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Research article

# Nocturnal avian migration drives high daily turnover but limited change in abundance on the ground

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Every night during spring and autumn, the mass movement of migratory birds redistributes bird abundances found on the ground during the day. However, the connection between the magnitude of nocturnal migration and the resulting change in diurnal abundance remains poorly quantified. If departures and landings at the same location are balanced throughout the night, we expect high bird turnover but little change in diurnal abundance (stream-like migration). Alternatively, migrants may move simultaneously in spatial pulses, with well-separated areas of departure and landing that cause significant changes in the abundance of birds on the ground during the day (wave-like migration). Here, we apply a flow model to data from weather surveillance radars (WSR) to quantify the daily fluxes of nocturnally migrating birds landing and departing from the ground, characterizing the movement and stopover of birds in a comprehensive synoptic scale framework. We corroborate our results with independent observations of the diurnal abundances of birds on the ground from eBird. Furthermore, we estimate the abundance turnover, defined as the proportion of birds replaced overnight. We find that seasonal bird migration chiefly resembles a stream where bird populations on the ground are continuously replaced by new individuals. Large areas show similar magnitudes of take-off and landing, coupled with relatively small distances flown by birds each night, resulting in little change in bird densities on the ground. We further show that WSR-inferred landing and take-off fluxes predict changes in eBird-derived abundance turnover rate and turnover in species composition. We find that the daily turnover rate of birds is 13% on average but can reach up to 50% on peak migration nights. Our results highlight that WSR networks can provide real-time information on rapidly changing bird distributions on the ground. The flow model applied to WSR data can be a valuable tool for real-time conservation and public engagement focused on migratory birds' daytime stopovers.

Keywords: bird migration, eBird, flow model, stopover, turnover, weather surveillance radar

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## Introduction

Seasonal bird migration is a complex spatio-temporal phenomenon resulting in the mass displacement of billions of birds between their breeding, stopover and nonbreeding locations (Hahn et al. 2009, Dokter et al. 2018). One fundamental attribute of nocturnal migration systems is the large daily variation in the number of birds aloft, characterized by a few nights per season with extremely high migration volumes (Erni et al. 2002, Horton et al. 2021). This pattern of temporal concentration lends itself to targeted conservation measures during nights of peak passage, such as 'lights out' alerts to reduce collision risks for birds in flight (Loss et al. 2023). Temporally targeted measures may also be effective during birds' migratory stopovers on the ground (e.g. cat indoors schemes (Loss et al. 2015), timing of pesticide use (Hedges 2001) or temporary wetland establishment (Reynolds et al. 2017)). Such measures are particularly important in the context of staggering global declines in migratory bird populations (Sanderson et al. 2006, Vickery et al. 2014, Rosenberg et al. 2019).

Designing maximally effective conservation strategies requires quantifying the predominant patterns of bird migration and linking these to changes in patterns of bird abundance on the ground. The association between numbers of birds in migratory flight and numbers on the ground will fall between two extremes (Fig. 1). The first, we define as the wave-like regime, where birds depart from a defined area and migrate to a destination area that is largely distinct from the area of departure, thereby changing local abundances on the ground. The second, we define as the stream-like regime in which birds depart from a region that is much broader than their nightly travel distance. In this case, net changes on the ground are minimal because the arrival and departure fluxes balance each other out. While both regimes would see the same overall displacement over the season, the wave-like regime would result in more fluctuation through time in the numbers of birds on the ground at any given location, whereas in the stream-like regime densities on the ground would change only gradually or not at all. To date, we do not know which of these two regimes best describes continental-scale migrations of birds.

Note that we focus here on waves and streams as observed in the daily changes in bird density on the ground. This differs from how the alternatingly large and small migration nights observed in the air by radars has been referred to as wave-like with the waves denoting the intense migration nights (Erni et al. 2002, Horton et al. 2021). In the context of our manuscript, a wave is a density aggregation of birds on the ground that propagates in space as a result of nocturnal migration, which can abruptly change local bird densities when the wave arrives at a given location.

A wave-like regime could be expected in light of studies showing a correlation between nocturnal migration passage and the diurnal abundance of birds on the ground, especially at migration funneling points (Zehnder and Karlsson 2001, Simons et al. 2004, Peckford and Taylor 2008, Komenda-Zehnder et al. 2010). This regime would also be consistent with studies showing that birds align their migration to weather patterns (Alerstam and Lindström 1990, Liechti 2006, La Sorte et al. 2015, Shamoun-Baranes et al. 2017), assuming that these conditions vary spatially. Indeed, this would result in birds departing, flying, and landing together where and when conditions are optimal (Nilsson et al. 2019). Conversely, adverse weather conditions prevent birds' continued migration and lead to the gradual accumulation of

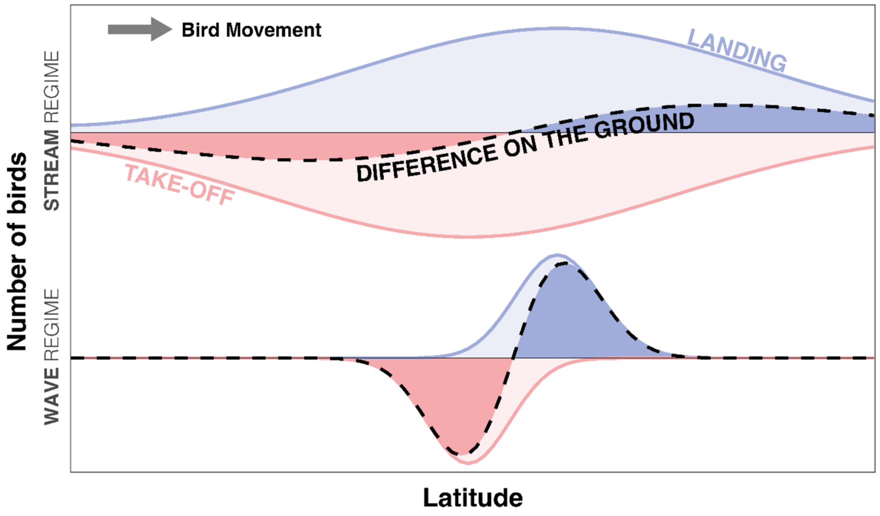

Figure 1. Schematic illustration of the two conceptual flow movement regimes of birds within a single night at a regional scale. In the stream-like regime (top), birds depart across an area that is large compared to the typical nightly flight distance resulting in little change in numbers on the ground (dotted line) compared to the absolute number of take-off and landing (light blue and red). Conversely, in the wave-like regime (bottom), the majority of birds depart from a more localized area that can be overflown within a single night, resulting in a large difference in the number of birds on the ground (dark red and blue), with take-off numbers (light red) closely matching the net loss number (dotted line) and landing numbers matching the net gain number.

