Arctic tern flyways and the changing Atlantic Ocean wind patterns

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A R T I C L E   I N F O

A B S T R A C T

Migratory bird trajectories are the result of their own speed and direction in combination with wind speed and direction. Several studies have focused on the interplay between bird migration and general wind patterns, however, the majority of them did not take into account climate change and used a small number of individuals. By integrating tracking data from two populations of Arctic terns ($n = 72$) with ERA5 and Earth System Model (ESM) wind data, we were able to study the current conditions and the potential effects of climate change on them.

The Svalbard birds experienced wind support values around 3 m/s with a relatively low variability, while the Dutch population experienced almost no wind support with a greater variability. Svalbard terns exhibited better adjustment of their flyways to daily and annually varying wind conditions, and responded to crosswinds by drifting over extended periods/regions (median Drift Ratio $\pm$ standard deviation: 0.51 ± 0.18) while the Dutch population mostly compensated (0 ± 0.31). We suggest that the Svalbard birds will be able to adapt their flyways to future Atlantic Ocean wind pattern changes, while we are uncertain whether the Dutch population can keep compensating for future changes or not.

We examine the robustness of our results by using a selection of ESMs and by including metrics for several uncertainty sources (ESMs, wind variability, tracking method etc.). This study highlights the importance of wind as a flyway-shaping factor and points out the possibility for different responses to wind by different populations of the same species, in different Ocean regions and seasons.

Introduction

Birds spend their lives in a thin layer around our planet: the atmosphere. This dynamic medium influences all aspects of their migration and physiology [1]. During flight, birds need to contend with atmospheric conditions and adapt to general wind circulation patterns such as the jet stream, which is associated with much of the midlatitude weather and climate, and the tropical trade winds [2,3]. Wind speeds are in the same order of magnitude as the birds' airspeed and thus can have a large impact on their groundspeed and overall flying efficiency [1,4]. This is a challenge that birds address by adapting their behaviour: adjustment of departure time, selection of optimal flight height, use of appropriate flight speed, adjustment of direction, and exploitation of favourable (tail) winds [5].

The climate is changing [6], influencing the atmospheric circulation, and forcing birds to make decisions based on changing wind direction while flying. This becomes even more challenging for seabirds since they fly mainly over oceans, where wind speeds are generally higher than over continents but where direct observations are sparse [1]. Therefore, it is important to utilize the possibilities offered by Earth System Models (ESM) to assess the relation between bird flight and wind patterns, to make projections about future changes in wind conditions, and to investigate possible bird behaviour adjustments. ESMs combined with movement data from tracking devices can give an insight to the migration patterns of smaller birds. Despite their low accuracy, the use of a larger sample size (more bird locations) provides distributions of

locations and angles, which are used to infer the response to wind and flight behaviour. This approach of using distributions, median values and uncertainty measures rather than individual measurements, leads to more robust findings. The large number of location data will additionally allow us to create maps that can be used to investigate spatial patterns.

Birds travelling long distances, across all climatic zones make suitable candidates for studying the effect of wind patterns on migratory birds, since the exploitation of winds must be of importance to them [7]. One such bird is the arctic tern (*Sterna paradisaea*), performing one of the most spectacular migrations: up to 80,000 km in a round trip between the two poles [8]. It exploits the seasonal resources and profits from the favourable weather conditions in their Arctic breeding grounds, while it winters along the Antarctic pack ice [9–11]. So far, studies have focused on several arctic tern populations, using the Atlantic and the Pacific Ocean highways: Svalbard [12], Netherlands [13], Alaska [7,9], Greenland, Iceland [8], Baltic Sea [11] and White Sea [14]. The importance of wind in shaping their flyways and in their flight behaviour in general has been highlighted by studies using small tracking devices (geolocators) that yield insight into this small-sized seabird's migration patterns [8,11,12,15,16].

Usually, the effect of atmospheric winds on bird flight is estimated using the concept of wind support, being the wind vector in the direction of the bird's flight, with positive values representing tailwinds and negative values headwinds [17]. It influences the bird's groundspeed, the overall migration speed and energetic expenses, and has been used for studying flight speeds, flight altitudes, flight range, migration intensity and stopover behaviour. Moreover, wind support (and crosswinds) can help us elucidate the relationship between winds and the migration corridors of arctic terns, while the response of arctic terns to lateral flows (compensation/drift) can provide insights into the orientation behaviour of the birds at any moment (or location). Even though we found a limited number of studies focusing on the response of arctic terns to wind [11,12,16,18], we failed to find studies that include the effects of climate change on the migration behaviour of this formidable bird. As a matter of fact, very few studies have addressed the effects of changing wind circulation on migratory birds, with one such study being the one by La Sorte et al. [19], albeit for unknown bird species since weather surveillance radar data were used.

We use geolocator data from two arctic tern populations (Svalbard and Netherlands) integrated with wind data from ERA5 reanalysis (representing the present-day climate) in order to analyse their flight behaviour and the wind support along their migratory paths. The large number of tracking data (Svalbard: 61 birds, Netherlands: 11) allows us to create wind-support maps for a large part of the AO, by treating tracking data as individual points rather than bird trajectories. This approach allows to identify regions and patterns of interest that might be otherwise masked. Furthermore, we employ CMIP6 ESM wind data for future projections of wind support per population, season and AO region. Finally, we combine all analyses in an attempt to assess possible flyway changes in the future. In this paper, we aim to address a) The response of the two arctic tern populations to global wind patterns and b) The impact of projected future wind patterns from ESMs on these populations.

Methods

Bird data

Dutch population

Adult arctic terns were captured on their nests in Eemshaven (53°33′ N, 6°94′ E) and Punt van Reide (53°31′ N, 7°10 E). A total of 21 birds were given a geolocator (Migrate Technology Ltd., Intigeo, type: 3.12.4); 16 birds in 2014 and 5 in 2017. The geolocators sampled the light intensity every minute and recorded the max light every 5 mins, and could record data for a maximum of 15 months. A total of 12

geolocators were retrieved (57%); 9 from 2014 (56%) and 3 from 2017 (60%). For this study, we had access to data from 11 geolocators, each of which had been recording data for at least 364 days. We used the R language package FLightR [20] for position calculations, and the BAStag package [21] for annotating sunrise and sunset, with a light threshold value of 1.5. The geolocators recorded data for 422 days on average (range 364–500), but we used only the first 12 months from each device.

Svalbard population

A total of 150 light loggers (type Intigeo W65 and Intigeo C65 from Migrate Technology Ltd) were attached to Arctic terns during the breeding seasons of 2012 to 2016 in Ny Ålesund, Svalbard. In the following breeding seasons a total of 73 loggers were retrieved. No logfiles could be downloaded from 11 retrieved loggers and one logger only had three months of data and was omitted from this study. Eventually, a total of 61 loggers was used in this study. Light levels were sampled every minute with maximum light recorded every 5 minutes.

The light level data were processed using Intiproc (Geolocation Processing Software) estimating the average location of each bird at night and day. We used a threshold of 10, an elevation angle of -3.7° and a period of 10 days before and after the equinox. Locations were unavailable at periods of the year when birds were experiencing 24-hour daylight and around equinoxes, when day length is similar throughout the world. The filtered data contained between 214 and 395 points of locations for all birds (mean = 302, SD = 46.1).

Staging areas

Migrating animals stop in suitable habitats (staging areas) in order to refuel or rest, before continuing their journey, ideally making use of environmental assistance (e.g. wind) in order to migrate successfully. This results in zero or low distance covered, periods that need to be excluded from the analyses. Degrees of longitude [22] and latitude [7,8] covered have been used to distinguish between moving and stationary (breeding range, wintering range, staging areas) periods. However, we found that such approaches might underestimate the number of stationary positions in some cases. For example, using 0.8° of longitude per 12 hours as a threshold [22] results in fewer stationary points for birds flying meridionally (from N to S or vice versa) compared to the ones that fly zonally (W to E or vice versa), covering more degrees of longitude per 12 hours. The opposite was observed when 0.8° of latitude per 12 hours were used as a threshold: meridionally flying birds covered more degrees per 12 hours (resulting in more stationary points) compared to the ones flying zonally. This lead us to adopting an alternative approach: combining longitudinal and latitudinal distance into a single vector: 1.6° covered per 12 hours.

An additional challenge was the fact that one degree of longitude at the equator translates roughly to 111 km but not at higher latitudes (~55 km at 60° latitude, for example). After performing linear regression, using all the distances covered per 12-hour section in degrees (independent variable) and in km (dependant variable), we calculated a slope of ~105 km/degree. Our final step was to convert degrees to km, and acquire a new threshold: 168 km (1.6° * 105 km/degree) per 12 hours. If birds did not cover a distance of more than 168 km between two consecutive locations (12 hours), in any direction, for at least two and a half days (five locations, cf. [22]), we classified this location as "stationary".

Svalbard subpopulations

During autumn migration, the Svalbard arctic terns fly over the Greenland Sea between Greenland and Iceland into the North AO and later approach the North African coast. They then split into four main routes: American coast, African coast, America – Africa and Africa – America. For the two last routes, America – Africa and Africa – America, the terns cross the AO zonally, between 20°S – 40°S. We omitted the data points from this crossing during autumn migration, by excluding all datapoints between 20°S – 40°S, and 20°W – 10°E. We assigned the rest

of the data points, close to the coasts, to two subpopulations: Svalbard-Am (datapoints close to the American coast) and Svalbard-Af (close to the African coast). This resulted in two subpopulations sharing the same data points north of the equator during autumn, while having different datapoints south of the equator.

