

Seasonal effects of climate and land use changes on ecological niche of a migratory bird

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Abstract

Background: The habitat selection strategies followed by migratory populations are a major concern for conservation and management. Consequently, the ability to predict their distribution and potential changes in migratory behaviour is a pressing challenge for ecological modelling in a changing world. There are two main strategies of habitat selection adopted by migratory animals: tracking optimal conditions or acclimatizing to a changing environment between seasons. In this study, we investigate the variations in ecological niche of gps-tracked American White Pelicans (AWPE) associated with their seasonal migration. We also investigated whether recent changes in food resources in their wintering grounds have exerted an impact on the habitat selection behaviour of AWPE.

Methods: We developed Maximum Entropy (MAXENT) Species Distribution Models (SDM) using data from GPS-tracked AWPE. We then compared climatic and land-cover niche breadth and overlap between their breeding and wintering grounds in relation to the facultative migratory behaviour of AWPE.

Results: Our climatic, land-cover, and combined SDMs obtained a high predictive performance. Several lines of our findings support our hypothesis that AWPE habitat selection strategy follows the “niche switcher” theory. American White Pelicans showed little climatic niche overlap between nesting and wintering seasons. Migrants in the breeding grounds showed broader climatic niche than residents and migrants in the wintering grounds. Finally, declines in availability of food resources provided by commercial aquaculture in their wintering grounds appeared to affect the niche variations of AWPE, with land-cover niche being narrower before than after the decline in aquaculture.

Conclusions: If AWPE can effectively adapt and occupy different niches when they migrate instead of tracking suitable climate conditions, this can have important implications in the context of Global Change, since they might respond unexpectedly to anthropogenic changes, like the recent decline in aquaculture as a food resource reported here.

Background

Understanding the habitat selection and optimal use of available resources (such as food or shelter) by species represents a key topic in theoretical and applied ecology (Boyce and McDonald 1999, Manly et al. 2002, McLoughlin et al. 2010, Bell 2012). In recent years, many studies have focused on how animals use these resources and their ability to adapt to a changing environment (Martin 2001, Araujo et al. 2004, Hoffmann and Sgro 2011). The classical conception of environmental niche implies that if a set of conditions (dimension) are used more frequently than expected from availability, they are considered selected by the organism (Aebischer et al. 1993) and each of these conditions/resources defines a dimension of the ecological niche of that organism (Hutchinson 1957). Given the potential for ecological niche shifting, studies based on empirical data from migratory populations that can select different environmental and land-cover niches between seasons may provide more representative scenarios under which the species are able to change their ranges (Mau-Crimmins et al. 2006).

Seasonal migration is one of the most important behaviours in animal life cycles, particularly for avifauna (Berthold 2002). Among these migratory movements, the latitudinal long-distance migrations between breeding/nesting and non-breeding/wintering grounds (Cox 1985, Newton 2008) represent an ideal scenario to study variations in the ecological niche of these species as well as their seasonal acclimatization to different environmental conditions throughout their annual life cycle. Much has been debated on the origin of migration and its evolution (Marini et al. 2013, Gomez et al. 2016, Winger et al. 2019). Migratory birds face the situation of living in different environments during different seasons. The strategy that migratory birds follow to deal with this physiological challenge will vary between two basic extremes: they either track a single set of conditions year-round (“niche tracker”) or adapt to the new environment when changing from one ecological regime to another (“niche switcher”) (Nakazawa et al. 2004, Laube et al. 2015). For niche “switchers” (sensu Nakazawa et al. 2004), migration is ultimately not motivated by tracking optimal conditions. Niche switchers are better prepared to adapt to changing conditions, and therefore have a much broader ecological niche (Wiens et al. 2010). As an opposite behaviour, niche trackers are expected to have more constant, narrow niches throughout the year (hence, greater niche overlap between seasons) for the dimension they are forced to track.

Ultimately, evidence for whether migrating populations track or adapt to climatic conditions between different seasons can be found in their niche breadth and the amount of overlap between the climatic conditions they experience between these seasons (Nakazawa 2013). However, for many migratory species, the niche selection strategy in their migration is not known; consequently, little is known about their ability to cope with the ongoing climate and land use changes. This is the case of our study species, the American white pelican (*Pelecanus erythrorhynchos*, hereafter AWPE), which has a substantial economic importance due to its alleged impacts on human activities such as aquaculture (King 2005). Approaches to studying long distance migration include year-round surveys of specific localities (e.g., Breeding Bird Survey system [Sauer et al. 2017], Remsen and Parker 1990) or tracking of individuals through their migratory route (e.g., Davenport et al. 2012). In this study, we based our analyses on data from 36 AWPE that were equipped with GPS tracking devices.

American white pelicans are divided into eastern and western metapopulations by the Continental Divide (Anderson and King 2005). We focused on the eastern metapopulation of the AWPE, which shows a facultative, mid-range migration between the Northern Great Plains (the nesting grounds) and the Southern Gulf of Mexico (the wintering grounds) along the Mississippi and Ohio River Valleys (King et al. 2017, Shannon et al. 2002). The mechanisms that control this facultative migration (e.g. resident individuals at the wintering or nesting grounds year-round) is still unknown (King et al. 2017). Since the 1990’s, AWPE has been known to use commercial aquaculture ponds consistently for feeding primarily on catfish (King 2005). Because of relatively shallow depth and high density of food resources, fish ponds in Alabama, Arkansas, Louisiana, and Mississippi, USA, provide an ideal foraging environment for the AWPE (Glahn et al. 1995, King and Werner 2001, King et al. 2010). The aquaculture industry had expanded with an increase in water acreage from 1980 until 2005, when a sharp decline ensued from rising feed prices and declining fish prices. The south-eastern US is the predominant region where AWPE populations have their wintering grounds (King et al. 2016). Furthermore, there has been a consistent decline in

precipitation for temperate climates (Walther et al. 2002, IPCC 2014), which may be exacerbated in the southern part of North America (Seager et al. 2007). The alterations of water regimes, in conjunction with changes in land use, are likely to affect the habitat selection and land-cover niche of waterbirds such as the AWPE. For these reasons, we investigated the potential effects of the reduction in aquaculture activities in the wintering range of AWPE on their habitat selection patterns, with the expectation that AWPE may look for alternative food and shelter resources where the aquaculture water acreage has declined.

We propose the following research questions in this study: (i) is the migratory behaviour of the studied AWPE populations better explained as niche trackers or niche switchers? (ii) do migratory populations at the breeding grounds show wider climatic niche but narrower land-cover niche (temporally more stationary) in comparison to the wintering grounds and the resident populations? (iii) is there a greater land-cover niche overlap than climatic niche overlap between the AWPE in breeding and wintering grounds? and (iv) has the land-cover niche of the AWPE in the wintering grounds expanded after the decline of aquaculture activities?

To answer these questions, we developed species distribution models in conjunction with measurements of niche similarity and breadth to predict the geographic distribution of the AWPE and to examine differences in their ecological niches between breeding and non-breeding grounds. We characterized the suitable habitats of these populations using climatic and land cover variables, and predicted the potential distribution of AWPE in North America and the niche breadth and niche overlap for both breeding and non-breeding populations. We account for environmental differences to address questions on ecological niche variation and habitat selection conducted across large spatial scales.

