetland	−0.007	0.003	0.089
Species target			
No species – Other species	−0.007	0.003	0.057
No species - Waterbird	−0.007	0.003	0.157
Other species - Waterbird	0.000	0.003	0.995

differed with the habitat target of conservation projects an IWC site was associated with (year:habitat-target effect in Appendix A.4). On average sites associated with conservation targeting wetlands (CTI change: 0.017 °C/year, SE = 0.001) showed two times faster CTI increase than sites associated with projects not targeting any habitat type (0.008 °C/year, SE = 0.002). Sites associated with conservation targeting other habitats (0.010 °C/year, SE = 0.003) showed no significant differences in CTI change compared with sites associated with any of the other two habitat conservation targets (wetland or no habitat, Fig. 3, Table 2 and Table 3). Between the three categories of species target no significant differences were observed (Table 3 and see year:species-target effect in Appendix A.4). However, we also found an effect of the interaction of habitat target and species target on CTI change over time (year:habitat-target:species-target effect in Appendix A.4). There was great variation in CTI change at sites associated with other habitat conservation depending on the species target (Appendices A.5 and A.6). Sites associated with conservation targeting other habitat and no species showed a CTI change of −0.002 °C/year (SE = 0.005), while sites in the category other habitat and other species showed a CTI change of 0.016 °C/year (SE = 0.005) and sites associated with conservation targeting other habitats and waterbirds showed a CTI change of 0.014 °C/year (SE = 0.006) (Appendix A.5). This large variation in rate of CTI change can make comparing average CTI increase for sites associated with other habitat conservation misleading. The relatively large standard error values suggest heterogeneity in the patterns described in this three-way interaction. For sites associated with LIFE projects targeting wetlands or no habitat, not such a strong variation with species target was observed and all sites associated with wetland conservation showed faster CTI increase than sites associated with no habitat conservation (Appendices A.5, A.6 and A.7).

Temperature values ranged from −8.77 °C to 16.47 °C, with a mean of 4.84 °C. Temperature increased across all sites, but was between three to six times faster than CTI temporal change (Fig. 3, Appendices A.8 and A.9), which lead to substantial climatic debt for all sites. The latitudinal gradient for temperature was −0.425 °C/° (SE = 0.008) and the latitudinal gradient for CTI was −0.320 °C/° (SE = 0.008). Temperature spatial shifts ranged from 10.40 km/year in sites associated with other species conservation to 15.27 km/year in sites receiving funding for waterbird conservation. CTI spatial shifts ranged from 2.36 to 5.8 km/year, with the largest shift observed in sites receiving wetland targeting conservation and the smallest shift in sites with no species target (Fig. 4). Climatic debt was highest in sites associated with waterbird conservation (10.60 km/year), while sites receiving funding for conservation targeting other species showed the lowest climatic debt with 5.62 km/year and in sites associated with no species conservation the climatic debt was 8.23 km/year. Sites associated with wetland conservation showed the second lowest climatic debt with 6.18 km/year. Sites associated with conservation targeting other habitats (9.12 km/year) and sites associated with no habitat conservation (9.16 km/year) showed very similar climatic debt (Fig. 4). For the entire study period of 28 years

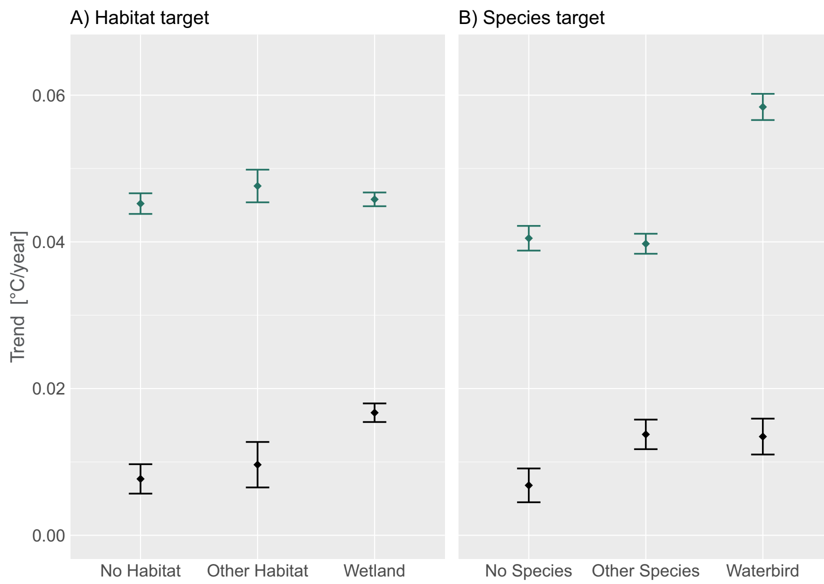

Fig. 3. CTI (black, lower row) and temperature (green, upper row) trend in °C per year. A shows effect sizes for the three habitat target categories averaged over the levels of species target. B shows effect sizes for the three species target categories averaged over the levels of habitat target. (Whiskers = SE). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