Wind data

Wind data preparation

Arctic terns typically migrate at low altitudes, near the water surface [16,18], so we used the zonal (u10) and meridional (v10) surface wind components from the ECMWF Reanalysis v5 (ERA5), as actual wind conditions and for validating the CMIP6 ESMs. Ten years of data (2011–2020) were used [23] at a spatial resolution of ~25 km and at an hourly temporal resolution. For future projections, we downloaded the zonal (uas) and meridional (vas) surface wind components from 29 ESMs. For present conditions (2011–2020), we selected the historical run and for future (2076–2085), the Shared Socioeconomic Pathway 5–8.5 (SSP585), at various spatial resolutions (depending on the model) and at a daily temporal resolution. The 29 ESMs and the ERA5 data were eventually used at a daily temporal resolution and re-gridded to a spatial resolution of ~100 km [24].

ESM validation

We validated all 29 ESMs against the ERA5 surface wind data, using two methods (Fig. 1). Firstly, we calculated the monthly zonal and meridional wind component means for the entire AO using ERA5 wind data and compared these to the ones calculated with each of the 29 ESMs, employing Root Mean Square Errors (RMSE), correlation co-efficients (r), and differences in monthly standard deviation (σ). Finally, we averaged all three metrics over the two wind components, acquiring a single RMSE, r and σ value. The best performing models are considered the ones with relatively low RMSE, high r and low σ difference.

Secondly, we followed the Reichler & Kim [25] approach, a method in which annual mean climatologies from gridded fields of models (29 CMIP6 ESMs) and validating data (ERA5) are used. We first calculated for each model and wind component (zonal and meridional) a normalized error variance by squaring the weighted grid-point differences between ESMs and ERA5, for the 2011–20 period. We used bird occurrences as weights: grid cells with more bird location data had higher weight than grid cells with fewer birds, and grid cells with no birds (minimum weight used = 1). Then, the individual model variances were normalized by dividing them with the average CMIP6 variance and finally, the mean over both wind components was taken using equal weights. According to this method, the best-scoring ESMs are the ones with lowest MPI values.

In the last step, we selected the models that fulfilled four criteria: a) MPI < 1, b) RMSE < 0.3 m/s, c) r in the top 50% and d) σ difference in the bottom 50%. Eventually, we selected the five best performing models (MIROC6, EC-Earth3-Veg, HadGEM3-GC31-MM, HadGEM3-GC31-LL, UKESM1-0-LL) and used these to calculate future wind support and crosswind changes.
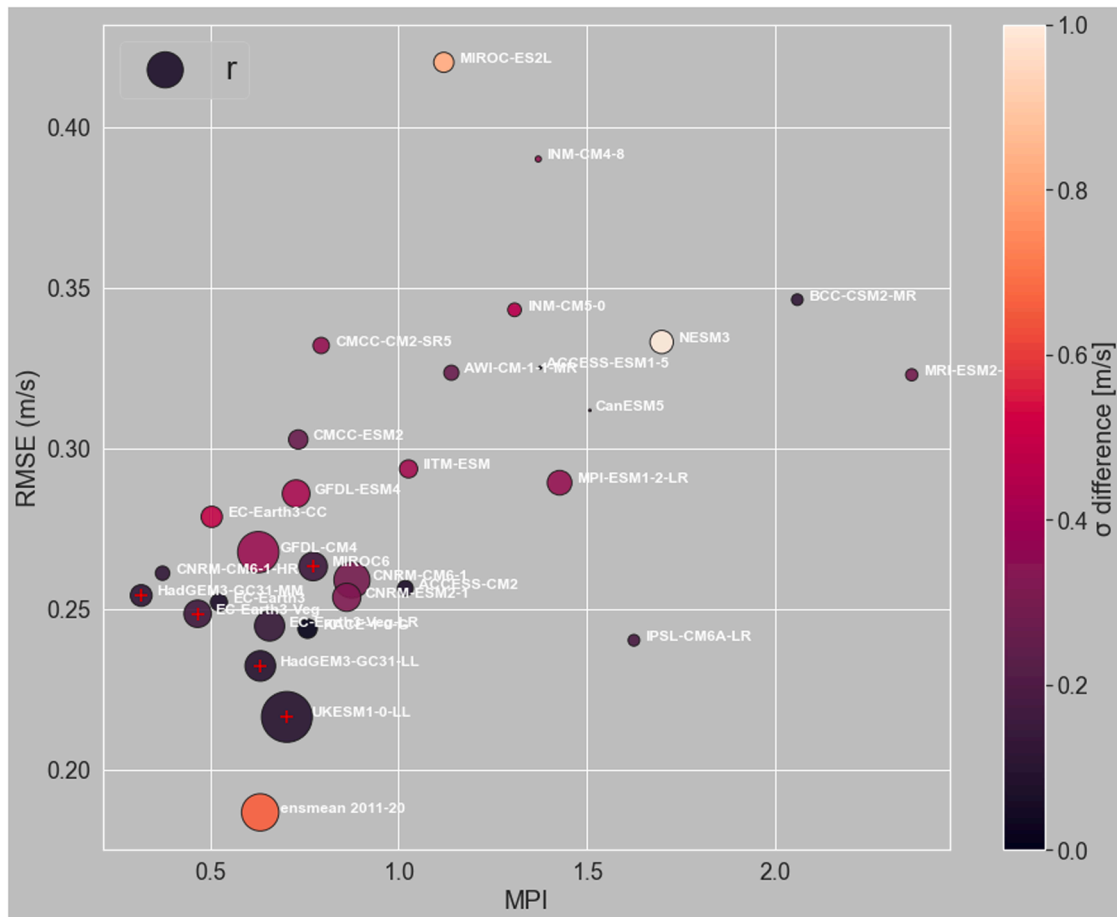

Fig. 1. Scatterplot of both validation methods used for selecting the five best Earth System Models (ESM). The x-axis depicts the Model Performance Index (MPI), as calculated using the Reichler & Kim (2008) method. The root mean square error (RMSE, y-axis), correlation coefficient (r, dot size) and the standard deviation (σ) difference (dot colour) were used to compare each ESM's ability in predicting the wind (u- and v-components) conditions over the AO to ERA5. Best performing models, located at the bottom left corner (low MPI and RMSE values), have large dot size (high r values) and dark colour (small difference in σ with the ERA5 data). The five models selected are depicted by the red crosses.

Wind support, crosswind and drift ratio

Wind support and crosswind calculation

We calculated the bird moving direction (groundspeed vector) from each location to the next [26,27]. We then combined zonal and meridional wind components of the climate data (ERA5 and CMIP6) [28] into an overall wind vector ($\overrightarrow{w}$) with speed and direction. The angle between the wind and the groundspeed vectors (θ) was used for estimating wind support and crosswind. These were calculated for each bird location, during both migrations (spring and autumn), as follows:

$$windsupport = |\overrightarrow{w}| \times cos\theta \qquad (1)$$

Positive wind support values imply tailwinds, while negative imply headwinds

$$crosswind = ||\overrightarrow{w}| \times sin\theta| \qquad (2)$$

Crosswind is always positive, irrespective of whether it comes from left or right, relative to the groundspeed's direction.

ERA5 wind support and crosswind datasets

We calculated the actual wind support and crosswind that the birds experienced using the ERA5 reanalysis wind data for each bird location and date (ERA5_actual dataset, see Fig. 2). We then created an "artificial interannual variability" dataset by calculating the wind support that the birds would have experienced if they flew the same route on the same day of the year for 10 consecutive years, from 2011 until 2020 (ERA5_10 yr). This resulted in an additional dataset with ten wind support and ten crosswind values per bird location (Fig. 2).

ESM wind support and crosswind datasets

We calculated the bird's wind support and crosswind on the actual dates using the ESM wind data for each bird location and date (CMIP6_actual dataset), and the wind support that they are projected to experience 75 years into the future, between 2086 and 2095 (Fig. 2), resulting in the CMIP6_proj dataset. Furthermore, the difference between future and present wind conditions was calculated by subtracting the two ESM datasets, resulting in the CMIP6_diff dataset: CMIP6_diff equals CMIP6_proj minus CMIP6_actual.

Finally, three "artificial interannual variability" CMIP6 datasets were created, by calculating the wind support that the birds would experience if they flew on the same day of the year for 10 consecutive years, from 2011 until 2020 (CMIP6_actual_10 yr) and from 2086 until 2095 (CMIP6_proj_10 yr). The difference between these two datasets was then taken: CMIP6_diff_10 yr = CMIP6_proj_10 yr – CMIP6_actual_10 yr. This resulted in three additional datasets with ten wind support and ten crosswind values per bird location (Fig. 2).

Daily variability datasets

We also created an "artificial daily variability" dataset by calculating the wind support that the birds would experience if they flew on each of the twelve days before and twelve days after the actual date (day 0), resulting in an additional dataset with 25 wind support and 25 crosswind values per bird location (ERA5_25d, see Fig. 2).