birds on the ground, referred to as 'Zugstau' (Schuz 1952). When extreme unexpected weather events occur, especially in front of geographical barriers, this can halt migration and lead to substantial aggregations of birds on the ground, described as fallouts (Duncan 1994, Ryan et al. 1997). These processes could generate waves and have been corroborated with anecdotal observations of high numbers of migrants moving through the landscape (Bagg et al. 1950). More recently, a similar wave-like movement was documented propagating over several days and hundreds of kilometers in western Europe based on weather radar data (Fig. 2 in Nussbaumer et al. 2021).

However, alternative findings suggest that migration can occur under a stream-like regime, where a similar number of birds depart and land at each location, resulting in minimal daily change in the number of birds on the ground during

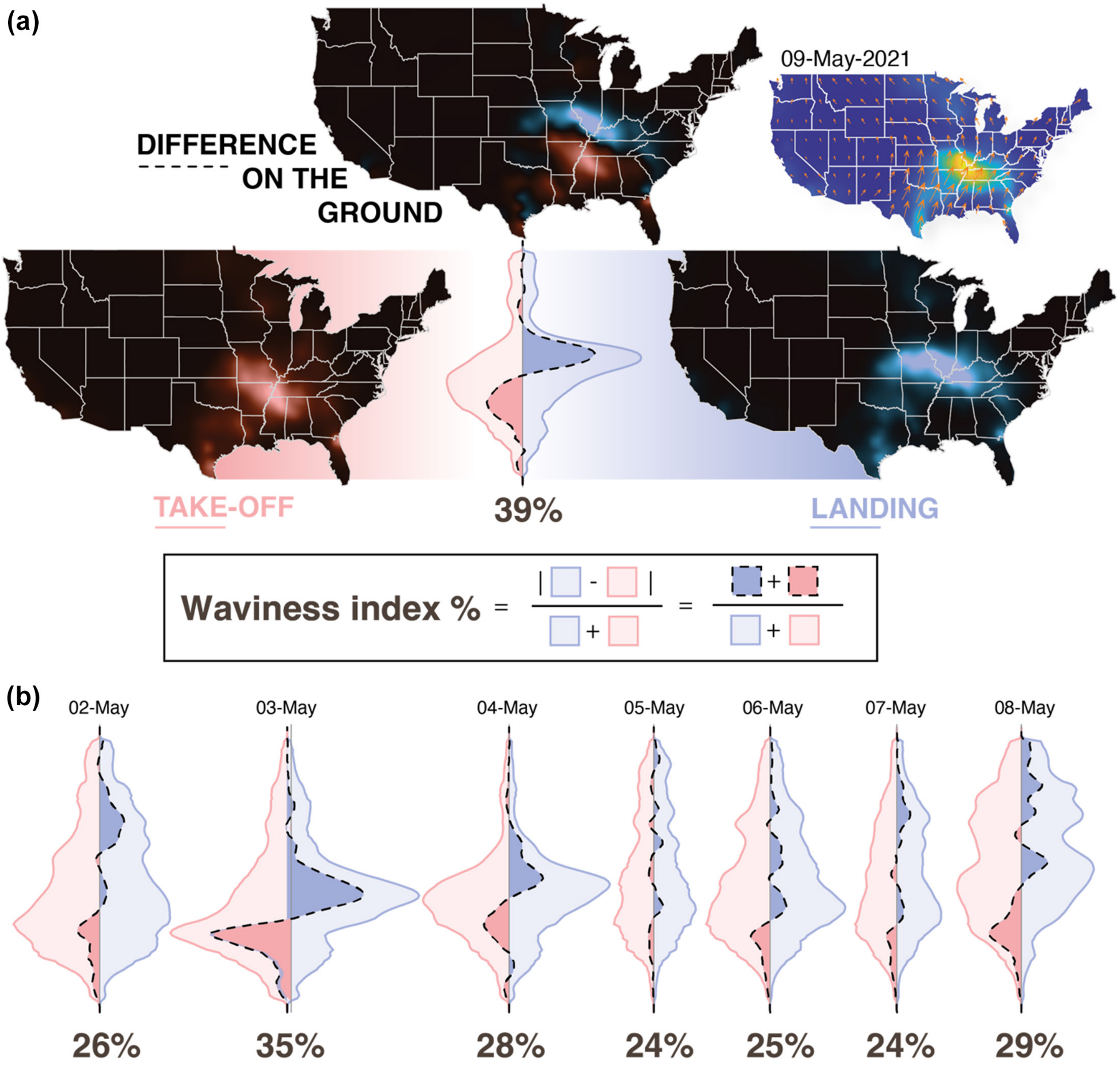

Figure 2. Illustration of the waviness index, used to quantify migration regime (Fig. 1). (a) Based on bird density and flight speed (top right), we computed a map of landing (left) and take-off (right) during spring migration (Nussbaumer et al. 2021). The difference between these two maps quantifies the net change on the ground (top). The same figures for all nights of April–May 2021 are available in the Supporting information. The waviness index (% values in the figure) quantifies the relative change in the number of birds on the ground compared to the fluxes of taking-off and landing. (b) The waviness index values are shown for several nights during early May 2021 together with the longitudinal aggregation of nightly maps of take-off, landing, and difference on the ground. These plots mirror Fig. 1, illustrating the variation in the spatio-temporal patterns of migration. he maps for all nights during spring 2021 can be found in the Supporting information.