Methods

The study area included the entire geographic distribution range of the eastern metapopulation of American white pelicans in North America (Fig. 1). We used data from 36 AWPE satellite tracked for one, two or a maximum of three years from 2002 to 2010 (King et al. 2016) and analysed the recorded locations in their breeding grounds (only migrants) and non-breeding grounds (including migrants and year round residents). Potential usefulness of satellite tracked animal data in Species Distribution Models (SDMs) has been increasingly addressed in the scientific literature (Jiguet et al. 2011), where even a limited number of tracked individuals can produce accurate and reliable predictive models (Gschweng et al. 2012). However, examples of reliable SDMs based on satellite tracked animals are still scarce (Gottschalk et al. 2005, Jiguet et al. 2011, Bridge et al. 2011). In addition, most SDMs are developed using static, sparse data (museum, collections and/or observational counts) which are susceptible to bias in sampling intensity and detection ability (Gschweng et al. 2012). Conversely, satellite tracked data are mostly free of these problems (Hebblewhite and Haydon 2010). In our study, the number of tracked individuals is well above the minimum suggested (6) which is generally accepted to minimize the limitations of bias resulting from behaviour of specific individuals rather than the entire population (Aebischer et al. 1993, Proosdij et al. 2016).

To control for spatial bias and unbalanced number of tracked locations per individual (Phillips et al. 2006), we found the individual with the smallest number of locations, and reduced the number of locations of the other individuals to equal it by randomly selecting from all available locations. We also resampled each subset of presence records so each location was separated from the nearest one by a minimum of 5 kilometres. For the objectives of this study, we combined the location of the migrants and the residents at the wintering grounds during winter into one unique population. We first analysed, however, the two groups separately (migrants in winter and residents), and the results of model fitting and niche analyses did not differ in either direction or significance. Thus, in further analyses, we considered and compared breeding versus non-breeding populations. Because we wanted to analyse the use of habitat by AWPE in their breeding and wintering grounds, we excluded from analyses the tracking locations during seasonal migration. A given individual was considered in spring migration (departure from wintering range) when it crossed 35°N latitudinal line northward, defined as the northern boundary of the wintering range, until it reaches the breeding grounds (see King et al. 2017), and vice versa in autumn. For the purposes of this study, we assumed that migration ended when the given individual entered the breeding (spring) or wintering (autumn) region and began moving locally as it searched or settled into a particular breeding site (King et al. 2017). In addition, and to ensure that we exclude from analyses those locations where AWPE were flying at higher altitude above ground, we also excluded from analyses those locations in the upper decile of flying speed (Gutierrez Illan et al. 2017). In order to test for the effects of aquaculture in the AWPE wintering range, we divided our bird data into two subsets of satellite-tracked locations, before and after the peak of aquaculture activities in the region (here used as 2005). All comparative analyses were based on models developed with these two sets of data (pre- and post-aquaculture) with the expectation that species distribution models will show different contribution of predictor variables (particularly land cover) before and after the aforementioned peak of aquaculture. There were limited individuals for migrants in winter after the peak of aquaculture, and that was the main reason why we combined migrants in winter and residents in one group for further analyses.

Environmental variables

We used two types of predictor variables in raster format: (i) Climatic (14 variables) and (ii) Land cover (5 variables). Variable multicollinearity in ecological modelling can be an important problem because the effects on the response variable can be due to either true synergistic relationship among the predictors or spurious correlations (Graham 2003). To account for multicollinearity, we used a backwards stepwise process to calculate the variance inflation factor (VIF) with the initial pool of 19 predictor variables, and only selected those below a value of 4 (O'Brien 2007, Kock and Lynn 2012). With the resulting set of variables, we calculated a correlation matrix (Pearson's r) and discarded those showing values above 0.7. Before the analyses, all environmental layers were resampled to correspond to the 30 arc-seconds grid cell size of the environmental variables with coarser resolution (Merow et al. 2013).

Climate: Climatic variables were obtained from the WorldClim (version 2) database (Hijmans et al. 2005; <http://www.worldclim.org>), which provides a variety of monthly climatic data averaged over the years 1970–2000. Two main reasons persuaded us to develop our models based on the WorldClim data

source. First, wind direction and strength is one of the main drivers of AWPE movements and behaviour (Gutierrez Illan et al. 2017) and none of the alternative climate data source include data on wind currents at the desired spatio-temporal scale, which was considered a serious limitation. Second, we regressed data obtained from two alternative climate sources, Climate Research Unit (CRU) of University of East Anglia (Harris et al. 2014) and PRISM from Oregon State University (PRISM Climate Group 2012) against same variables from WorldClim data and found that the correlations were highly significant ($R^2 > 0.8$; $p < 0.001$ in all cases) which led us to believe that the results would not have changed neither qualitatively nor quantitatively if alternative climatic data sources would have been used.

The choice of climate predictors reflected energy and water constraints on the distribution range of birds. We initially selected the following variables for the warmest (July) and coldest month (January), which accounted for the time of the year when the pelicans were in the breeding and wintering ranges: minimum, maximum and average temperature, total precipitation, solar radiation, water vapour pressure and wind speed.

Land cover: We used North American Land Change Monitoring System (NALCMS, 2005; Homer et al., 2015) (<https://landcover.usgs.gov>) based on MODIS satellite imagery to obtain the land cover data. The classification of land cover types is designed in three hierarchical levels using the Food and Agriculture Organization (FAO) Land Classification System (Homer et al, 2015). Given the importance of the presence of water for our study species, we used a variable called "wetlands" (which discriminates between different types of wetlands) from the Global Lakes and Wetlands Level 3 Database (GLWD-3) (Lehner and Döll, 2004). We also calculated the variable "distance to water" as the Euclidean distance from every tracked location to the nearest permanent water body. For each individual and for each tracked location point we extracted the land cover variables selected for analyses using ArcMap spatial analyst (ESRI, 2014).

Modelling and statistical analysis

We aim to identify the main factors defining the potential distribution of AWPE in North America by developing climate, land use and climate-land use combined models based on their ecological niche requirements. To achieve this, we used the Maximum Entropy Model (MAXENT) for the SDM of AWPE (Phillips et al. 2006). MAXENT software was chosen because it has been shown to outperform other algorithms (i.e. GARP, CART) for building SDMs from presence-only data (Elith et al. 2006) and it is designed to integrate with GIS software thus making data input and predicted (mapped) output easier to handle (Elith et al. 2010). It compares presence locations with randomly selected points to find the largest spread (maximum entropy) of the current conditions relative to an available 'background' of environmental variables, in order to create maps of habitat suitability for each grid cell across the study region and determine the contribution of each environmental variable to a species occurrence. Maximum entropy is essentially the same as maximizing the log likelihood of the data associated with the presence sites minus a penalty term, conceptually similar to information criteria like Akaike Information Criterion (AIC) (Akaike 1973).