Drift ratio calculation

We assume that in very light (or lack of) winds, arctic terns fly along the shortest possible route from each location to the next. The Preferred Direction of Movement (PDM) of both populations during both seasons was then defined as the shortest possible route (great-circle distance) between two locations (Fig. 3, blue squares, circles and triangles). Each migration was subdivided into a number of legs by connecting wintering grounds (average position of Svalbard wintering birds: 26.4°W, 66.5°S, Dutch birds: 0.3°E, 69.6°S), staging sites (average position of Svalbard staging birds in N. Atlantic staging site: 34.1°W, 53.2°N, Uruguay-Argentina staging site: 40.5°W, 38.2°S and South African staging site: 10.7°E, 37.1°S) and breeding grounds (coordinates of the Svalbard bird colony: 11.9°E, 78.9°N, Dutch bird colony: 7°N, 53.3°N). During the autumn migration, we used the African staging site as the destination of the Dutch birds instead of Antarctica. This was done because the Dutch birds continue their trip to the Indian Ocean (IO), a region outside the scope of this study, instead of crossing directly the SO.

Drift ratio (DR) is the ratio between the bird's sideward (to the PDM) ground speed (in m/s) and the sideward (to the PDM) wind speed (in m/s). As Vansteelant et al. [29], we omitted locations with weak sidewinds (< 0.5 m/s). Furthermore, we removed locations with outlier groundspeeds (more than three standard deviations above or below the mean (z-score > 3) and locations with absolute DR values greater than two, as the low accuracy of geolocators [30,31] potentially influences the accuracy of the groundspeed and consequently of the sideward groundspeed calculations, resulting in a number of outliers. Finally, we calculated the DR using the following formula:

$$DR = \frac{sidewardgrounspeed}{sidewind} \qquad (3)$$

A DR-value of zero indicates full compensation (the bird does not move sidewards), and a value of one indicates that the bird moves sidewards (drifts) with the same speed as the wind (full drift strategy). Everything between zero and one is a partial compensation/partial drift strategy. Values below 0 indicate an overcompensation behaviour (the bird compensates more than necessary for keeping its course), and values over 1 indicate overdrifting (the bird moves sidewards with a higher speed than the wind).
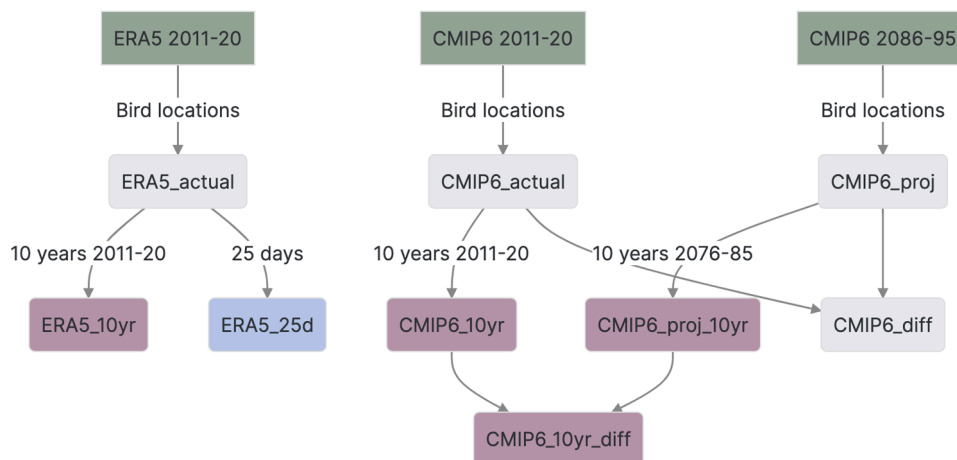

Fig. 2. All wind support and crosswind datasets used in this study, created by combinations of the original ERA5 and CMIP6 wind data.
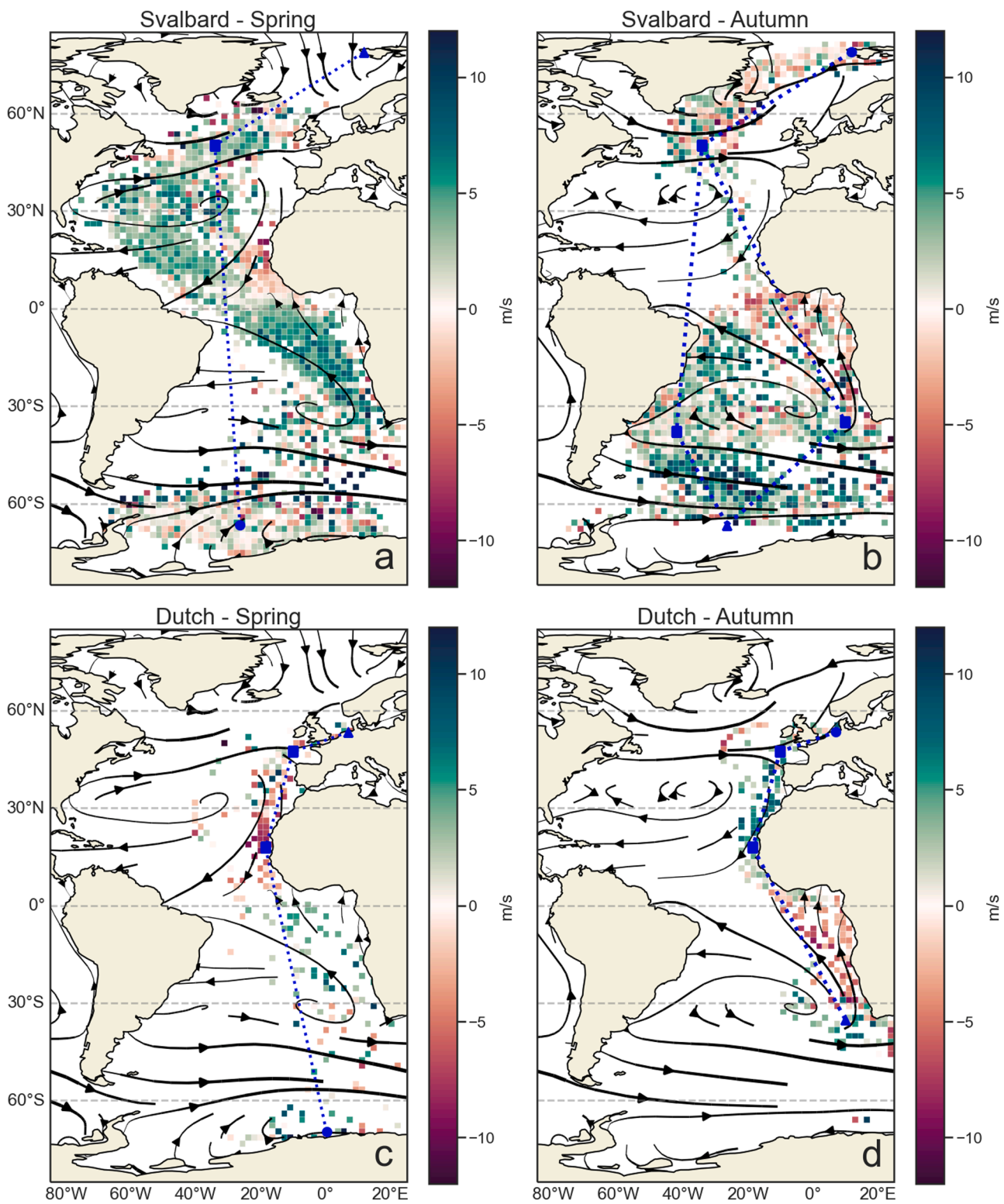
Fig. 3. Wind support gridded maps for a) spring and b) autumn migration of the Svalbard population, and c) spring and d) autumn migration of the Dutch population. The wind support values of each bird location are averaged per 2°x2° bin. Green colour depicts positive support (tailwind) and red, negative support (headwind). Black arrows show the decadal mean (2011–2020) of ERA5 surface wind (u and v components) for spring (left column, months of March, April and May) and autumn (right column, months of September, October and November), with their width representing wind magnitude. The blue circles depict the starting point of the migration, the blue triangles the end point and the blue squares the staging sites. The dotted lines connecting them represent the preferred direction of movement (PDM), defined as the great circle distance.

Population comparison and sample sizes

Due to the smaller size of the Dutch population (*n* = 11 against *n* = 61 for Svalbard) all comparisons between the two populations were performed either using the entire datasets (all location data, Figs. 4, 6 and 9) or large bins (5, 10 and 20° of latitude, Figs. 5, 7 and 8), covering hundreds to thousands of kilometres, and providing a good balance between spatial resolution and statistical power (sample size).

The non-parametric Mann-Whitney U Test was used to compare the distribution of the angles between the groundspeed and the wind vectors (Fig. 4), of the two populations. We reject the null hypothesis that distributions are identical, when *p*-values are lower than the confidence level α = 0.05. Bootstrapping (resampling 1000 times with replacement) provided 95% confidence intervals for the median value per bin (Figs. 5 and 7). t-tests were performed per bin or lag, in order to detect significant differences between the actual wind support and the 10-year mean

(Fig. 5), the actual wind support (lag 0) and the other 24 lags (Fig. 6) and the drift ratio of the two populations (Fig. 7). We reject the null hypothesis that median values are identical, when *p*-values are lower than the confidence level α = 0.05.