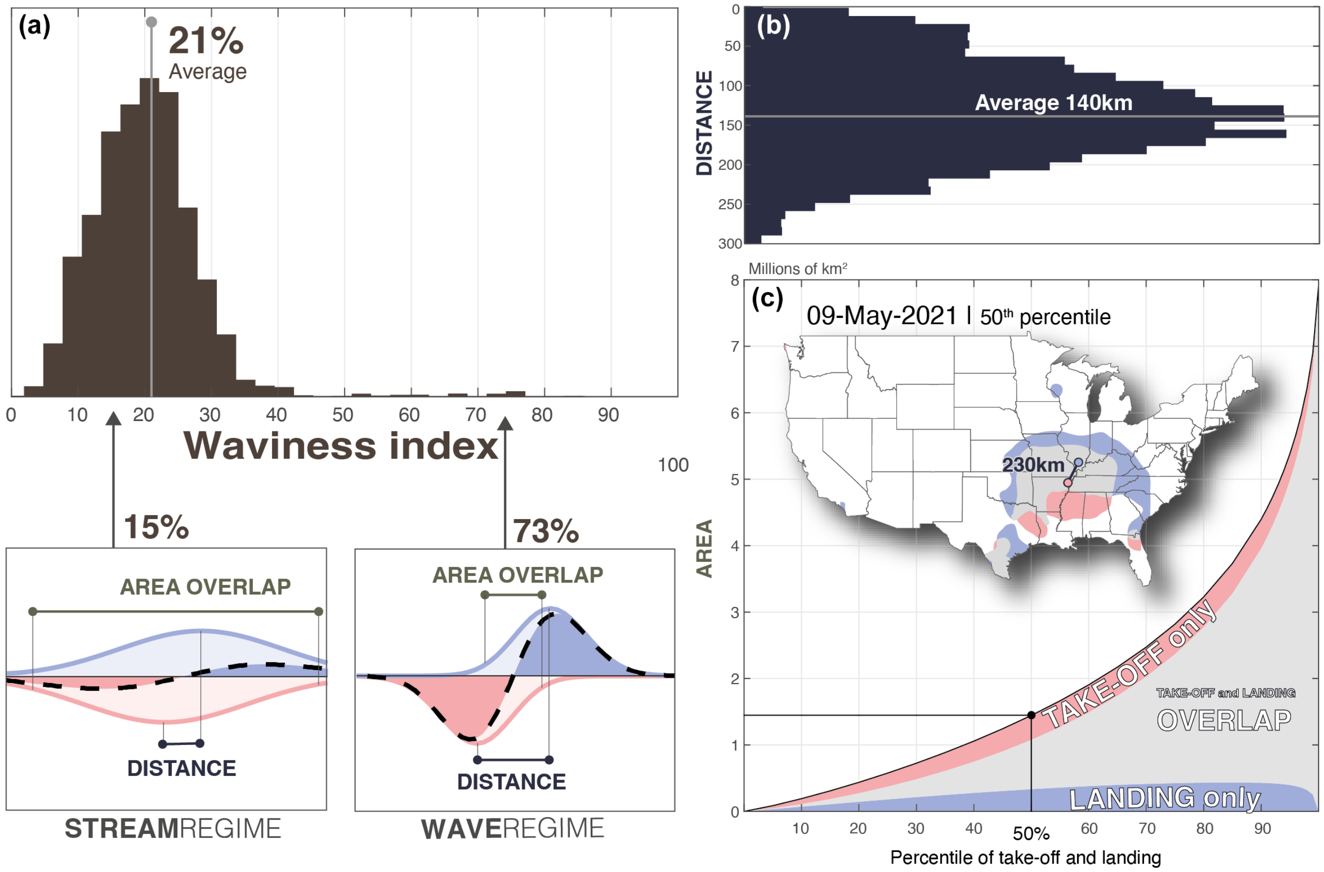

Figure 3. (a) Histogram of the nightly waviness index computed using 20 years of data and weighted each night by the quantity of take-off/landing. The two schematic examples of stream and wave-like regimes presented in Fig. 1 correspond to a waviness index of 15 and 73% respectively. (b) Histogram of the distance between the center of mass of take-off and landing for each night, weighted by take-off and landing. (c) Area with overlapping take-off and landing depending on a threshold of percentile of the total take-off and landing. The insert map illustrates these areas for the 50th percentile on 9 May together with the position of the center of mass of take-off and landing. For the bulk of migration, the take-off and landing zones are large and mostly overlap, with less than 100 km between the take-off and landing center of mass (characteristic of the stream regime). However, for the peak location of migration, the overlap is smaller (characteristic of a wave-like regime).

the entirety of a migratory season. Indeed, when looking at the daily scale and not considering funneling points, the relationship between the total number of birds passing through by night and those found on the ground by day is complex (Nisbet and Drury 1969, Fischer et al. 2012, Horton et al. 2016). High migration passage overnight could signify large departures, large arrivals, or both, the latter resulting in high turnover of individuals but little change in absolute numbers on the ground. Additionally, the anecdotal observations describing migration waves moving across multiple nights usually relate to specific barriers, such as the coastal effect or exceptional weather events, which may not be representative of general migration patterns. Indeed, large-scale studies using weather surveillance radar (WSR) have shown that the majority of migratory passage occurs inland during nights with clear skies (Erni et al. 2002, Dokter et al. 2018). As such, while waves may occur under specific conditions, most birds might still be migrating in a stream-like fashion.

With broad spatial sampling and continuous, standardized measurements, WSR networks are well-positioned to inform our understanding of nocturnal bird migration (Gauthreaux and Belser 2003, Dokter et al. 2011, Shamoun-Baranes et al. 2014). While they constitute a powerful tool to provide near real-time large-scale information on birds in flight, WSR are not able to directly observe the resulting change in number of birds on the ground (Buler and Diehl 2009). However, recent advances in WSR data analysis have made it possible to connect large migration movements with bird numbers on the ground through a fluid dynamics model that invokes mass conservation (Nussbaumer et al. 2021). By integrating departures, flight, and arrivals into a cohesive framework, changes in bird numbers on the ground can be tracked in near real-time, making flow models a promising tool for conservation planning and public engagement. In addition, this modeling approach can be used to assess the degree to which bird migration occurs according to a wave- or stream-like pattern, by quantifying both the fluxes of birds departing and landing over night at high temporal resolution throughout the continent.

The eBird citizen science dataset (Sullivan et al. 2009, 2014) lends itself to estimating the diurnal abundance of birds on the ground, providing a complementary source of information for detecting daily changes on the ground at regional scales. This offers the opportunity to ground truth the density changes on the ground estimated by WSR, leveraging the large temporal extent and spatial coverage of both datasets. Furthermore, relating these fluxes to the total number of birds observed on the ground allows us to estimate the turnover of bird abundance, i.e., how many birds on the ground are changing from one day to the next relative to the total number on the ground. As the daily change in the total number of birds per checklist cannot distinguish coinciding take-off and landing, it is challenging to detect migration occurring under a stream-like regime, where take-off and landing tend to be balanced. Yet, through quantifying changes in species composition, eBird may offer a proxy of nightly turnover. We therefore explore the correlation between turnover (WSR) and species compositional changes (eBird), which we expect to be stronger in stream-like regimes.