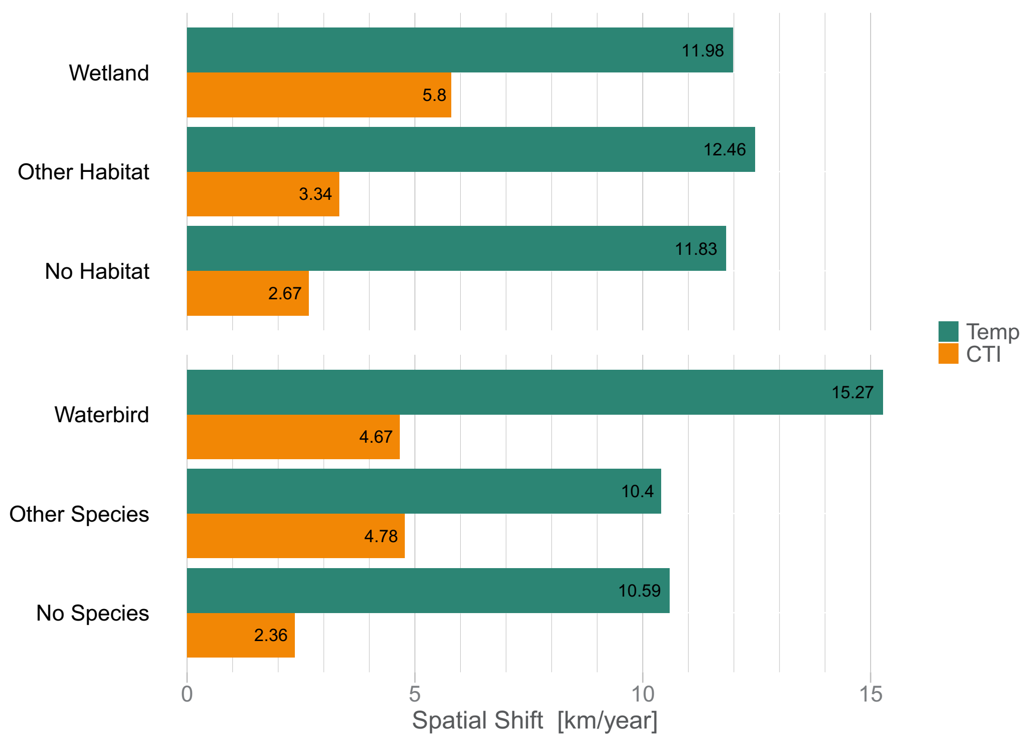

Fig. 4. Spatial shifts of CTI and temperature per year for the different conservation target categories. Difference between CTI and temperature in each group equals climatic debt.

this climatic debt amounts to a lag ranging from 157.36 km (other species) to 296.80 km (waterbirds), and reaching 173.04 km when wetland conservation was targeted (see Appendix A.10 for all climatic debts). For results on species-habitat interactions see supplementary material (Appendix A.10).

4. Discussion

Our study is part of a global effort looking for solutions to reduce negative impacts of climate warming on biodiversity (IPCC, 2022; Pörtner et al., 2023). Naturally, the most efforts should go towards lowering greenhouse gas emissions and reducing the speed of climate warming (IPCC, 2022). However, despite all efforts, we are already experiencing the impacts of a changing climate and these will likely increase in the future (United Nations Environment Programme, 2023). Typically, studies that work on climate warming adaptations for biodiversity require large temporal and spatial scales to detect a consistent effect of warming (Adrian et al., 2012), and are therefore challenging to carry out owing to data limitations. Here, we conducted a pan-EU study at large temporal and spatial scales with information on waterbirds (IWC), protected areas (N2K) and conservation management projects (LIFE) with data that was consistently collected under standardized monitoring and reporting frameworks. This design offers good opportunity to investigate the potential of conservation projects to improve biodiversity responses to climate warming.