Results

The present

Wind support

In order to explore the importance of the Atlantic Ocean (AO) wind patterns on the migration of the two populations, we visualise the distribution of the birds and quantify wind support per bird location (averaged over 2°x2° bins). The sigmoidal shape is a characteristic of the Svalbard population's spring migration (Fig. 1a). It follows the general circulation patterns, the prevailing westerlies and trade winds, and
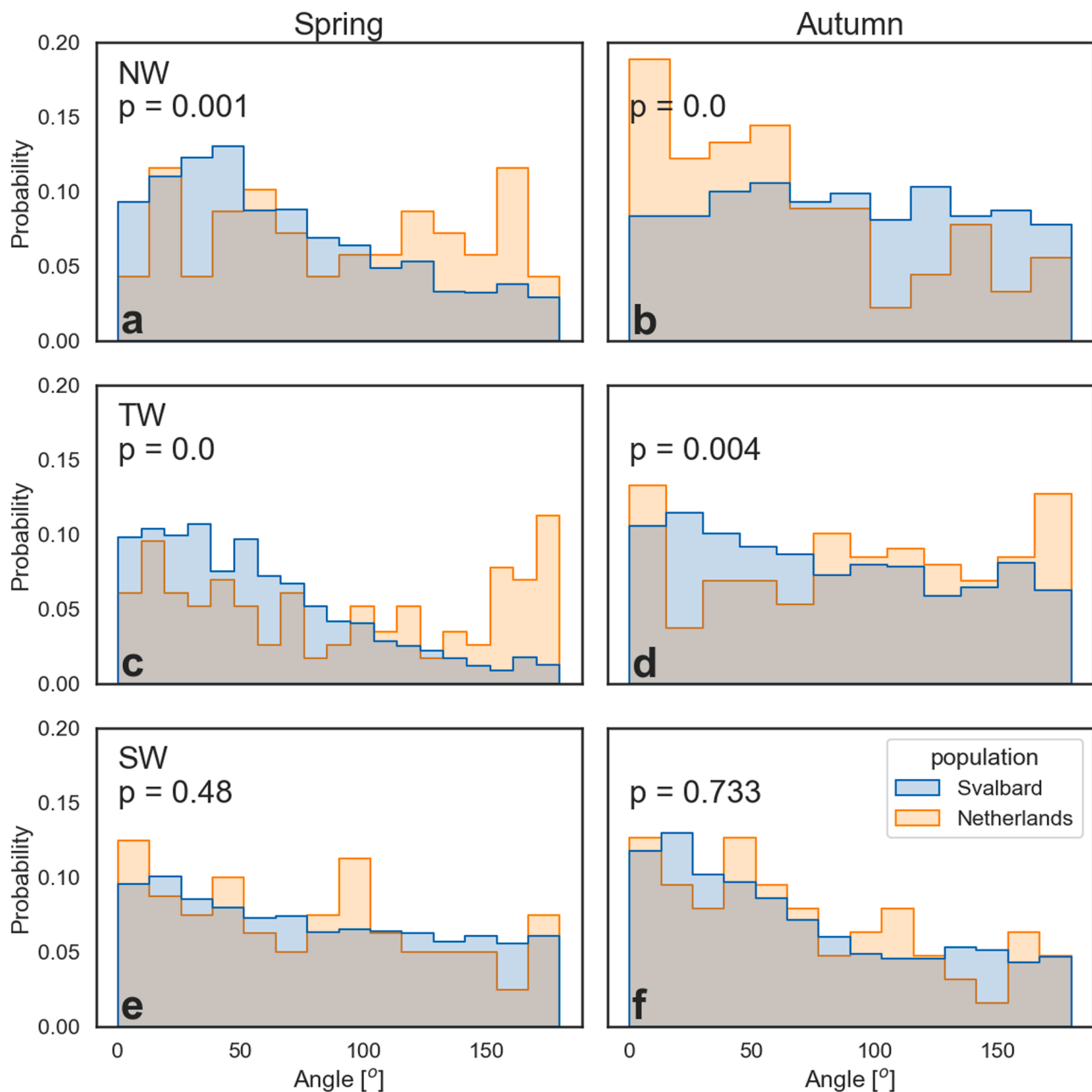

Fig. 4. Probability distribution of angles between the groundspeed and the wind vectors, per population (colours), season (columns) and AO region (rows, NW: NH westerlies, TW: trade winds, SW: SH westerlies). *p*-values below 0.05 show significantly different distributions between the two populations (Mann-Whitney U Test).
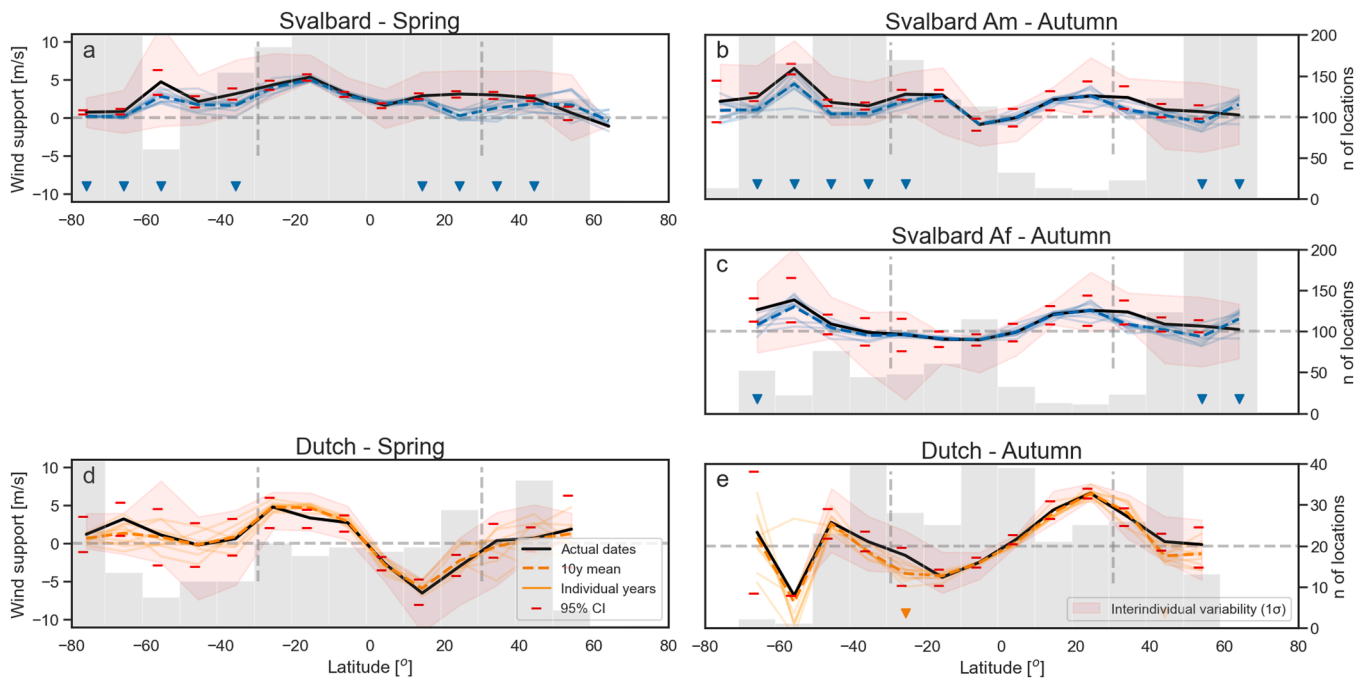
Fig. 5. Wind support zonal means per 10° bin for the ERA5_actual and ERA5_10 yr datasets for a) spring migration of the Svalbard population, b) autumn migration of the Svalbard Am subpopulation, c) autumn migration of the Svalbard Af subpopulation and d) spring and e) autumn migration of the Dutch population. The black continuous line depicts the actual date support (ERA5_actual), the dotted black line the 10-year mean (of ERA5_10 yr) and the coloured lines the individual years of the ERA5_10 yr dataset. The grey bars depict the number of bird locations used per 10° bin. The red lines depict the 95 % confidence interval for each 10° bin and the triangles highlight the bins for which a significant difference (*t*-test, *p*-values < 0.05) has been detected between the population's actual wind support, and the 10-year mean. Inter-individual variability per bin is shown as a red shade (median ± 1σ).
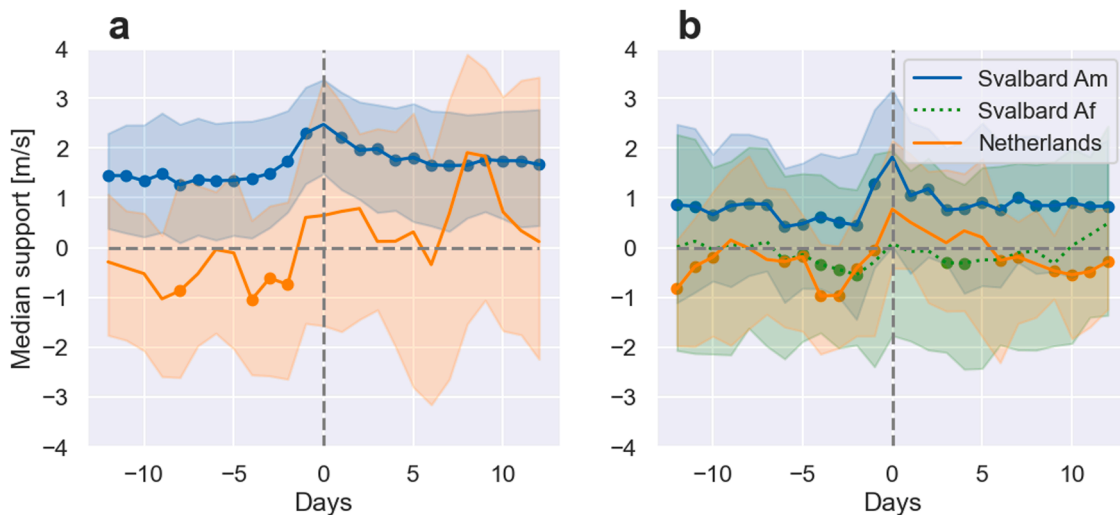

Fig. 6. Lagged median trajectory wind support for a range of 12 days before and after the actual date of flight (day 0) for both populations (ERA5_25d dataset), during a) spring and b) autumn migration. Dots depict the lags with significant (*t*-test per lag, *p*-values < 0.05) difference from lag 0, shades represent inter-individual variability (median ±1σ).

provides the highest wind support (median ± standard deviation: 3.09 ± 1.52 m/s). A notable feature of this shape is the "wind highway" from approximately 30°S to 30°N, a region of high support (4.24 ± 1.35 m/s) in which Arctic terns exploit the SE (between 30°S and 0°) and the NE trade winds (between 0° and 30°N). The Dutch population follows a straighter migratory path (Fig. 3c), partially exploiting the trade winds (between 30°S and 0°) but choosing to stay close to the African coast in the second leg of their journey. This strategy results in considerably lower wind support (0.22 ± 3.51 m/s) but shorter median migration length and duration (16,894 km and 50 days respectively) compared to

the Svalbard population (30,615 km and 106 days respectively) in spring.