As recently proved by Renner and Warton 2013, MAXENT is equivalent to a Poisson point regression and therefore is related to Poisson Point Process Model (PPM) for spatial count data, depending only in the intercept term (which is scale-dependent in MAXENT). Consequently, we changed MAXENT default settings following recommendations from Renner et al. 2015 to develop our PPM with presence-only data derived from our satellite tracked AWPE. Hence MAXENT setting was set to retain presence records in the same cell. Then, the raw output (not the default logistic output) can be interpreted as a relative intensity, proportional to a Poisson PPM intensity. All other MAXENT settings relating to model construction were left at their default values. For each of the populations (breeding versus non-breeding), we built MAXENT models using the resampled number of locations standardized by the minimum number of locations for a given individual. We used 10,000 randomly selected background locations for MAXENT. Thirty percent of occurrence records were withheld from each model to be used as independent testing data in a cross validation. For our models, background points were selected within the boundaries of the breeding and wintering grounds of the AWPE eastern population, respectively, following King et al. (2016). Then we projected the models to Canada, the United States, and the Southern Gulf of Mexico to cover all areas potentially reachable by the eastern metapopulation of the AWPE. The overall performance of models was evaluated via the True Skill Statistic metric (TSS) (Allouche Tsoar and Kadmon 2006). We calculated the TSS for each of our models from the MAXENT output using “rocr” (Sing et al. 2005) and “boot” (Canty and Ripley 2017) statistical packages in R (R Development Core Team 2017). TSS takes into account both omission and commission errors, and ranges from - 1 to + 1, where + 1 indicates perfect agreement and values of zero or less indicate a performance no better than random. In contrast to other performance scores (e.g. kappa), TSS is not affected by either prevalence or the size of the validation set (Allouche et al. 2006). We performed a 10-fold cross-validation procedure and calculated the average TSS values for each model.

Alternatively, we used the Area Under the threshold-independent Receiver-Operating Characteristic (ROC) Curve (AUC) in order to compare between the performance of the model types. The AUC metric has been widely used to compare model type performance between the same species and geographical context (e.g. Araujo and Guisan 2006, Marmion et al. 2009, Deblauwe et al. 2016), although potential limitations have also been identified (see Lobo et al. 2008). These values range from 0.5 to 1.0, with 0.5 indicating fit to the data no better than random, 1.0 indicating perfect model performance, and values > 0.9 indicating high fitting to data (Pearce and Ferrier 2000).

We calculated the niche overlap of the selected populations using the I statistic implemented in ENMTOOLS (Warren et al. 2008, 2010) and also calculated Schoener’s D (Schoener 1968). Both metrics are based on a species suitability score in each grid cell after suitabilities are standardized and range from 0 to 1, with 0 indicating no niche similarity between species and 1 indicating complete similarity (Broennimann et al. 2012, Warren et al. 2008). Following an analogous protocol, we calculated the niche breadth of the populations (Quintero and Wiens 2013) using the Levin’s concentration metrics implemented in ENMTOOLS. This statistic takes the habitat suitability values for each grid cell across the range and calculates niche breadth according to the inverse concentration. The Levin’s concentration metric also ranges from 0 to 1, indicating minimum to maximum niche breadth, respectively. We

developed 10 MAXENT models for each of the wintering and breeding AWPE populations and then calculated the niche breadth and niche similarity (overlap) between them via Levin's metric and Schoener's D and I statistic respectively (Warren et al. 2010).

Results

The final numbers of locations per individual selected for analyses were: 96 locations for migrants during winter, 193 for migrants during breeding seasons and 114 for residents at the wintering ground. The number of individuals that satisfied criteria for analyses were: 19 migrants in breeding season (8 pre-aquaculture; 11 post-aquaculture); 19 migrants in winter (7 pre; 12 post); 11 residents (8 pre; 3 post). Migrants during winter and residents were combined into a non-breeding population and treated as a unique group to increase sample size in further analyses. After the variable selection process (via VIF and multicollinearity matrix), the resulting final set of explanatory environmental variables (4 climatic and 4 land cover) is listed in Table 1.

Table 1

List of final environmental variables included in the habitat suitability modelling of American white pelicans.

Environmental variable	Code	Mean (min-max)	Original resolution	Source	Units / classes
a) Climatic	tmin07	11.3 (-21.7–	30 arc-sec	Worldclim	°C
Minimum Temperature	ppt07	40.8)	30 arc-sec	Worldclim	mm
(July)	rad07	71.2 (0–967)	30 arc-sec	Worldclim	kJ/m ²
Total Precipitation (July)	wind01	20305 (123–	30 arc-sec	Worldclim	day
Total radiation (July)		28340)			m/s
Wind speed (January)		3.5 (0.5–19.1)			
b) Land cover	hidro	17.3 (0–174.5)	250 m	USGS	km
Distance to water	lc2005	categorical	250 m	MODIS	16
2005 land cover	lchange	categorical	250 m	MODIS	NA
Land cover change (2005–2010)					
Wetlands	wetland	categorical	30 arc-sec	GLWD	10

Model performance evaluation in the 10-fold cross-validation showed TSS values above 0.64 for all model types (Table 2), which are considered very good performance for SDM (Allouche et al. 2006). The average AUC values of the three different model types ranged from 0.848 to 0.949 (Fig. 2; Fig. S1), which is considered high to excellent in terms of model fitting (Fielding and Bell 1997, Manel et al. 2001). The evaluation results indicated that all the models successfully discriminated presence from background locations, and strongly rejected the null hypothesis that test points are no better than a random prediction for all thresholds implemented in MAXENT. Model comparison showed that climate and combined models performed marginally better than land cover models (Table 2; Fig. 2) but the difference in performance was not qualitatively different.

Table 2

Results of the model evaluation of American white pelican habitat suitability using the True Skill Statistic (TSS). Average values for the 10 replicates and the associated standard deviation are shown for each model type.

Model	Pre-aquaculture	Post-aquaculture
a) Breeding	0.841 ± 0.012	0.872 ± 0.031
Climatic	0.806 ± 0.029	0.853 ± 0.024
Combined	0.654 ± 0.053	0.662 ± 0.037
Land cover		
b) Non-breeding	0.902 ± 0.022	0.901 ± 0.033
Climatic	0.898 ± 0.023	0.893 ± 0.026
Combined	0.637 ± 0.060	0.644 ± 0.048
Land cover		
Figure 1. Map of the geographical context of the study system showing land cover types and American white pelicans (AWPE) GPS-tracked locations separated in three populations: Migrants in breeding range (black dots); Migrants in wintering range (white dots) and residents (blue dots).		
Figure 2. Results of the Maximum Entropy (MAXENT) models of the seasonal geographic range distributions of American white pelicans (AWPE). Maps show in warmer colours the higher environmental suitability for each model type and each range.		
Figure 3. Seasonal niche analyses of niche tracking and switching in American white pelicans. Columns show the niche overlap between breeding and non-breeding populations (panel a) and niche breadth (panel b) for each model dimension and each population, before (blue) and after (grey) the decline of aquaculture activities in the region. Niche overlap is measured via Schoener's D (D) and the I statistic (I), whereas niche breadth is measured via the Levin's concentration metrics in all cases.		
Figure 1		

The similarity measures (overlap) between the breeding and non-breeding populations was much greater for the land cover niche than for the climatic niche (Fig. 3a). Mean I statistic was 0.23 for climatic niche versus 0.78 for land cover niche (Schoener's D: 0.08 versus 0.54). Our results showed the lowest niche overlap for combined models, which appears to be more in agreement with the niche switcher hypothesis (Fig. 3a).