Species communities are expected to change towards more warm-dwelling species as a response to climate warming. Thus, at any given locality the community temperature index (CTI; Devictor et al., 2008) is expected to increase. Here we used extensive data on waterbird abundance and the CTI concept to test how conservation projects under the EU's LIFE funding scheme implemented within N2K areas affect waterbird community adjustment to climate warming. We investigated how impacts differ between conservation projects with different levels of habitat and species target specialization. Overall, we found CTI and temperature to be increasing over time. In sites where conservation targets wetland habitats, waterbird CTI increased faster than in sites where conservation projects do not target specific habitat types. In contrast, we found no clear evidence that waterbird-specific projects lead to faster CTI increase, when compared to less waterbird specific conservation projects. However, across all sites CTI increase lagged behind temperature, leading to climatic debt, as is commonly observed for non-breeding waterbirds (Gaget et al., 2021), breeding birds (Devictor et al., 2012) and other terrestrial taxa (Lenoir et al., 2020).

As expected, we found CTI to be increasing over time. We interpret CTI increase as a community reshuffling in response to climate warming, indicating a relative species turn-over according to species thermal niche, as well as reflecting changes in species abundance (Devictor et al., 2008). Such changes in community composition have been observed for many bird communities (Devictor et al., 2012; Stephens et al., 2016) and other taxa (Löffler et al., 2019; Termaat et al., 2019) across study sites in Europe and North America Only one combination of conservation targets (other-habitat + no-species target) did not show a significant increase in CTI. This latter result could suggest that, when observed, changes in community composition were not reflecting a community adjustment to temperature increase. However, it is very likely that also other factors driving species responses are interacting with temperature change (Parmesan, 2006).

Additionally, although we did not detect an effect of the year of first implementation, many sites in the above-mentioned category (other-habitat + no-species target) received LIFE funding only recently and effects of conservation actions might not be visible yet (Watts et al., 2020). Including the year of first implementation of LIFE conservation projects to account for variation in the duration of conservation efforts may not fully capture the potential impact of longer implementation (see also Appendix A.13). Conservation efforts may not have been continuous since the initial implementation. Furthermore, while the results presented here are at EU scale, information on the spatial scale of the projects or the intensity of implementation efforts is lacking, all of which could significantly influence bird community responses regionally.

We found wetland targeted conservation to lead to faster CTI increase in waterbird communities compared with sites associated with conservation not targeting specific habitat types. CTI change in sites associated with conservation targeting other habitat types, did not differ significantly from the other two habitat target categories. Habitat conservation likely plays an important role in facilitating community adjustment to climate warming (Synes et al., 2020; Fartmann et al., 2022), which is one major conclusion from studies contrasting community change inside versus outside protected areas, were change was observed to be faster inside PAs (Gaüzère et al., 2016; Hintsanen et al., 2023). Such results have also been observed for non-breeding waterbirds (Gaget et al., 2021). Protected areas have often been linked with higher rates of species colonization (Thomas et al., 2012; Hiley et al., 2013; Gillingham et al., 2015), which is one driver behind observed community shifts. In our study targeting habitats in general (other habitat category) did not lead to faster CTI increase compared with no habitat targets. It should be mentioned here, that the target category no-habitat consisted of the lowest number of sites, which might influence results as a higher number of sites could increase the probability of beneficial conservation. However, even though the actual actions implemented under the LIFE projects are not included in this study, projects targeting wetlands specifically seem to be more beneficial for waterbird community shifts. These are the preferred habitat types of the considered species group and conservation targeting wetlands are likely to have a greater impact on waterbirds compared to actions targeting other habitat types.

Unlike our expectations, conservation projects more specialized on waterbirds did not lead to faster CTI increase when compared with projects targeting other species or no specific species. Indeed, no difference in CTI increase was observed between the three categories.

In a previous study, PAs designated for waterbirds were found to be most efficient in increasing waterbird community adjustment to climate warming, especially if the PA had a management plan (Gaget et al., 2022). In contrast to Gaget et al. (2022), we here only considered PAs that have received LIFE funding, regardless of designation, in an attempt to link realized conservation actions done in PAs to community changes.

Taken together, these studies imply that N2K areas designated to protect a certain community with an intent to manage the site can be successful in aiding that community to adjust to climate warming. However, on the management level actions targeting a community's habitat (rather than actions targeting the species group directly) seem to provide the most benefits for the community's adjustment to climate warming.