In summary, the aims of this study are to 1) apply flow modeling to characterize whether continental bird migration occurs primarily through substantial daily changes in bird numbers on the ground at locations along the migration front (waves), or through a more balanced flow of individuals across the landscape (stream), 2) compare and ground-truth the estimated changes in bird numbers on the ground with eBird data, and 3) combine WSR daily fluxes of take-off and landing with eBird abundance information to estimate a daily turnover rate on the ground.

## Material and methods

### Data

#### *Daily estimates of take-off and landing from WSR*

We downloaded NEXRAD data from 143 WSR station locations in the contiguous US for the years 2004–2021 (NOAA National Weather Service (NWS) Radar Operations Center 1991). We processed the polar volume data at each WSR station to generate vertical profiles of bird density and speed based on data within 5–35 km range of the radar, and subsequently integrated these over altitude into vertically integrated timeseries (Dokter et al. 2018, 2019). We then interpolated bird density and flight speed across the contiguous US following the approach developed by Nussbaumer et al. (2019). In this approach, we first learn from the data the spatio-temporal pattern of migration through a covariance model, and then produce estimated bird density value on a 0.25° spatial map for each timestep (15 min), producing smoothed maps of bird speed and density. Finally, we ran a flow model to produce gridded daily estimates of take-off and landing within the contiguous US following the approach presented by Nussbaumer et al. (2021). By requiring that bird numbers must be conserved between consecutive timesteps (mass conservation) and by assuming that bird densities in the air can only change by moving in the direction of the speed field or by exiting/entering the airspace to/from the ground, this approach allows to estimate maps of the take-off and landing flux at each timestep. More details on the WSR data processing and interpolation model can be found in the Supporting information.

#### *Daily estimates of bird abundance on the ground from eBird*

We use the eBird dataset (Sullivan et al. 2009, 2014) to estimate 1) the number of nocturnally migrating birds on the ground for each day and 2) the change in species composition from one day to the next. More details on the processing of eBird data can be found in the Supporting information.

Analyzing the daily change in the number of birds requires a high volume of data. We therefore limited our analysis to the geographic regions and seasons with the largest number of eBird checklists. Temporally, we focused our assessment on spring migration (1 April–1 June) occurring during the period 2010–2021 as checklist submissions and bird detections were highest during spring migration. Spatially, checklists tend to be concentrated around urban areas. We therefore selected the 16 urban areas that have five years of data, where each year included a maximum of 10 days with less than 10 checklists/day over the spring migration period (Supporting information) and use only the checklists located within a 0.75° (~ 80 km) radius around these areas. Because the number of individuals varies greatly with observation effort, we applied basic filtering of the checklist data based on effort variables (Johnston et al. 2021) and limit our analysis to nocturnal migrant landbirds.

First, to estimate the number of nocturnally migrating birds on the ground for each day, we apply the following steps: 1) sum the total counts of all species in each checklist, 2) model these total counts based on effort variables, 3) normalize the total counts to a standard effort using the model, and 4) for each urban area, retrieve a daily number of birds on the ground computed as the 75th quantile of all normalized total counts for this day. The 75th quantile was selected because it empirically shows the best match with weather radar data. Second, we estimate the change in species composition from one day to the next as the beta diversity index (Koleff et al. 2003) computed from the species reporting rates (i.e. proportions of checklists reporting each species) between two consecutive days. To compare WSR and eBird data, we spatially aligned both datasets by aggregating the WSR maps of take-off and landing over each urban area with a Gaussian kernel (SD = 2°).

### Analysis

#### *Description of the migration regime using the waviness index*

To discriminate between wave-like and stream-like migration regimes, we used a waviness index defined as the normalized difference between take-off and landing, corresponding to the ratio between the absolute difference between take-off (T) and landing (L) (i.e. change on the ground) divided by the sum of birds taking off and landing (Eq. 1),

$$\text{Waviness index} = \frac{|T - L|}{T + L}$$

A waviness index close to 0 indicates that there is a small change in the number of birds on the ground compared to a high number of birds taking off and landing at that same place (i.e. high replacement rate); this corresponds to a stream-like regime. By contrast, a wave-like regime is characterized by a waviness index value close to 1, representing an extreme case with no overlap between regions of take-off and landing. We computed this index for each night across the entire continental US using the take-off and landing fluxes derived from WSR data.

To further characterize the spatio-temporal structure of migration, we quantified 1) the distance between the center of mass of take-off and of landing and 2) the overlap between the take-off and landing areas. When calculating these centers of mass, we must take into account the boundaries of our study area and the fact that birds entering the study area are only reflected in the landing map, and similarly, birds leaving the area only contribute to the take-off map. We therefore add the birds entering and leaving the study area to the maps of take-off/landing respectively, at the pixel they entered/left. We quantified the overlap between regions of take-off and landing by finding the minimum area that includes various percentiles of the total take-off and landing fluxes over each night.

### *Relating take-off and landing (WSR) to change on the ground (eBird)*

We sought to compare and assess the relationship between the number of birds taking off and landing overnight estimated with WSR data with the change in the number of migrant birds estimated using eBird data during consecutive days. This involved calculating the Pearson correlation between: 1) the WSR landing minus take-off and 2) the difference in the corrected eBird counts between the days prior to and following the night of the WSR data. In order to account for the high variation in the number of checklists available, we only considered the days and urban areas with at least 50 checklists a day and weighted the correlation by the number of checklists available during the two consecutive days (Supporting information). To provide context and assess the benefit of using the flow model, we also computed the weighted correlation between passage and daily change on the ground. Passage is estimated by the total number of birds crossing a 1 km transect perpendicular to the direction of movement over the course of a night.