In autumn, the Svalbard terns follow two different flyways (Fig. 3b): the American (Svalbard – Am) and the African (Svalbard – Af), with lower wind support (1.81 ± 2.57 m/s against 2.07 ± 2 m/s). Another important segment of the southbound migration is the crossing of the Southern Ocean (SO), here defined as the region between 60°S and 45°S, a leg with almost triple the median wind support of the Svalbard southbound migration (6.13 ± 1.88 m/s) and with influence on the shape of the flyway, as most birds choose to make the SO crossing west
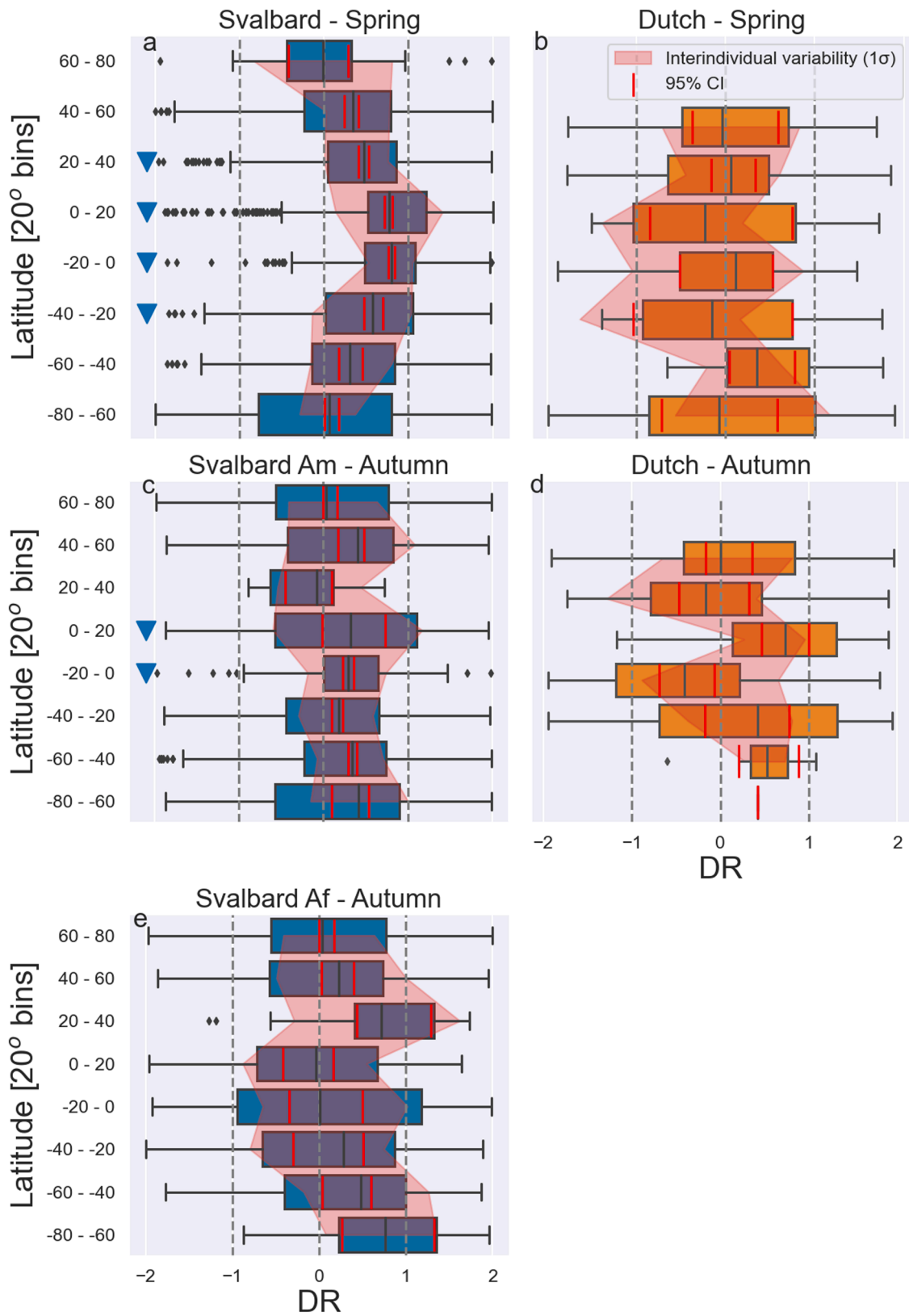
Fig. 7. Drift ratio (DR) of 12-hour bird locations per 20° latitude bins, for spring migration of the a) Svalbard and b) Dutch population, and autumn migration of the c) Svalbard Am, d) Dutch and e) Svalbard Af population. The boxplots visualize the distribution of the 12-hour DR-values: The box shows the three quartiles of the distribution, the bars extend to points that lie within 1.5 IQRs (interquartile range) of the lower and upper quartile, and values outside this range are considered outliers. The red lines depict the 95% confidence interval for the median value of each 20° bin, the triangles highlight the bins for which a significant difference (*t*-test, *p*-values < 0.05) in DR has been detected between the two populations. Inter-individual variability per bin is shown as a red shade (median ± 1σ).

of 0° ($n = 50$), following a SE direction. The Dutch terns once again follow an approach that makes them face headwinds in the second half of their AO migratory path by staying close to the (highly productive) African coast. This results in a low median support (1.14 ± 2.95) but at the same time in lower median crosswind compared to the Svalbard - Am population (2.89 m/s versus 3.87 m/s) due to the weaker winds prevailing in the area (5.69 m/s versus 7.02 m/s). The length of the Dutch population's path is once again shorter (15,067 km versus 28,065 km), at least partly because of the omission of datapoints East of the tip of S. Africa.

Alignment with the prevailing wind

Partly responsible for the differences in wind support is the alignment of each bird with the wind, i.e. the angle between the bird's groundspeed vector and the wind vector. In low latitudes (trade wind zone between 30°S and 30°N, middle row in Fig. 4), the Dutch birds show either poor alignment with the wind direction (uniform distribution) or a bimodal distribution, indicating the switch from tailwinds to headwinds after crossing the equator. It is indeed the selection of low wind magnitude areas combined with the preference for either tailwinds or headwinds, that results in lower crosswinds for the Dutch population in the trade wind zone compared to the Svalbard one (2.44 m/s versus 3.78 m/s). Overall, the Svalbard population aligns better with wind direction (larger percentage of small angles) compared to the Dutch one in low latitudes ($p = 0$ and $p = 0.004$) and in the Northern hemisphere westerlies during spring ($p = 0.001$, Fig. 4). However, there is no clear difference in the region of the Southern hemisphere westerlies, with both populations showing a preference for alignment with the wind direction. Smaller angles between the groundspeed and the wind vectors lead to more consistent crosswinds across most regions for the Svalbard birds (approximately between 4 and 5 m/s). By adjusting their direction, birds can regulate the magnitude of crosswinds and consequently wind support and energetic expenses. On the other hand, the more uniform distribution of angles for the Dutch population results in strong crosswinds in areas with high wind magnitudes (south of 30°S: 3.40 ± 3.67 m/s) and weaker in low-wind-magnitude areas (north of 30°S: 2.83 ± 3.41 m/s), making them act as a "mirror" of the prevailing wind conditions, especially of the zonal wind component.

Wind support: interannual variability

The fact that the Svalbard birds adjust their groundspeed direction to the prevailing wind conditions, results in significantly higher wind support for the actual dates than the 10-year mean, in the mid-latitudes (Fig. 5a and b, spring migration and autumn migration of the Svalbard – Am subpopulation). Had they chosen the same locations on any other year or a similar flyway by habit, their actual-date wind support would have been close to the 10-year mean. Instead, they have clearly higher values than most of the individual 10 years in many cases, and especially in two "key" regions: the crossing of the SO (between 45 and 60°S), and the transition between the Hadley cell and the Ferrell cell, roughly between 20 and 40°N. The mid-latitudes exhibit higher interannual and daily variability in wind conditions than the trade wind regions, and the Svalbard population succeeds in exploiting the tailwinds during both migrations. Daily adjustments in groundspeed become even more important in the two aforementioned "key" regions; there, adjustments in direction can lead to large differences in wind support for areas with strong westerlies (SO) or areas that influence the final leg of spring migration (20°N – 40°N).