Niche breadth analyses revealed the breeding population showed a greater climatic niche breadth (pre-aquaculture: 0.070 ± 0.001 ; post-aquaculture: 0.055 ± 0.001) than the non-breeding population (pre-aquaculture: 0.025 ± 0.001 ; post-aquaculture: 0.022 ± 0.001) (paired t-test, $P < 0.01$, $n = 10$), but the difference between pre and post aquaculture was not statistically significant. In the case of land cover models, the breeding populations showed a significantly narrower niche (pre-aquaculture: 0.061 ± 0.005 ; post-aquaculture: 0.232 ± 0.007) than the non-breeding populations (pre-aquaculture: 0.113 ± 0.001 ; post-aquaculture: 0.251 ± 0.001) (paired t-test, $P < 0.01$, $n = 10$). Land cover niche breadth significantly differed before and after the decline in aquaculture activities, for both breeding and non-breeding populations (paired t-test, $P < 0.01$, $n = 10$) (Fig. 3b). Finally, niche breadth for combined models was also significantly

wider for breeding than non-breeding populations (paired t-test, $P < 0.05$, $n = 10$), but there was no statistically significant difference between pre and post aquaculture peak of activity.

Discussion

Ecological niches need to be considered dynamic entities over the seasonal cycle of migrants in order to better understand the temporal variability of individual and population needs (Martinez-Meyer et al. 2004). In our study, we developed species distribution models and analyzed the ecological niches of AWPE populations in two different phases of their annual life cycle. Our tracking results show high consistency with the known distribution of AWPE in North America (Knopf and Evans 2004, Rodewald 2015). More crucially, we found seasonal differences in their ecological niche patterns. Climatic, land cover and combined models demonstrated very high predictive power of the AWPE distribution (TSS ranged from 0.64 to 0.90; AUC ranged from 0.85 to 0.95); however, the niche patterns described by the climate, landcover, and climate-landcover combined models differed considerably indicating different roles of these habitat dimensions.

The results of our study indicated that the migratory behavior of the AWPE was better explained by the climatic “niche switcher” than the “niche tracker” hypothesis. Several study findings support this conclusion. First, the climatic niche suitability models estimated little overlap between the breeding and the winter ranges (Fig. 3a) indicating that climatic conditions were substantially different between the two ranges, but land-cover niche overlap was much greater indicating that pelicans tended to select similar land cover between the wintering and nesting grounds. Second, climatic niche breadth was greater in the breeding grounds than in the non-breeding grounds indicating the ability to adapt to different climatic conditions. Finally, AWPE showed a narrower land-cover niche breadth before compared to after the decline in aquaculture activities.

In the current literature there are examples of studies that were able to identify climatic “niche trackers” that follow the same climatic conditions year-round (e.g. Joseph and Stockwell 2000, Nakazawa et al. 2004, Gomez et al. 2016), as well as “niche switchers,” which switch climatic niches between seasons (Marini et al. 2013, Laube et al. 2015). Recently there has been a strong debate over this question and it is still unclear whether migrants are forced to switch niches due to geographical climatic variability between breeding and non-breeding regions (often not allowing for climatic niche tracking) or they actively do so by selecting climatically distinct environments in different seasons (Warren et al. 2008, Broennimann et al. 2012). Independent results from different studies should be interpreted cautiously because of differences in the amount and types of spatial distribution data among the studies. For example, Gomez et al. 2016 found predominant niche tracker behavior in migrant warblers. In that study, they emphasized the necessity of incorporating data on population-level geographical ranges, migratory connectivity and actual migration routes in order to accurately interpret the true breeding and non-breeding range of species as well as the migration paths followed by the birds. Here we presented a study that dealt with these questions based on year-round distribution and migration routes at population and individual level.

This study rejects the hypothesis that migratory behavior of AWPE would be motivated by tracking climatic conditions between the nesting and wintering grounds, where the individual would experience a restricted range of environmental conditions (Shaw and Couzin 2012). On the contrary, AWPE appear to switch climatic niches between seasons, which sheds light on the evolutionary origin of their facultative medium-distance migration (Kendall et al. 1996, Bell 2000). Results presented in this study seem to support the hypothesis that the harshness of late summer and autumn temperatures at the nesting grounds forced AWPE to face the decision of leaving at the cost of increasing mortality risk and energy expenditures in the migration, or staying at the cost of reduced survival under extreme climatic conditions, but it might not be enough to trigger migratory behavior (Salewski and Bruderer 2007, Winger et al. 2014). Unlike some passerine species (Gomez et al. 2016), AWPE do not seem to compensate the migration costs by the physiological benefits of living under the same climatic conditions (Wiens and Graham 2005). The tendency to track climatic niches across seasons in breeding populations may be partially explained by their wider climatic niches relative to that of residents and wintering populations (Fig. 3b) as well as by their life experience of climatic changes forcing them to search for more favorable conditions (Louchart 2008). The reasons to migrate may be more related to the higher reproductive success in the breeding grounds accompanied by less predation risk (Alerstam et al. 2003, Mckinnon et al. 2010) and by processes related to biotic interactions (Lawson and Weir 2014) and dispersal ability (Laube et al. 2013). This may help explain the facultative migration observed in some AWPE individuals, who completed the migration one year but remained in the wintering grounds the following one. Thus, the decision of facing migration or staying in the non-breeding grounds must be subject to a tradeoff between migration (individual) cost and long-term survival.

Consistent with the “niche switcher” hypothesis, individuals in the breeding range showed broader climatic niche than those in the non-breeding range. Land-cover niche was narrower in the breeding range than in the non-breeding range. This result may also reflect the temporal stationarity of land cover conditions in comparison to climate (Currie et al. 2017, see Broennimann et al. 2012). Migrants will need to adapt to changing climate conditions at the nesting grounds, whereas residents and individuals in the wintering grounds will face less climatic variability (Marini et al. 2013, Laube et al. 2015, Pérez-Moreno et al. 2016).

There was a much greater overlap in land-cover niche between the breeding and non-breeding populations in comparison with the climatic niche. The low climatic niche overlap between breeding and non-breeding grounds suggests that a hypothetical overwintering on the breeding grounds would require physiological tolerance deviations that will expose AWPE to unproductive winters (Gomez et al. 2016). This is probably the reason why the tendency of the facultative migration strategy is to remain in the wintering grounds when the physiological condition of the pelican is not optimal (e.g. immature or weak individuals).