### *Estimate of the daily turnover rate*

Relating the number of birds taking off and landing to the number of birds on the ground provides insight into the dynamics of the daily turnover in bird abundance. We estimate the abundance turnover rate, corresponding to the proportion of birds which are replaced overnight, by combining WSR data and eBird data. We compute the turnover rate θ (Eq. 2) as:

$$\theta = \gamma \frac{\left(T_{t\rightarrow t+1} + L_{t\rightarrow t+1}\right)/2}{\left(S_t + S_{t+1}\right)/2},$$

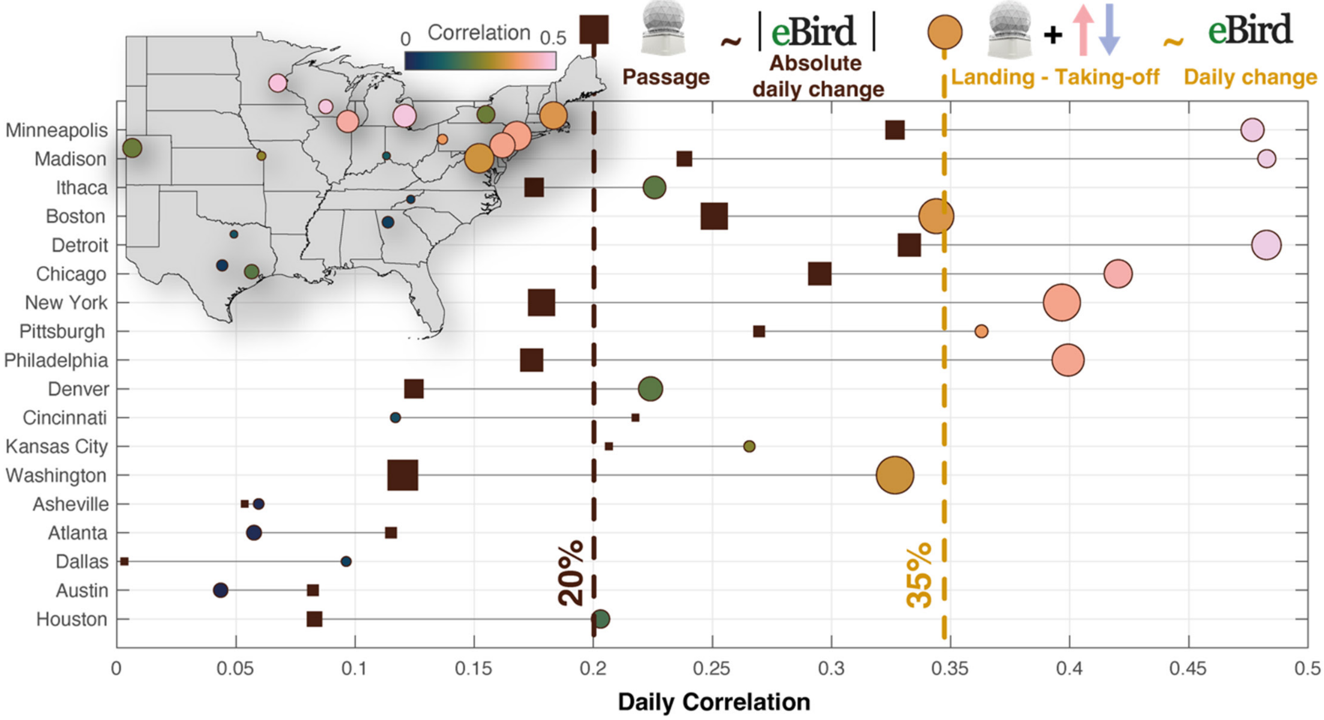

Figure 4. Correlation between eBird daily change in bird abundance on the ground with (1) WSR passage (density × speed) in squares and (2) the change derived from the flow model (landing-departure) in circles. Cities are ordered on the y-axis by latitude. The diameters of the symbols are proportional to the number of checklists used in the computation of the correlation. We find a stronger average correlation (r = 0.35) between eBird and the flow model than with passage only (20%).

where $T_{t\longrightarrow t+1}$ and $L_{t\longrightarrow t+1}$ are the take-off and landing fluxes between day $t$ and $t+1$ estimated from WSR data while the storage $S_t$ and $S_{t+1}$ are the total number of birds on the ground at day $t$ and $t+1$ estimated as the 75th percentile of the corrected eBird count. The coefficient $\gamma$ is a proportionality factor that quantifies by how much the net flux of take-off and landing (bird km$^{-2}$) translates into a net change of individual birds counted in a checklist (bird/checklist normalized for 1 km – 1 h), e.g. $\gamma$ bird km$^{-2}$ = one bird/normalized checklist. We estimated this coefficient $\gamma$ as the slope of a linear fit of the daily change on the ground from WSR and eBird (Eq. 3),

$$\gamma\left(L_{t\to t+1} - T_{t\to t+1}\right) \sim S_{t+1} - S_t.$$

We fitted a different coefficient for each combination of the following grouping variables: 1) each year / each urban area, 2) all years / each urban area and 3) all years / all urban areas (Supporting information). The turnover rate was computed using the coefficients estimated from all years / each urban area.

To test if our flow-approach is predictive of species composition changes, we computed a turnover in species composition (Supporting information) and correlated this with both the passage and the absolute values of departure and landing for each urban area.

In order to obtain metrics representative of migration nights and avoid over-influence of nights with little to no passage, we chose to weigh all histograms and average values at the daily scale by the sum of the number of birds departing and landing over the night.

## Results

### Waviness index indicates a stream-like regime

The flow model was able to quantify fluxes of bird take-off and landing at a continental scale. These results revealed the sheer scale of bird migration: we found that, for each year within the continental US, during each of the top three nights, over 1 billion birds took off in the autumn and 800 million took off in spring. The maximum daily take-off and landing density in a year was 700 birds km$^{-2}$ (median for the period 2004–2021), which is equivalent to 1 bird taking off within every 38 × 38 m$^2$. However, the amplitude and location of bird movement varied strongly from one day to the next (Fig. 2; for all nights see Supporting information).

Remarkably, regions of departure and arrival tended to overlap, resulting in small net change on the ground. We used the waviness index to quantify the degree to which take-off and landing overlapped (Fig. 3a) and found an average value of 21% (SD = 7%), indicative of a predominantly stream-like migration. In regions and on nights with intense migration, we found a narrow transition zone between areas of net departure to areas of net arrival (Fig. 2). Migratory passage was well correlated with take-off or landing (r = 0.60), but poorly correlated with the resultant change in bird numbers on the ground (r = 0.08) (Supporting information). Passage alone is thus a poor predictor of on-the-ground change, demonstrating the added value of a comprehensive model that tracks fluxes of take-off and landing and the narrow transitions in their net balance.