These results highlight the potential of habitat targeted conservation projects to facilitate community responses to warming temperatures. However, the benefits of species targeted conservation should not be dismissed so easily, as we here considered general conservation targets while the specific actions included in our categories and their impacts might differ greatly.

Inside the N2K network, examples of LIFE projects targeting specific waterbird species, include for example the implementation of patrol schemes to reduce illegal hunting of red-breasted geese, *Branta ruficollis*, (LIFE09 NAT/BG/000230), improvement of the breeding habitat of the dalmatian pelican, *Pelecanus crispus*, by installing breeding platforms (LIFE18 NAT/NL/000716) or control of predator species, such as the yellow-legged gull, *Larus michahellis* which preys on Audouin's gull, *Ichthyaetus audouinii* (LIFE03 NAT/E/000061). Such species conservation projects might not be as beneficial in facilitating community adjustment to climate warming, as they often aim at conserving the current range of the targeted species (Greenwood et al., 2016) and benefits are often limited to the targeted species (Bowgen et al., 2022), which can blur patterns of community response to climate warming. Conservation projects targeting wetland habitats on the other hand, include actions such as restoring natural river characteristics by widening the river bed or removing gravel barriers (LIFE00 NAT/A/007053), raising lake water levels to former conditions to restore marshes and wet meadows in lake surroundings (LIFE00 NAT/D/007038) or raising water levels in previously drained bogs (LIFE14 NAT/IE/000032). Such projects are altering habitats and are thereby more likely to affect the entire waterbird community. These examples highlight the variety of actions found within the broad target categories. The effects of such a variety of actions on CTI can be very different. However, standardized information on implemented actions is not available in the LIFE database complicating the evaluation of impacts of specific actions and highlighting the need for more detailed reporting of management actions. Additionally, we cannot rule out that other management actions, independent from LIFE projects were enforced in the studied PAs. These can interact with LIFE actions and have effects not detectable with this study design. Although challenging to compare across countries, the amount of funding allocated to different management actions should also be taken into consideration in future research. There are likely differences in budgets between conservation actions (Appendix A.3), which might be related to effects of management actions but can also influence the implementation and practicability of certain actions (Giakoumi et al., 2019).

We found temperature to be increasing across all sites, yet much faster than CTI increase, leading to climatic debt in all study sites. Climatic debts observed in this study are comparable to climatic debts observed for bird communities in similar studies (Devictor et al., 2008; Devictor et al., 2012; Gaget et al., 2021). In our study, sites with wetland conservation showed the smallest climatic debt when compared to the other two habitat conservation categories (other-habitat and no-habitat), which is not surprising as sites associated with wetland conservation also showed the fastest CTI increase. However, as the climatic debt takes both, CTI and temperature change, into account, climatic debt is not necessarily linked only to the rate of CTI change. Indeed, although CTI change did not differ between the three species-specific conservation categories, sites with waterbird conservation showed the highest climatic debt due to the fast temperature increase in these sites. This is an interesting result indicating potential bias in the allocation of waterbird conservation funding. It should be investigated further whether sites receive more waterbird targeted conservation funding because waterbird populations at such sites experience more severe threats and whether conservation strategies adequately deal with such threats resulting from climate change.

The great lag of CTI change behind temperature change indicates, that the magnitude of warming pressure exceeds the maximum rate by which communities are able to change, which has been observed in numerous studies for terrestrial species (Devictor et al., 2008; Lenoir et al., 2020; Gaget et al., 2021).

However, it should be highlighted that while a smaller climatic debt through increase of CTI might indicate faster adaptation of communities, the CTI does not capture the mechanisms driving community shifts and CTI increase might result from decrease in cold-dwelling species only, reducing species richness. Alternatively, increase in warm-dwelling species without decrease in cold-dwelling species increases CTI values. While this initially increases species richness, this can be an indicator of delayed distribution shifts in cold-dwelling species, which increases their climatic debt (Gaget et al., 2021 and see Appendix A.14). Differences between species in their responses to warming could possibly also increase the risk of biotic homogenisation (McKinney and Lockwood, 1999, but see Gaget et al., 2020). Nevertheless, the CTI captures general community changes and can be an important tool for assessing biodiversity responses to changing temperatures. However, the impacts of conservation projects, including LIFE conservation projects, on species specific population responses are important to understand the mechanisms behind the community shifts we detect here and should be the focus of future research.