Finally, our findings supported our expectations that the recent drastic decline in aquaculture activities starting around 2005 (King 2005) had impacted the land-cover niche of the AWPE populations. We found that land-cover niche breadth had expanded considerably at the wintering grounds after 2005, suggesting

that AWPE were forced to find new sources of nourishment and/or shelter due to the disappearance of the aquaculture ponds. However, we also found land-cover niche expansion in the nesting grounds. A plausible explanation is that migrants will show change in land-cover niche during their breeding season as a carryover from the wintering grounds. We believe this is one of the most important results of the present study, and has considerable economic implications for the fish farming in the South-eastern US since these aquacultural activities, apart from being an economic driver in the region, may be acting as a sustainable system to maintain viable long-term populations of AWPE. Finding a balance between the economic viability of aquaculture and the maintenance of the near perfect foraging habitats for the pelicans and other commensal species of waterbirds seems crucial for the sustainability of the ecosystem (Murphy 2005, King and Anderson 2005).

Conclusions

The present study addressed important concerns in the conservation and future management of AWPE populations regarding their ability to cope with ongoing climate change. Our results suggest that AWPE might respond unexpectedly to global change, as they might not track climatic changes (Barbet-Massin et al. 2009), but adapt to new conditions in similar environments, changing their migratory patterns and/or geographical distribution, like other taxa (Hickling et al. 2006, Marini et al. 2009). Furthermore, if global change has an impact on habitat availability, as predicted for some future scenarios (IPCC 2014), existing migration routes and migration strategies may disappear due to alterations in the migration paths and/or stopover sites. Further research should explore how recent climate changes will potentially affect the facultative migratory behaviour and how this condition evolves under such complex constraints.

Abbreviations

AWPE

American White Pelican; MAXENT:Maximum entropy; SDM:Species distribution model; VIF:Variance inflation factor; CRU:Climate research unit; NALCMS:North American Land Change Monitoring System; FAO:Food and Agriculture Organization; GLWD:Global Lakes and Wetlands; AIC:Akaike Information Criterion; PPM:Poisson point process model; TSS:True Skill Statistic metric; ROC:Receiver-Operating Characteristic; Area under the curve:AUC;

Declarations

Ethics approval and consent to participate

The authors declare that no animal was harmed or hurt during the development of the present study.

Consent for publication

Not applicable.

Availability of data and materials

All the datasets used during this study are fully available without restriction from the corresponding author upon request. AWPE gps-tracked locations, climate data and MaxEnt input files will be publicly and permanently accessible through Dryad repository (<https://datadryad.org>).

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

All authors conceived the ideas and designed methodology. DTK and FC collected the data. JGI and GW analysed the data. JGI led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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References

- Aebischer NJ, Robertson PA, Kenward RE. Compositional analysis of habitat use from animal radio-tracking data. *Ecology*. 1993 Jul;74(5):1313-25.
- Akaike H. Information theory as an extension of the maximum likelihood principle. *Second International Symposium on Information Theory, Budapest, Akademiai Kiado*. 1973. pp. 276-281.
- Alerstam T, Hedenström A, Åkesson S. Long-distance migration: evolution and determinants. *Oikos*. 2003 Nov;103(2):247-60.
- Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology*. 2006 Dec;43(6):1223-32.

Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global change biology*. 2004 Sep;10(9):1618-26.

65. Bell C. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology*. 2000 May;31(2):258-65.

Barbet-Massin M, Walther BA, Thuiller W, Rahbek C, Jiguet F. Potential impacts of climate change on the winter distribution of Afro-Palaeartic migrant passerines. *Biology Letters*. 2009 Feb 25;5(2):248-51.

Bell WJ. *Searching behaviour: the behavioural ecology of finding resources*. Springer Science & Business Media; 2012 Dec 6.

Berthold P. Bird migration: the present view of evolution, control, and further development as global warming progresses. *Acta Zoologica Sinica*. 2002;48(3):291-301.

Boyce MS, McDonald LL. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*. 1999 Jul 1;14(7):268-72.

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD, Wikelski M. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *Bioscience*. 2011 Sep 1;61(9):689-98.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global ecology and biogeography*. 2012 Apr;21(4):481-97.

Cox GW. The evolution of avian migration systems between temperate and tropical regions of the New World. *The American Naturalist*. 1985 Oct 1;126(4):451-74.

Currie DJ, Venne S. Climate change is not a major driver of shifts in the geographical distributions of North American birds. *Global Ecology and Biogeography*. 2017 Mar;26(3):333-46.

Davenport LC, Bazán IN, Erazo NC. East with the night: longitudinal migration of the Orinoco Goose (*Neochen jubata*) between Manú National Park, Peru and the Llanos de Moxos, Bolivia. *PloS one*. 2012 Oct 4;7(10): e46886.

Deblauwe V, Droissart V, Bose R, Sonké B, Blach-Overgaard A, Svenning JC, Wieringa JJ, Ramesh BR, Stévant T, Couvreur TL. Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. *Global Ecology and Biogeography*. 2016 Apr;25(4):443-54.

E.S.R.I., ArcGIS, 2014. 10.2. 1 for Desktop. Redlands, CA: Environmental System Research Institute

- Elith* J, H. Graham* C, P. Anderson R, Dudík M, Ferrier S, Guisan A, J. Hijmans R, Huettmann F, R. Leathwick J, Lehmann A, Li J. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*. 2006 Apr;29(2):129-51.
- Elith J, Kearney M, Phillips S. The art of modelling range-shifting species. *Methods in ecology and evolution*. 2010 Dec;1(4):330-42.
- Fielding AH, Bell JF. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation*. 1997 Mar;24(1):38-49.
- Glahn JF, Dixson PJ, Littauer GA, McCoy RB. Food habits of Double-crested Cormorants wintering in the delta region of Mississippi. *Colonial Waterbirds*. 1995 Jan 1:158-67.
- Gómez C, Tenorio EA, Montoya P, Cadena CD. Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences*. 2016 Feb 10;283(1824):20152458.
- Gottschalk TK, Huettmann F, Ehlers M. Thirty years of analysing and modelling avian habitat relationships using satellite imagery data: a review. *International Journal of Remote Sensing*. 2005 Jun 20;26(12):2631-56.
- Graham MH. Confronting multicollinearity in ecological multiple regression. *Ecology*. 2003 Nov;84(11):2809-15.
- Gschweng M, Kalko EK, Berthold P, Fiedler W, Fahr J. Multi-temporal distribution modelling with satellite tracking data: predicting responses of a long-distance migrant to changing environmental conditions. *Journal of Applied Ecology*. 2012 Aug;49(4):803-13.
- Gutierrez Illan J, Wang G, Cunningham FL, King DT. Seasonal effects of wind conditions on migration patterns of soaring American white pelican. *PloS one*. 2017 Oct 24;12(10):e0186948.
- Harris IP, Jones PD, Osborn TJ, Lister DH. Updated high-resolution grids of monthly climatic observations—the CRU TS3. 10 Dataset. *International journal of climatology*. 2014 Mar 15;34(3):623-42.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*. 2005 Dec;25(15):1965-78.
- Homer C, Dewitz J, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold N, Wickham J, Megown K. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*. 2015 May 1;81(5):345-54.
- Hoffmann AA, Sgro CM. Climate change and evolutionary adaptation. *Nature*. 2011 Feb;470(7335):479.