While the total area of take-off and landing spanned millions of km$^2$ (Fig. 3b), the weighted average distance between the center of mass of take-off and landing for a night was only 139 km (Fig. 3a) (156 km in spring and 134 km in autumn). Nights with higher numbers of birds migrating are correlated with increased distances between the centers of mass of take-off and landing, such that the average distance of the 5% of the nights with the highest movement was as high as 180 km. The overlap between the area of take-off and landing was also scale-dependent: the smallest regions containing 50% of the take-off and landing overlapped by 80%, while the smallest regions containing 10% of take-off and landing overlapped only by 15% (Fig. 3c).

### Take-off and landing fluxes corroborate observed changes on the ground

To ground truth our WSR-based estimates of departure and arrival, we related the nightly change in the number of birds on the ground estimated from WSR to diurnal changes in bird abundance on the ground estimated using eBird data.

At the daily scale, we found a positive correlation (r = 0.35) between the daily change in the number of birds estimated by the flow model (i.e. landing minus take-off) and daily change in bird abundance estimated using eBird data (Fig. 4). This correlation was stronger when more checklists were available and in the northern urban areas. In comparison, the correlation between the absolute change on the ground with passage was much weaker (r = 0.20), demonstrating the benefit of explicitly accounting for the spatio-temporal variation of density and flight speed to estimate change on the ground.

We estimate the seasonal change in number of birds on the ground with WSR data by calculating the cumulative summing of the daily difference between take-off and landing, allowing us to compare eBird and WSR data over longer periods. At this seasonal scale, we observed a good correspondence of the time series and year-to-year fluctuation (Fig. 5, Supporting information).

### Low daily abundance turnover rate

We combined information on fluxes (from WSR) and bird abundance on the ground (from eBird) to estimate the proportion of migrant birds changing during a night (i.e. turnover rate). Across all urban areas, the best fit resulted in a $\gamma$ coefficient of 16 birds km$^{-2}$ for one bird/checklist indicating that on average a net increase on the ground of 16 birds km$^{-2}$ detected by WSR resulted in one more bird counted per checklist (standardized effort to 1 h and 1 km). However, this coefficient fitted separately per year and urban area showed consistent variability among urban areas (Supporting information), indicative of systematic differences across years and

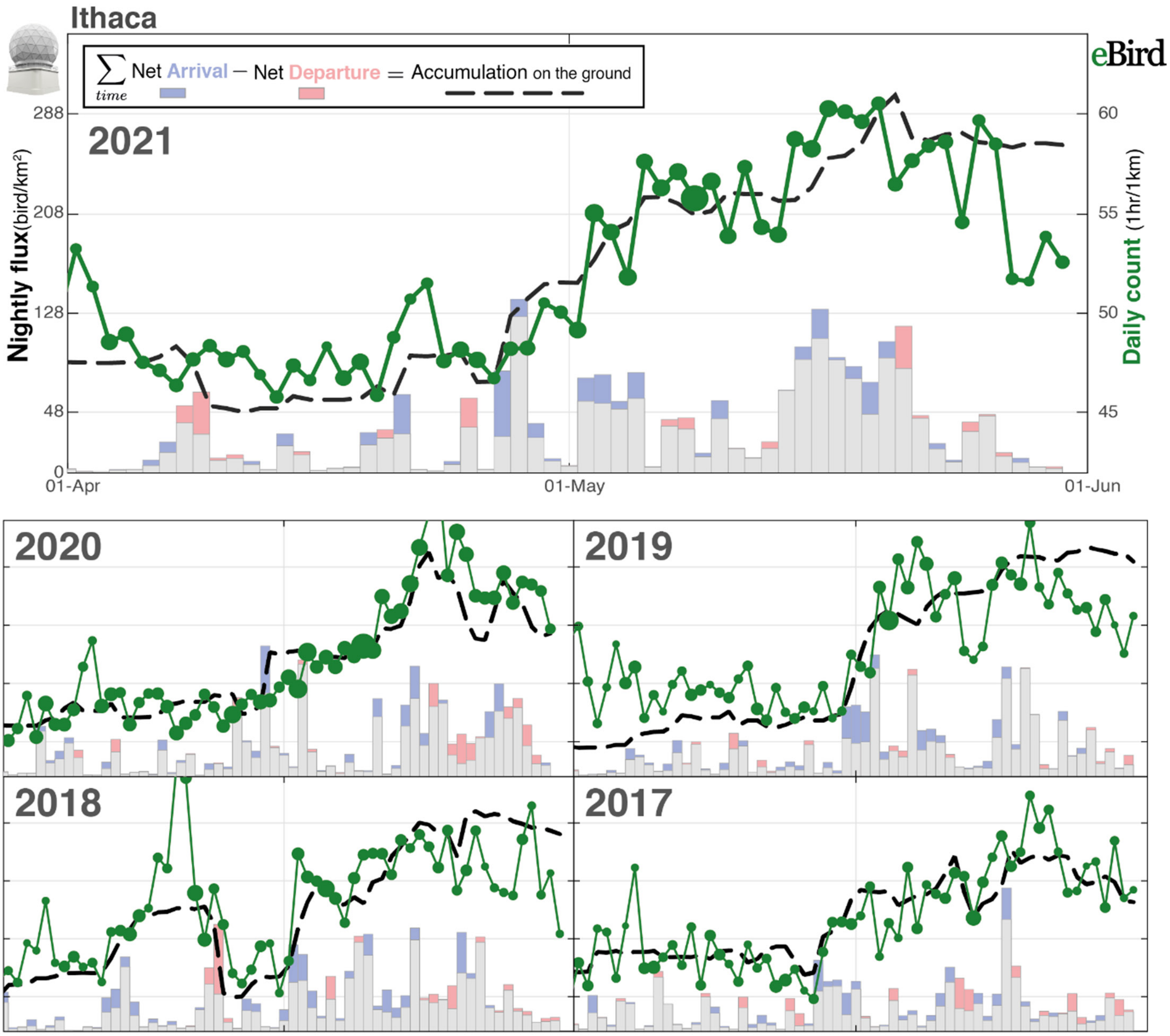

Figure 5. Comparison of the 75th quantile of the corrected on the ground counts of bird abundance from eBird (green) with the accumulation of birds aloft from WSR (black dotted line. The accumulation was computed as the cumulative sum of landing (blue) minus take-off (red). The two lines match at the seasonal level, showing similar year-to-year fluctuation in their general shape (e.g. end April 2018). This figure shows the results for Ithaca. Similar figures for all years and radars can be found in the Supporting information.

urban areas in either the WSR fluxes or eBird counts. These values range from 6 to 23 birds km$^{-2}$ (Supporting information). We therefore used of 16 birds km$^{-2}$ calculated across all of our data for the computation of the turnover rate.