We acknowledge that spatial differences in the attribution of funding exist (Hermoso et al., 2018). Here, we considered the potential benefits as being homogeneous inside N2K areas and we only looked at sites that have received LIFE funding. Considering the distance between management actions and wetlands monitored for waterbirds, inside and outside protected areas, might help to quantify direct and indirect effects of management actions on community adjustment to climate warming. For instance, a network of sites that have received funding to conduct similar management actions might result in a synergetic effect at network scale, especially as waterbirds are very mobile and can easily move. The spatial dependency in the influence of protected area networks on the effects of conservation actions should be further investigated.

5. Conclusion

Our results provide some insight on the potential of conservation on waterbird community responses to climate warming. In sites where wetland habitats were targeted by conservation projects, community change was faster compared to sites without conservation targeting habitats. Conservation targeting waterbird species did not lead to faster community change compared to less specialized species conservation. While protected areas and their designation for target species are important to facilitates waterbird community adjustment to warming temperatures (Hiley et al., 2013; Gaüzère et al., 2016; Hintsanen et al., 2023; Wauchope et al., 2022; Gaget et al., 2022), our results imply that on the management level conservation targeting a community's habitat (rather than targeting the species group directly) is more likely to provide benefits for a community's adjustment to climate warming. However, more detailed information on conservation actions is necessary to study the impacts of specific actions in order to be able to design successful future conservation strategies. Additionally, similar approaches studying other species groups and habitats would be valuable to further examine the impacts of conservation on species responses to climate warming.

Nevertheless, community change was lagging behind temperature (climatic debt) in all sites, highlighting again the need for conservation facilitating community responses to climate warming. While the EU LIFE program was originally not designed to support community responses to climate warming, it is encouraging to find positive effects of existing LIFE conservation projects on these responses. This study demonstrates the potential of current conservation projects within PAs to support waterbird communities responding to climate warming, while highlighting the need for more detailed reporting of implemented conservation actions.

CRediT authorship contribution statement

Leonie Jonas: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Jon E. Brommer:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Martin Jung:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Michal Baláž:** Writing – review & editing, Writing – original draft, Resources. **John J. Borg:** Writing – review & editing, Writing – original draft, Resources. **Luka Božič:** Writing – review & editing, Writing – original draft, Resources. **Preben Clausen:** Writing – review & editing, Writing – original draft, Resources. **Antoine Deroux:** Writing – review & editing, Writing – original draft, Resources. **Koen Devos:** Writing – review & editing, Writing – original draft, Resources. **Cristian Domșa:** Writing – review & editing, Writing – original draft, Resources. **Sándor Faragó:** Writing – review & editing, Writing – original draft, Resources. **Niamh Fitzgerald:** Writing – review & editing, Writing – original draft, Resources. **Valeri Georgiev:** Writing – review & editing, Writing – original draft, Resources. **Fredrik Haas:** Writing – review & editing, Writing – original draft, Resources. **Menno Hornman:** Writing – review & editing, Writing – original draft, Resources. **Christina Ieronymidou:** Writing – review & editing, Writing – original draft, Resources. **Tom Langendoen:** Writing – review & editing, Writing – original draft, Resources. **Aleksi S. Lehikoinen:** Writing – review & editing, Writing – original draft, Resources. **Kim Lindner:** Writing – review & editing, Writing – original draft, Resources. **Leho Luigujõe:** Writing – review & editing, Writing – original draft, Resources. **Włodzimierz Meissner:** Writing – review & editing, Writing – original draft, Resources. **Tibor Mikuska:** Writing – review & editing, Writing – original draft, Resources. **Blas Molina:** Writing – review & editing, Writing – original draft, Resources. **Filipe Moniz:** Writing – review & editing, Writing – original draft, Resources. **Zuzana Musilová:** Writing – review & editing, Writing – original draft, Resources. **Danae Portolou:** Writing – review & editing, Writing – original draft, Resources. **Gwenaël Quaintenne:** Writing – review & editing, Writing – original draft, Resources. **Juhani Rantanen:** Writing – review & editing, Writing – original draft, Software. **Laimonas Šniaukšta:** Writing – review & editing, Writing – original draft, Resources. **Antra**

Stīpniece: Writing – review & editing, Writing – original draft, Resources. **Norbert Teufelbauer:** Writing – review & editing, Writing – original draft, Resources. **Marco Zenatello:** Writing – review & editing, Writing – original draft, Resources. **Elie Gaget:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111213.

Data availability

Data will be made available on request.

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