We did not find significant differences between the actual wind support and the 10-year mean for the largest parts of both migrations of the Dutch birds and the Svalbard – Af subpopulation in autumn(Fig. 5c, d and e). This could mean two things: either our sample size was too small for detecting significant differences or the population's actual wind support indeed follows closely the 10-year mean. The 95% confidence intervals remain close to the 10-year mean (except for the Southern hemisphere westerlies in spring), and combined with the facts

that the Dutch population shows poorer (than the Svalbard one) alignment with the wind (Fig. 4), and that the Svalbard – Af subpopulation also follows closely the 10-year mean, hint towards the African flyway being followed by birds that exhibit a different behaviour: these birds show less adaptability to wind direction (flexibility to wind conditions), and would rather follow a similar migratory path each year instead of adjusting their speed and direction based on wind conditions. Had they aligned better with the prevailing wind directions during the actual flight dates, they would have higher wind support values than the 10-year mean (similar to the Svalbard population).

The majority of the observed differences takes place in the highly variable mid-latitudes. The more consistent trade winds (low interannual variability) offer a reliable region for the birds, where wind speed and direction do not vary considerably on an annual basis. This phenomenon is exploited best by the northbound migration of terns flying to Svalbard, as they create the aforementioned (Fig. 1a) "wind highway" in this area.

Wind support: daily variability

The highest median trajectory support values were achieved when the actual dates were used for the Svalbard population in spring, the Svalbard – Am subpopulation in autumn and the Dutch population in autumn as well (Fig. 6a and 6b, day 0), as seen by the significant differences between day 0 and multiple days before and after. This highlights the importance of adjustments as a response to daily wind variability, during both migrations. Moreover, during the aforementioned migrations, the lowest inter-individual variability was observed: 1.09, 1.42 and 1.29 m/s for (Svalbard spring, Svalbard – Am autumn and Netherlands autumn). In spring, the Svalbard birds show a gradual decrease of 0.82 m/s (33%) in wind support, in the following (after day 0) seven days suggesting that the days they actually flew are clearly part of a short, optimal time window for the specific flyway they followed. This small window of opportunity highlights the importance of direction adjustments for these birds: the specific set of locations and directions used by the Svalbard birds produce high wind support values only combined with the wind conditions during the actual time of flying. It is noteworthy that even though wind support decreases during the preceding or following twelve days (maximum decrease = 49%), it never approaches negative values or even zero.

This is in contrast with the Dutch population's spring migration, whose median wind support is not only lower on day 0 (0.65 m/s) but does also exhibit higher daily variability (0.77 m/s versus 0.31 m/s), few days with significantly lower (than day 0) support values, and additionally much higher inter-individual variability (2.02 m/s). This translates to short time windows of wind support over 0.5 m/s (from day -1 until day 2, and from day 7 to day 10), dispersed amongst days with values close to zero or even negative, small wind-related advantages in terms of cost saving, and a larger variety of behaviours amongst the individuals

A similar picture can be described for the autumn migration: Svalbard -Am birds experience the highest wind support on day 0 (1.80 m/s), which is higher than the Dutch population's (0.77 m/s), and exhibit lower daily variability (0.32 m/s against 0.42 m/s). Once again the Dutch population's support values fluctuate around zero. However, both populations now show significantly higher support values on day 0, compared to multiple days before and after, and a more uniform behaviour of the population (inter-individual variability: 1.42 m/s and 1.29 m/s for Svalbard – Am and Netherlands). What is noteworthy here, is the behaviour of the Svalbard – Af subpopulation, following partly a similar path as the Dutch birds: Their actual median wind support is almost zero (0.08 m/s), with a relatively high daily variability (0.23 m/s), similar to the majority of the 25-day period, and with large inter-individual variability (1.85 m/s). This results in 25-day values fluctuating around 0 m/s, with large periods of headwinds (negative values).

Drift ratio

The Svalbard population mostly drifts in lower latitudes during spring migration (significantly higher DR values than the Dutch population, Fig. 7a), along the trade wind "highway", and partially compensates in the mid-latitude westerlies, when the birds need to reach the African coast (in the southern hemisphere) or their breeding grounds (in the northern hemisphere). This approach of drifting whenever possible continues in their autumn migration (Fig. 7c), but only for the birds following the American flyway (Svalbard – Am). For birds leaving Svalbard, the NH westerlies (roughly between 30°N and 60°N) are mostly a compensation region. After crossing the intertropical convergence zone (ITCZ, close to the equator), the American flyway provides more wind support and drifting while the Svalbard - Af subpopulation chooses to compensate more and potentially exploit the productive African coast. Finally, between 40°S-60°S, DR again attains a median value close to 0.5 for both Svalbard subpopulations, similar to the one in spring when birds once again partially compensate for the strong SO westerlies.

The Dutch birds begin their northward journey with partially compensating for the SO westerlies (no significant difference from the Svalbard population was found in this region); they switch to over-compensation after crossing the ITCZ in order to turn eastwards for the final leg of their migration, which allows them to employ partial or full compensation once more. A wider (than the Svalbard population) range of strategies is utilized during their southbound migration, with a striking drop in DR after crossing the ITCZ and turning eastwards, following the African coast. Eventually, between 20°S-40°S they exhibit another impressive increase of DR, close to the coast of Namibia and S. Africa, and just before crossing to the IO.

Overall, the spring migration of the Svalbard birds has the highest median DR (Table 1) and lowest inter-individual variability, suggesting that most birds followed a flying strategy between partial drift/compensation and full drift. This can indeed be seen in the "wind-influenced" S-shape (Fig. 1a), allowing for a better exploitation of tail-winds. During autumn, the median DR-value drops below 0.5 for both flyways: the American and African. The American flyway offers two regions where drift is a viable strategy: along the Brazilian coast (0°S - 30°S) and at the crossing of the SO. The African flyway although exhibiting lower DR values and higher inter-individual variability, (more compensation, table 1) presents different advantages, such as food availability and weaker winds. The migrations with the lowest DR are the ones performed by the Dutch terns. They follow shorter and straighter routes, and they overcompensate after crossing the ITCZ which results eventually in median DR values close to 0 (full compensation) for spring and 0.23 (close to full compensation) in autumn (Table 1). Not only are the Dutch population's median DR values low,

but their meridional variability (σ amongst the 20° bins) is high (Table 1), especially in Autumn. During their southbound migration they need to employ a wide variety of strategies, from overcompensation to almost full drift, making this journey more challenging. Moreover, the relatively high inter-individual variability suggests that the individuals opted for different strategies.

Future changes

Wind support

The zonal wind components of the Hadley and Ferrell atmospheric cells are projected to strengthen in the poleward half of the cells (Fig. 8, boxes 1, 5 and 8), and weaken in the equatorward half (Fig. 8, boxes 2, 4, 6 and 7). As a consequence, during spring migration, both populations are projected to experience stronger tailwinds in the beginning of their journey (Fig. 8, box 1, between 50°S and 60°S) and weaker in the last part of the SO crossing, before entering the trade wind zone (Fig. 8, box 2, between 30°S and 40°S). While the first leg of spring migration will be more supported, the opposite will happen in the last leg for both populations, due to the projected weakening of the NH westerlies (Fig. 8, box 4). One unique feature is the large increase in wind support between 10°S and the ITCZ (Fig. 8, box 3) as a result of stronger, westward, trade winds between 10°W and 40°W, a region that only the Svalbard birds cross on their way to the N. American coast. The uncertainty of the model projections (model spread) is higher for the Svalbard population in the SH, and decreases for the rest of the journey, while the opposite is the case for the Dutch ones.

For autumn, models in general agree (low model spread) on decreased wind support in the beginning of the Svalbard migration (Fig.8, box 5), because of stronger NH westerlies above 45°N. The models also agree on stronger tailwinds during the crossing of the SO for the Svalbard – Am subpopulation (Fig. 8, box 8, 45°S-60°S) thanks to the enhanced SO westerlies. Unfortunately, the large model spread does not allow for clear conclusions for the Svalbard – Af birds. The weaker NH westerlies (south of 45°N) will pose less resistance in the beginning of the Dutch southbound migration (Fig.8, box 6). Later on, the projected slowing down of the trade winds (Fig. 8, box 7) has a double effect on the population: weaker support close to the African coast above the ITCZ, and an increase in wind support below the ITCZ (low model spread for both changes). This can potentially increase the wind profitability of the "African coast" strategy in the AO and make it a successful feature of their autumn migration, which will remain in the future.

The median support per bin (one degree of latitude), is projected to decrease for the northbound (-0.21 m/s) and increase for the southbound (0.14 m/s) migration of the Svalbard population (Fig. 9a and 9b). In the first case 4 out of 5 models agree on the sign of the change, while in autumn 4 models agree on the increase (plus one with a value close to zero) giving more confidence that autumn migration will indeed become more wind-supported. The Dutch population's projected changes in wind support are close to zero (0.07 m/s for spring, 0 m/s for autumn, Fig. 9c and 9d), albeit with large uncertainty, both in model spread (spring: 0.59 m/s, autumn: 0.30 m/s) and in interannual variability (spring: 0.46 m/s, autumn: 0.38 m/s). This large uncertainty amongst models and years, combined with a small signal, makes general projections for the Dutch flyways hardly significant, and allows only for meaningful assessment of changes on a regional scale.