We estimated the turnover rate for each day and urban area, corresponding to the proportion of the total number of migrants on the ground that departed over the night (Fig. 6). Averaged across the entire period (2010–2021) and all urban areas, and each night weighed by the number of birds migrating, the daily turnover rate was 13% (SD = 9%). During peak migration nights, the turnover rate could reach up to 40–50%, indicating that, while the population of birds on the ground can change substantially in a single night, overall, mass migration nights only see a fraction of birds aloft (see the Supporting information for a sensitivity analysis of these results in relation to the uncertainty associated with γ-coefficient).

We found a high correlation (r = 0.53) between the turnover in species composition and the average magnitude of take-off and landing at the daily scale (Supporting information). This correlation was high for all urban areas, ranging between 0.43 and 0.74 (expect Houston).

## Discussion

### Migration as a stream

We found a stream-like pattern for the large majority of migration nights where take-off and landing fluxes were in

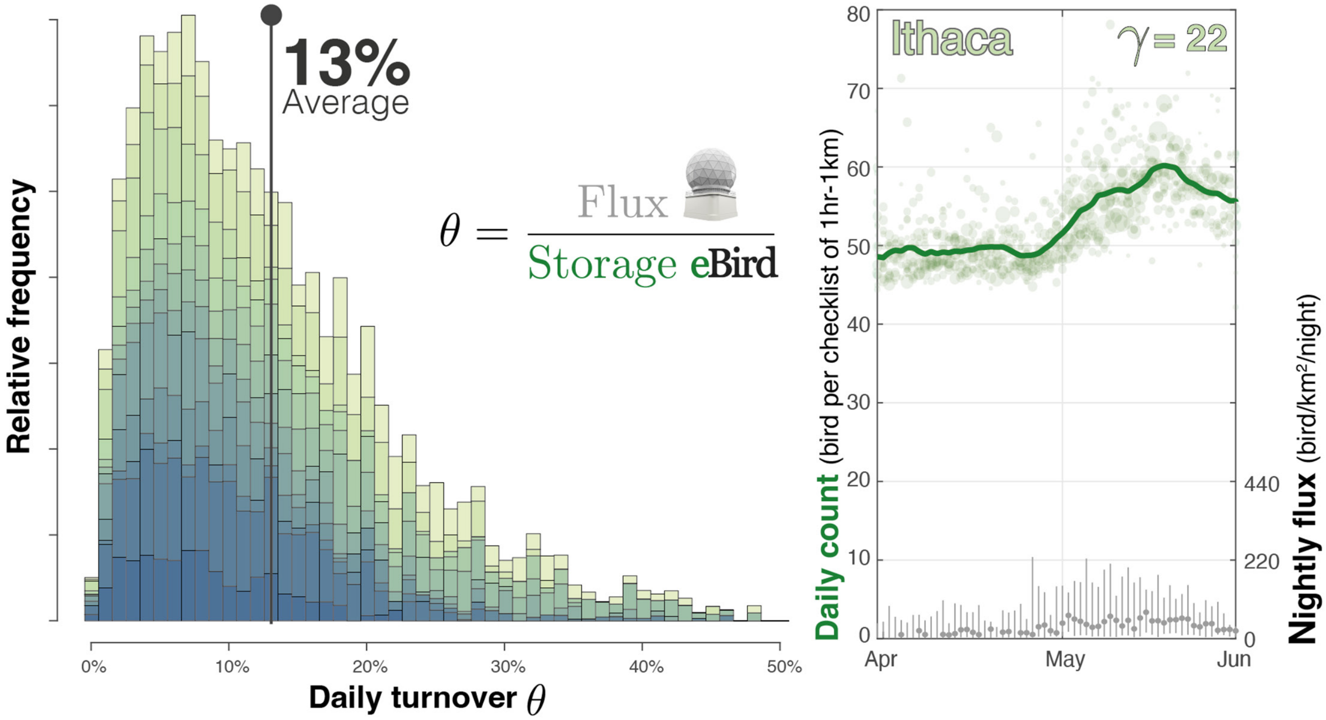

Figure 6. (left) Weighted histogram of the daily abundance turnover rate for migratory species for all urban areas combined (represented by different colors in the histogram). (right) Illustration of the storage (average seasonal variation of the number of birds per checklist across year) and flux (q10, q50 and q90) of the take-off across all years in Ithaca, NY.

near balance, such that there is relatively little change in the number of birds on the ground from one night to the next. In addition, areas with substantial take-off and landing tended to be much larger than the average distance traveled by birds each night. These findings show conclusively that migration chiefly follows a stream-like pattern and that large day-to-day density changes on the ground are relatively rare at the regional scale.

The stream-like regime is most evident from the fact that the daily change in the number of birds on the ground was only a fraction of the magnitude of birds taking off and landing (i.e. waviness index of 21% in Fig. 3a). We interpret this finding as a result of birds' general tendency to migrate in favorable weather conditions: the scale of synoptic high-pressure systems (~ 1000 km) matches the order of magnitude of the area of take-off, landing, and overlap, which is much larger than the distance typically covered by a bird during a given night. Our analysis found that the center of mass is displaced by an average of 140 km every night (Fig. 3b), suggesting that birds fly around 3 h 40 m per night on average, using the average speed of 38 km $h^{-1}$ estimated from WSR data. Our results strongly suggest that, in the absence of a barrier, both the average distance and duration of bird flight are significantly smaller than what a bird could theoretically achieve in a night (e.g. 380 km for a full 10 h flight). While peak take-off and landing occur typically at the beginning and end of the night respectively, we found that birds can also take off later and, more commonly, land earlier in the night (Supporting information). These results are in line with previous ringing, telemetry and multi-sensor geolocator studies which have found average flight distances ranging from 100 to 200 km (Cochran 1987, Ellegren 1993, Hall-Karlsson and Fransson 2008, Briedis et al. 2020, Rime et al. 2023), and short flight durations indicating that birds would take-off and land throughout the night (Müller et al. 2016, Bäckman et al. 2017).