Hutchinson GE. Cold spring harbor symposium on quantitative biology. Concluding remarks. 1957; 22:415-27.

IPCC Synthesis Report 2014. Intergovernmental Panel on Climate Change (IPCC).

Jiguet F, Barbet-Massin M, Chevallier D. Predictive distribution models applied to satellite tracks: modelling the western African winter range of European migrant Black Storks *Ciconia nigra*. Journal of Ornithology. 2011 Jan 1;152(1):111-8.

Joseph L, Stockwell D. Temperature-based models of the migration of Swainson's flycatcher *Myiarchus swainsoni* across South America: a new use for museum specimens of migratory birds. Proceedings-Academy of Natural Sciences of Philadelphia. 2000 Apr 14;150:293-300.

Kendall WL, Peterjohn BG, Sauer JR. First-time observer effects in the North American breeding bird survey. The Auk. 1996 Oct 1;113(4):823-9.

King DT, Werner SJ. Daily activity budgets and population size of American white pelicans wintering in south Louisiana and the delta region of Mississippi. Waterbirds. 2001 Aug 1:250-4.

King DT, Anderson DW. Recent population status of the American white pelican: a continental perspective. Waterbirds. 2005 Dec;28(sp1):48-55.

King DT. Interactions between the American white pelican and aquaculture in the southeastern United States: an overview. Waterbirds. 2005 Dec;28(sp1):83-7.

King DT, Belant J, Harrel B, Glahn J. Superabundant food at catfish aquaculture facilities improves body condition in American White Pelicans. Waterbirds. 2010 Jun;33(2):221-8.

King DT, Fischer J, Strickland B, Walter WD, Cunningham FL, Wang G. Winter and summer home ranges of American white pelicans (*Pelecanus erythrorhynchos*) captured at loafing sites in the southeastern United States. Waterbirds. 2016 Sep;39(3):287-95.

King DT, Wang G, Yang Z, Fischer JW. Advances and environmental conditions of spring migration phenology of American White Pelicans. Scientific reports. 2017 Jan 16;7:40339.

Knopf, F. L. and R. M. Evans 2004. American White Pelican (*Pelecanus erythrorhynchos*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bna.57>. Accessed 1/15/2019.

Kock N, Lynn G. Lateral collinearity and misleading results in variance-based SEM: An illustration and recommendations. Journal of the Association for Information Systems. 2012 Sep 26;13(7).

Laube I, Graham CH, Böhning-Gaese K. Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. Global Ecology and Biogeography. 2013 Feb;22(2):223-32.

- Laube I, Graham CH, Böhning-Gaese K. Niche availability in space and time: migration in *Sylvia* warblers. *Journal of Biogeography*. 2015 Oct;42(10):1896-906.
- Lawson AM, Weir JT. Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology letters*. 2014 Nov;17(11):1427-36.
- Lehner B, Döll P. Development and validation of a global database of lakes, reservoirs and wetlands. *Journal of Hydrology*. 2004 Aug 20;296(1-4):1-22.
- Lobo JM, Jiménez-Valverde A, Real R. AUC: a misleading measure of the performance of predictive distribution models. *Global ecology and Biogeography*. 2008 Mar;17(2):145-51.
- Louchart A. Emergence of long distance bird migrations: a new model integrating global climate changes. *Naturwissenschaften*. 2008 Dec 1;95(12):1109-19.
- Manel S, Williams HC, Ormerod SJ. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of applied Ecology*. 2001 Oct;38(5):921-31.
- Manly BF, McDonald L, Thomas DL, McDonald TL, Erickson WP. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media; 2002 May 8.
- Marini MÂ, Barbet-Massin M, Lopes LE, Jiguet F. Geographic and seasonal distribution of the Cock-tailed Tyrant (*Alectrurus tricolor*) inferred from niche modeling. *Journal of ornithology*. 2013 Apr 1;154(2):393-402.
- Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W. Evaluation of consensus methods in predictive species distribution modelling. *Diversity and distributions*. 2009 Jan 1;15(1):59-69.
- Martin TE. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts?. *Ecology*. 2001 Jan;82(1):175-88.
- Martínez–Meyer E, Townsend Peterson A, Navarro–Sigüenza AG. Evolution of seasonal ecological niches in the *Passerina buntings* (Aves: Cardinalidae). *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 2004 Jun 7;271(1544):1151-7.
- Mau-Crimmins TM, Schussman HR, Geiger EL. Can the invaded range of a species be predicted sufficiently using only native-range data?: Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States. *Ecological Modelling*. 2006 Mar 15;193(3-4):736-46.
- McKinnon L, Smith PA, Nol E, Martin JL, Doyle FI, Abraham KF, Gilchrist HG, Morrison RI, Bêty J. Lower predation risk for migratory birds at high latitudes. *Science*. 2010 Jan 15;327(5963):326-7.
- McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL. Considering ecological dynamics in resource selection functions. *Journal of animal ecology*. 2010 Jan;79(1):4-12.

- Merow C, Smith MJ, Silander Jr JA. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*. 2013 Oct;36(10):1058-69.
- Nakazawa Y. Niche breadth, environmental landscape, and physical barriers: their importance as determinants of species distributions. *Biological Journal of the Linnean Society*. 2013 Jan 17;108(2):241-50.
- Nakazawa Y, Peterson AT, Martínez-Meyer E, Navarro-Sigüenza AG. Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. *The Auk*. 2004 Apr 1;121(2):610-8.
- North American Land Change Monitoring System (NALCMS) at 250 m spatial resolution. 2005. Produced by Natural Resources Canada/Canadian Center for Remote Sensing (NRCan/CCRS), United States Geological Survey (USGS); Instituto Nacional de Estadística y Geografía (INEGI), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Comisión Nacional Forestal (CONAFOR).
- O'Brien RM. A caution regarding rules of thumb for variance inflation factors. *Quality & quantity*. 2007 Oct 1;41(5):673-90.
- Pearce J, Ferrier S. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological modelling*. 2000 Apr 20;128(2-3):127-47.
- Pérez-Moreno H, Martínez-Meyer E, Soberón Mainero J, Rojas-Soto O. Climatic patterns in the establishment of wintering areas by North American migratory birds. *Ecology and evolution*. 2016 Apr;6(7):2022-33.
- Phillips RA, Silk JR, Croxall JP, Afanasyev V. Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation*. 2006 May 1;129(3):336-47.
- Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. *Ecological modelling*. 2006 Jan 25;190(3-4):231-59.
- PRISM Climate Group 2012 Four-km monthly products. Oregon State University, Corvallis, OR, USA. <http://www.prism.oregonstate.edu/>. Accessed 04/25/2019.
- van Proosdij AS, Sosef MS, Wieringa JJ, Raes N. Minimum required number of specimen records to develop accurate species distribution models. *Ecography*. 2016 Jun;39(6):542-52.
- Quintero I, Wiens JJ. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. *Global Ecology and Biogeography*. 2013 Apr;22(4):422-32.

- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Remsen Jr JV, Parker III TA. Seasonal distribution of the Azure Gallinule (*Porphyryla flavirostris*), with comments on vagrancy in rails and gallinules. *The Wilson Bulletin*. 1990 Sep 1:380-99.
- Renner IW, Warton DI. Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics*. 2013 Mar;69(1):274-81.
- Renner IW, Elith J, Baddeley A, Fithian W, Hastie T, Phillips SJ, Popovic G, Warton DI. Point process models for presence-only analysis. *Methods in Ecology and Evolution*. 2015 Apr;6(4):366-79.
- Rodewald, P. 2015. The Birds of North America: <https://birdsna.org>. Cornell Laboratory of Ornithology, Ithaca, NY). Accessed 02/07/2019.
- Salewski V, Bruderer B. The evolution of bird migration—a synthesis. *Naturwissenschaften*. 2007 Apr 1;94(4):268-79.
- Sauer J, Niven D, Hines J, Ziolkowski Jr D, Pardieck KL, Fallon JE, Link W. The North American breeding bird survey, results and analysis 1966-2015. Version 2.07. 2017. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schoener TW. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology*. 1968 Jul;49(4):704-26.
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang HP, Harnik N, Leetmaa A, Lau NC, Li C. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*. 2007 May 25;316(5828):1181-4.
- Shannon HD, Young GS, Yates MA, Fuller MR, Seegar WS. Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. *Boundary-Layer Meteorology*. 2002 Aug 1;104(2):167-99.
- Shaw AK, Couzin ID. Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *The American Naturalist*. 2012 Nov 27;181(1):114-24.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. Ecological responses to recent climate change. *Nature*. 2002 Mar;416(6879):389.
- Warren DL, Glor RE, Turelli M. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution: International Journal of Organic Evolution*. 2008 Nov;62(11):2868-83.

Warren DL, Glor RE, Turelli M. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*. 2010 Jun;33(3):607-11.

Wiens JJ, Graham CH. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 2005 Dec 15;36:519-39.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes JA, Harrison SP, Hawkins BA. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters*. 2010 Oct 1;13(10):1310-24.

Winger BM, Barker FK, Ree RH. Temperate origins of long-distance seasonal migration in New World songbirds. *Proceedings of the National Academy of Sciences*. 2014 Aug 19;111(33):12115-20.

Winger BM, Auteri GG, Pegan TM, Weeks BC. A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews*. 2019 Jun;94(3):737-52.

Figures

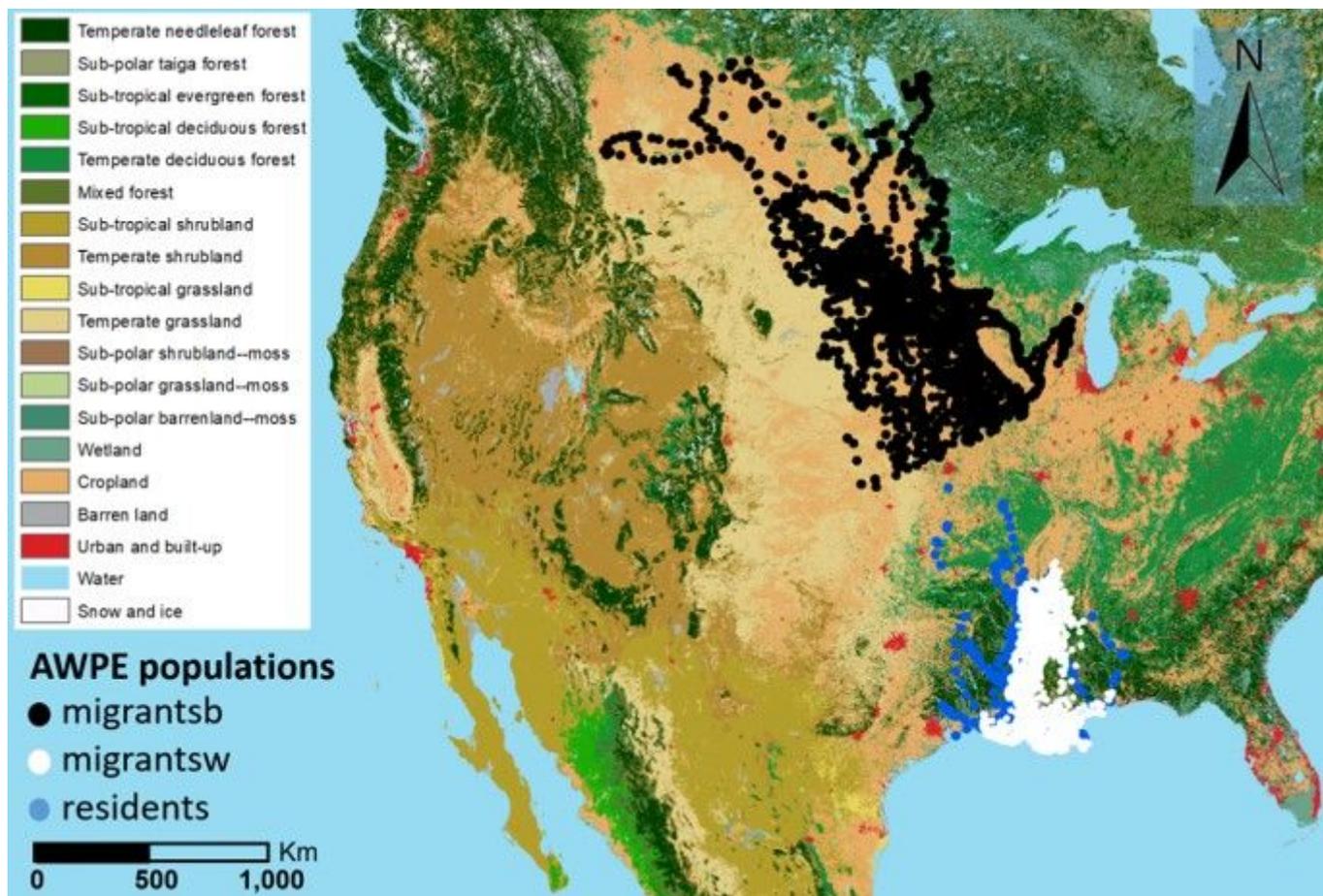


Figure 1

. Map of the geographical context of the study system showing land cover types and American white pelicans (AWPE) GPS-tracked locations separated in three populations: Migrants in breeding range (black dots); Migrants in wintering range (white dots) and residents (blue dots).