Discussion

With a large number of location data we investigated the flight strategy differences between two arctic tern populations following two different AO flyways: the American and the African flyway. Svalbard birds prioritised high wind support, by aligning their direction with the wind on an annual and on a daily basis. This resulted in more drifting, potentially lower metabolic costs during flight, but also in longer flyways over the open ocean. On the other hand, birds following the

Table 1

The Dutch population has lower individual median Drift Ratio (DR) values in both seasons and exhibits higher spatial (meridional) and inter-individual DR variability in autumn.

| Population	Season	Metric	Wind support (m/s)
Svalbard	Spring	Median	0.51
		Meridional σ (20° bins)	0.30
		Inter-individual σ	0.48
Svalbard - Am	Autumn	Median	0.25
		Meridional σ (20° bins)	0.18
		Inter-individual σ	0.56
Svalbard - Af		Median	0.16
		Meridional σ (20° bins)	0.32
		Inter-individual σ	0.74
Netherlands	Spring	Median	0
		Meridional σ (20° bins)	0.19
		Inter-individual σ	0.75
	Autumn	Median	0.23
		Meridional σ (20° bins)	0.41
		Inter-individual σ	0.58
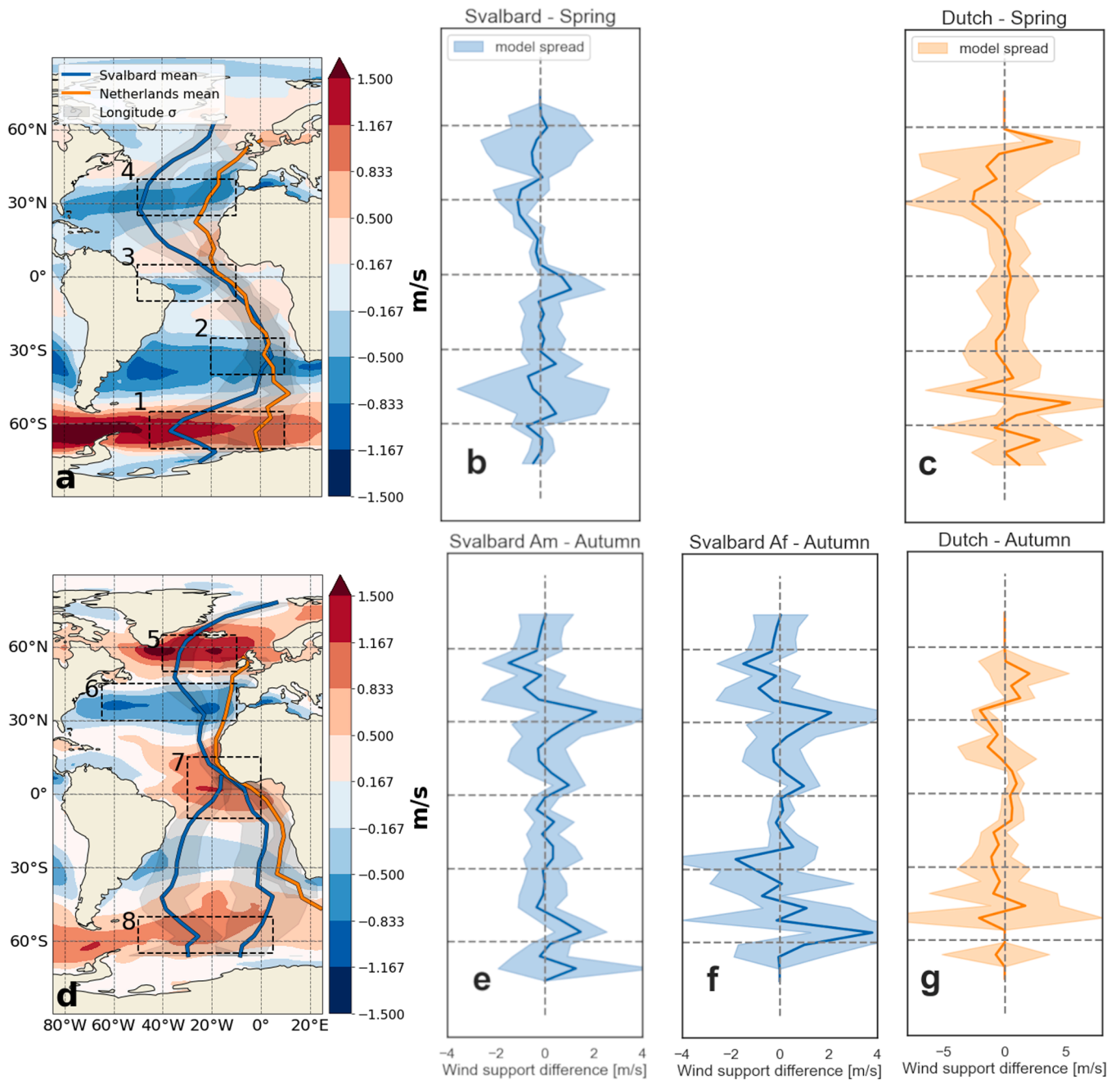
Fig. 8. Mean longitudinal position of the two populations (Svalbard: blue, Netherlands: orange, σ: grey shade), per 5° bin, during a) spring and d) autumn migration. The background of the two maps depicts the 10-year mean projected zonal wind component (U) changes by the 5-model CMIP6 ensemble (spring: March, April and May, autumn: September, October and November). The numbered rectangles (1 until 8) highlight areas of interest, described in the text. b) Zonal mean of projected changes in wind support per 5° bin for the Svalbard population in spring and e) (Svalbard Am), f) (Svalbard Af) Autumn, and for the Dutch population in c) Spring and g) Autumn migrations.

African flyway (Dutch population and Svalbard - Af subpopulation in autumn), prioritized distance and potentially feeding opportunities and ease of navigation (following the African coast) over wind support. Their alignment with the wind was poorer than the birds following the American flyway, and showed low wind flexibility on an annual or daily scale. Their strategy yielded shorter and straighter flyways, albeit with lower wind support and potentially higher metabolic costs during flight, due to higher compensation efforts. Furthermore, the majority of ESMs from our ensemble agree that Svalbard's population autumn migration will become more wind-supported while the opposite is projected for spring. As for the Dutch population, we can only talk about regional changes, as the overall signal is very low and the model spread large.

The Svalbard population in spring (and the Svalbard – Am subpopulation in autumn) follow a more "drift when possible – compensate only when necessary" strategy, by adjusting their journey to large-scale wind patterns. We did not observe a strategy of adaptive drifting but rather (partial) compensation in the higher latitudes and drift dominating in lower latitudes. A similar approach has been described in literature [32] as viable when the crosswinds are balanced over the migratory track, which was true in our case (spring mean zonal wind speed between 60°S and 60°N: 0.08 m/s, mean zonal wind speed experienced in spring by Svalbard birds: 0.34 m/s). Even though daily decisions are important for the Svalbard birds, their American flyway is more forgiving, in terms of optimal timing: following the general wind
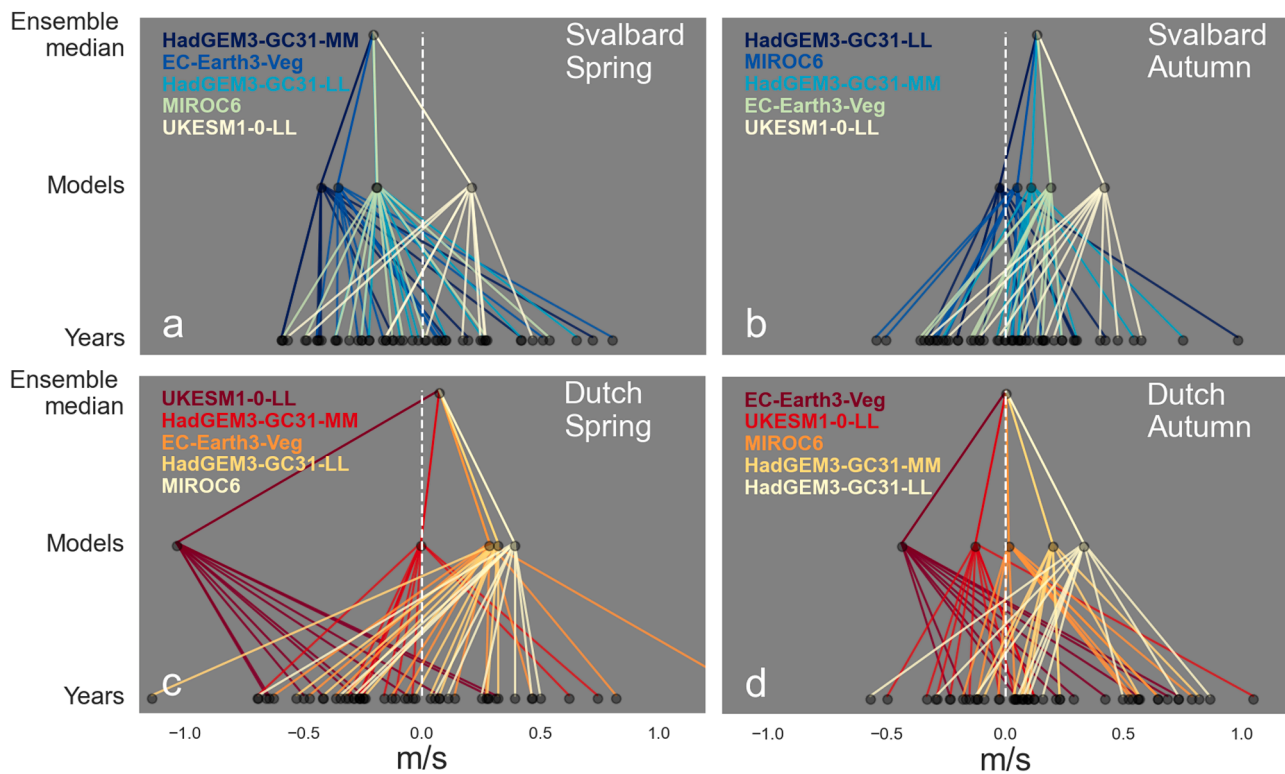
Fig. 9. Cascade of uncertainty in CMIP6 wind support difference (future minus present) for a) spring and b) autumn migration of the Svalbard population, and c) spring and d) autumn migration of the Dutch population. The differences are shown at three different levels of averaging: i, The five-model ensemble median. ii, The individual-model median, calculated using the actual dates, representing intermodel uncertainty. iii, The median for each year of the CMIP6_10 yr dataset, representing interannual variability.

patterns means that they always achieve positive median support values, albeit lower than the optimal values achieved on the actual day of flight. Their strategy might have the disadvantage of roughly doubling the length and duration of their travel but could potentially result in more informed decisions (possible when local conditions at departure are correlated with conditions further along the route, [33]) and lower wind-related risk for the birds.