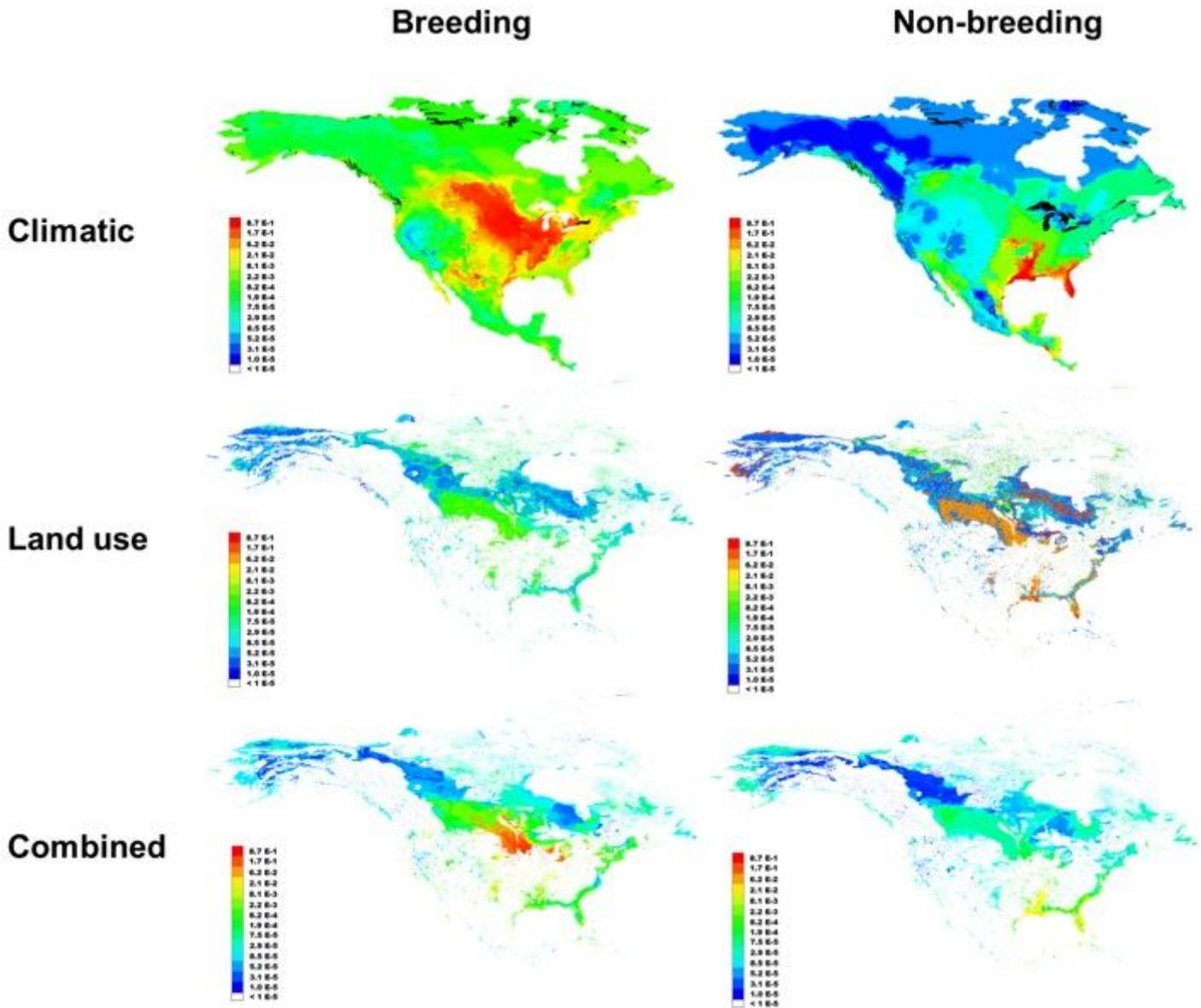
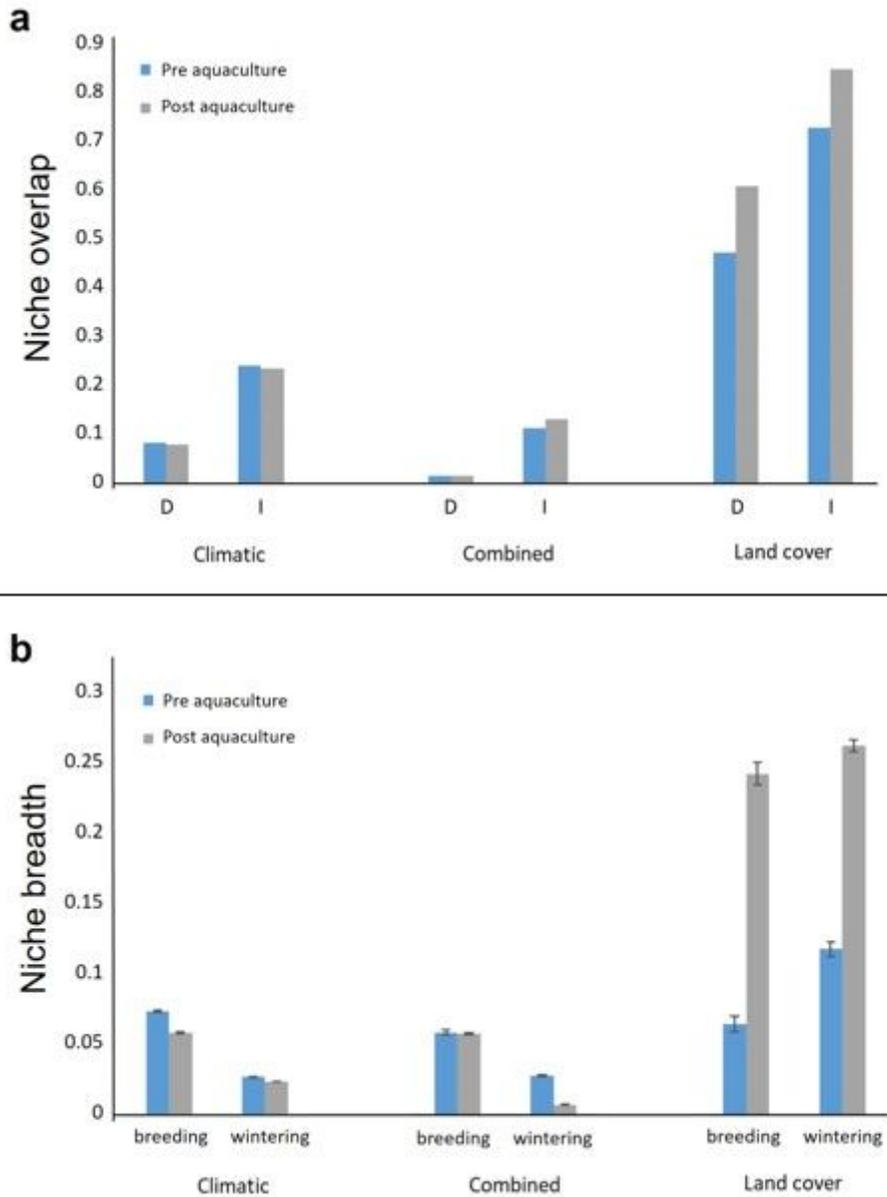


Figure 2

Results of the Maximum Entropy (MAXENT) models of the seasonal geographic range distributions of American white pelicans (AWPE). Maps show in warmer colours the higher environmental suitability for each model type and each range.



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Figure 3

Seasonal niche analyses of niche tracking and switching in American white pelicans. Columns show the niche overlap between breeding and non-breeding populations (panel a) and niche breadth (panel b) for each model dimension and each population, before (blue) and after (grey) the decline of aquaculture activities in the region. Niche overlap is measured via Schoener's D (D) and the I statistic (I), whereas niche breadth is measured via the Levin's concentration metrics in all cases.

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