The Dutch birds compensated more for crosswinds, on average, compared to the Svalbard ones. This behaviour can lead to higher airspeeds and energetic costs [3,32]. Compensation has been described as the main strategy for arctic terns by Hedenström and Åkesson [16] provided that they had a frame of reference, for example a coastline, and indeed in our data this energy-demanding flight strategy is combined with a shorter flyway and a frame of reference: the African coastline. Even though arctic terns are mostly diurnal foragers and fly at night [7, 12] their typically low flight altitude [16,18] might give them the opportunity to use the coastline as a visual aid for avoiding drifting into the AO. Moreover, the African coasts are highly productive during the period of arctic tern spring migration [11], and have lower wind (and consequently lower crosswind) speeds compared to the open Ocean. They follow a similar pathway during their autumn migration, which includes the highly productive Benguela current (Southwest Africa) and of course the IO (not used in this study). The IO provides ample wind support, thanks to the SH westerlies, and feeding opportunities [11] further changing the cost – benefit balance of the Dutch arctic tern migration.

The African flyway might be shorter and with more feeding opportunities, but correct timing seems to be of the essence; a few days could mean that the population will be flying against headwinds.

During our analysis, we found behaviours ranging from "drift when possible – compensate only when necessary" [34] in the American flyway, to full compensation with overcompensation in some parts

(African flyway). Other bird species or even subpopulations are likely to fall in one of these two categories or somewhere in between, while more extreme approaches can be observed in some cases (for example higher wind flexibility, see [5]). Groups following different strategies today might react differently in potential wind circulation changes (birds prioritizing tailwinds versus birds prioritizing distance, and ignoring poorer wind conditions). Understanding the present behaviour of organisms, allows us to discuss potential future changes on a more informed basis: any modelling attempt, should thus take into account these behavioural differences. Predicting large-scale changes in atmospheric circulation, and the extent to which migratory birds may adjust their behaviour, is important for long-term conservation efforts [33]. Expanding on that, we employed a large number of tracking data, created wind support maps of the AO and additionally identified "key" regions, where birds need to make important decisions on an (at least) annual basis. Still, a larger number of tracking data are necessary from a multitude of bird species and flyways in order to create a more complete picture of bird – wind interactions and potential future changes.

The Svalbard birds used in this study have exhibited excellent adjustment skills to wind conditions on an annual and even daily basis. Therefore, we would expect them to adjust to the future AO wind circulation, especially since it will take place gradually over a long time period (we used the period 2086 – 2095). For instance, during spring, a more pronounced S-shape in the trade wind zone and in the SH would be expected as a response to the wind patterns, while a straighter path would make sense in the NH as the weaker westerlies make a long journey from the N. American coast to Svalbard less profitable. The Dutch birds on the other hand choose to adjust their heading and airspeed in order to keep following the African coastline, meaning that in order to keep the same flyway and strategy in the future, they will have to compensate for the enhanced winds in the SO, amongst other changes. This begs the question: how much can they compensate? Is

there a tipping point after which they will not be able to compensate for crosswinds?

General atmospheric circulation has changed and will continue doing so. However, due to large internal variability and model uncertainty, confidence regarding future wind projections is not very high in most of the reference regions in the latest IPCC assessment report (AR6) [35]. This is an issue evident in studies dealing with future wind projections [36,37] and wind extremes in particular [38,39]. We believe that wind projections should, therefore, be treated with extra caution, and be reported with uncertainty metrics, such as the model spread used in this study. There are several climatic variables of direct or indirect interest to bird ecology: temperature has been found to influence plant growth and nitrogen content [40,41]. Moreover, the complex interplay between temperature, snow cover and food abundance controls the breeding success of birds migrating to the Arctic [42–44]. Precipitation, is another variable linked to primary productivity, and is expected to change in magnitude (for example the Arctic is becoming wetter) and in variability, leading to more unpredictable conditions in some cases [45, 46]. Finally, sea ice cover and ocean productivity are both crucial for arctic terns [7,47]. Future projections of all these climatic variables are publicly available form a large variety of ESMs and forcing scenarios, allowing for more studies combining climate science and ecology to be carried out in the future, which will greatly facilitate mitigation policies.

In our study, the uncertainty regarding climatic conditions came from model spread, and was used as an envelope in several steps of the study (Fig. 8 and Fig. 9). It will never be possible to quantify with precision future climate change at any point in time or space [48,49]. This uncertainty in multimodel projections of climate change comes from three sources: a) different forcing scenarios (SSPs), b) different models and c) internal variability, the natural variability of the climate due to its chaotic and nonlinear nature [50]. So, if models give different answers to the same questions, how do we choose which ones to trust? First of all, we believe that a careful evaluation of multiple ESMs for the variables, region and time period of interest is necessary, either for identifying potential biases and/or for model selection (as we did in the present study). Even the latest, state-of-the-art models are not immune to biases [51]. Secondly, characterizing the magnitude and sources of uncertainty can be helpful for effective decision-making, as it is important to know the full range of future possibilities [48,49]. Uncertainty has been included, by means of multiple models, in numerous applied studies, such as sea-level rise [52] and coastal erosion [49]. Data from a large number of ESMs are publicly available, and even statistical downscaling projects popular to ecologists, such as CHELSA [53], provide an ensemble of models and a selection of forcing scenarios. It is therefore possible for ecological studies to include climate-related uncertainty in their ecological impact studies, and hopefully lead to better informed decision-making.

Limitations of the study

Small sample sizes in scientific studies can pose significant limitations and introduce potential biases in the interpretation of results. With the limited number of Dutch birds in our study, there is a risk of random variation affecting our results, reducing the statistical power of the analysis. Moreover, small sample sizes may not adequately represent the diversity and variability present in the population under study, limiting the generalizability of our findings. Therefore, we used large regions containing multiple datapoints, and applied statistical tests and bootstrapping in order to enhance the robustness and reliability of our findings. Additionally, we provide uncertainty estimates over time (interannual and daily variability), space, individual birds (inter-individual) and ESMs (model spread).

ESMs models are used to simulate future climate conditions, and are complex mathematical representations of Earth's climate system. Due to the immense complexity of the climate system and the limited understanding of certain processes, uncertainties arise. Acknowledging and

accounting for these uncertainties is essential for robust decision-making in the face of climate change. Furthermore, the use of multiple SSPs recognizes the inherent uncertainty in predicting future societal choices and their impacts on emissions. In our study we used one pathway: SSP585. Finally, ESMs divide the Earth's surface into grid cells to represent various physical processes. However, due to computational constraints, these grid cells typically have a relatively coarse resolution, meaning that smaller-scale features and local variations are not adequately captured.

Outlook

In this study, we focused on the effects of wind on arctic tern migration. The climate system consists of multiple components with complex interactions and is changing [35], posing a challenge for climate scientists. Focusing on one climatic variable (for example wind), and studying its temporal variability (daily, interannual), model spread, effects on different populations, spatial patterns and projected changes, is already a tall order. However, we believe that the inclusion of additional migration aspects, such as stopover behaviour (staging sites, deposition rates), can lead to even more insights into bird behaviour, into the costs and benefits behind their decisions, and eventually into their future.

On top of the mean general wind circulation, changes in the Northern and Southern Annular Modes, the dominant source of variability in the mid-latitudes, are expected to take place, albeit with small confidence due to ESM limitations [35,54]. Changes in variability and/or extremes rarely receive the same attention as changes of the mean climate state, even though their effects can be large for migrating bird populations. Such potential, but uncertain, changes in the magnitude and frequency of extratropical cyclones and in the precipitation, might pause new challenges to arctic terns, and deserve to be studied in the future

Finally, it is possible to study the projected atmospheric changes effects on migratory behaviour, using models that have as input wind fields, for example anisotropic cost analysis (least-cost path modelling [55]) or Lagrangian approaches [56]. Such models allow the combination of projected climatic changes from ESMs, with migratory patterns from tracking devices and expert knowledge, in order to make better, and more informed projections.

CRediT authorship contribution statement

Nomikos Skyllas: Conceptualization, Methodology, Software, Writing – original draft, Visualization, Investigation. **Maarten J.J.E. Loonen:** Conceptualization, Methodology, Resources, Supervision. **Richard Bintanja:** Conceptualization, Methodology, Resources, Supervision.

Declaration of Competing Interest

The authors declare that they have no competing interests.

Data Availability

Data will be made available on request.

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