It should be noted that the data and method used in this study are best suited to describe regional-scale migration patterns (~ 50–100 km). This is because our analysis starts from point-based interpolations of vertical profile data, which makes the true spatial resolution of our data similar to the typical distance between radars (M = 174 km; SD = 56 km) (Nussbaumer et al. 2019). This is too coarse for capturing highly local effects such of rain, fine-scale orography or coast, or habitat selection. Our analysis therefore leaves open the possibility that wave-like patterns exist at highly local scales. We speculate that both dramatic fallouts and other strong fluctuations in bird numbers reported at coastal barriers (Duncan 1994, Ryan et al. 1997) may fall in this category. Because of our limitation in resolution, bird movements consistent with waves will not be detectable if the wave starts from a region not within the 35 km radius of detection of any radar or never propagates into the detection window of any upstream radar. Notwithstanding, these local wave-like patterns occur within the broader stream-like regime reported here and will therefore likely be short-lived and dissipate quickly. This is evidenced by the typically gradual change in bird densities observed by individual radar stations, which rarely detect the sort of high-density peaks in density that would be associated with fine-scale waves, and whose occurrence would be detectable by our method as long as the fine-scale wave passes through the 35 km detection radius of the radar stations. The low waviness index reported in our study indicates these waves, including fine-scale waves, must be relatively rare. Furthermore, wave-like events can be expected when migrating birds encounter an abrupt or unexpected barrier such as a precipitation front or coastline. Further investigation into these events, using local-scale radar products, is an exciting future avenue for flow-based analyses.

A limitation of our flow model is that it cannot distinguish take-off and landing occurring within a single timestep at the same pixel (Nussbaumer et al. 2021), exchanging birds landing with birds taking off at the same location. However, we expect this to occur infrequently as peak departures and landings generally occur at very different times of the night (Müller et al. 2016, Bäckman et al. 2017, Cooper et al. 2023, Kranstauber et al. 2023). We do not expect that ignoring these additional fluxes bias our conclusion of a predominantly stream-like migration regime in North America, as including them would only lead to higher take-off and landing fluxes with a net-zero difference on the ground, thereby producing an even more stream-like regime.

While the term 'migration wave' has been used casually in the literature to reference the strong night-to-night variability in aerial migration (Erni et al. 2002, Horton et al. 2021), this term differs from the wave-like regime described here. Our analysis indicates that such episodic mass movements are fully compatible within a stream-like regime. In the context of our work, mass migration events are best characterized as those nights where the large-scale stream of migration comes into motion.

## Radar predicts abundance changes and turnover observed on the ground

Results from the flow model applied to WSR data are corroborated by an independent dataset of bird observations on the ground ($r = 0.35$). This agreement is further confirmed by the fact that both datasets detect the same year-to-year variability in the seasonal accumulation of birds on the ground (Supporting information). This alignment demonstrates that WSR data can accurately predict changes in diurnal bird abundance on the ground.

Integrating these two datasets, we can estimate the nightly replacement of true migrants on the ground (daily turnover rate), which was previously difficult to achieve with alternative sources of data (e.g. banding, which cannot eliminate local dispersal effects). The fact that, on an average night, only 13% of birds on the ground are replaced by new birds, and even on peak nights, only up to half the birds are replaced, demonstrates that only a limited portion of the total bird mass participates in migration movements. In the context of a stream-like regime, where the numbers of birds taking off and landing are relatively similar, the high abundance turnover rate documented in this study offers valuable insights into the description of the change on the ground. Indeed, while the absolute number of birds might not change much, the replacement of individual birds is considerable. Our computation of the abundance turnover rate is sensitive to the $\gamma$ coefficient, which shows regional variation (Supporting information). However, a sensitivity analysis on $\gamma$ showed a limited impact on the overall distribution of the turnover rate (Supporting information).

The strong correlation ($r = 0.53$) between the turnover in species composition and the results from the flow model provides evidence that real-time WSR data can be used to inform about compositional changes on the ground. We find that WSR data are more strongly correlated with turnover in species composition than with the total count of birds per checklist ($r = 0.35$). This confirms a predominantly stream-like regime, where abundance changes on the ground are small (due to a balanced landing and departure fluxes) and therefore hard to detect (Supporting information).

## Implications for migratory bird conservation and public engagement

The positive correlation we find between the arrivals and departures estimated by WSR and observations on the ground estimated by eBird demonstrate that an accurate, real-time tool to inform birders and conservationists on daily changes in numbers of birds on the ground is feasible. The maps of daily arrivals and departures can be used to identify specific areas and periods with high arrival of birds on the ground, making it a relevant data product to inform temporal conservation measures on the ground. Integrating these maps into existing live migration tools such as the BirdCast dashboards (https://dashboard.birdcast.info/) has potential for strong public engagement, as they can inform observers on regional arrivals from the previous night as well as changes in overall numbers on the ground.

The stream-like regime identified in this study has implications for which type of conservation measures might be most effective for protecting migratory birds on the ground. We did not find evidence for regular regional-scale aggregations of large numbers of birds for short periods (April 2018 in Fig. 4). Rather, our analyses revealed a continuous smooth increase in the number of birds throughout the entire migration season. This suggests that conservation efforts for these species during migration should be geographically widespread, rather than based on specific hotspots, as well as temporally continuous throughout the season. This finding thus provides grounds to extend the 'shallow' widespread land-sharing conservation measures suggested by Vickery et al. (2023), not only to protect migratory birds on their wintering grounds, but also during their full migration journey. Such measures are complementary to the temporally focused measures targeting in-flight pulses of migratory birds. At the same time, conservation efforts may want to focus on protecting newly arrived birds instead of relying on absolute numbers of birds on the ground, as individuals who have recently landed might be particularly vulnerable while seeking to refuel in a new place. Our framework could help identify the few nights and areas characterized by a high number of birds landing and thus inform specific measures to protect migrants on the ground, such as pesticide control (Hedges 2001) and domestic cat programmes (e.g. https://abcbirds.org/program/cats-indoors).

Further research is needed to refine these findings at the local scale (< 100 km) and reveal fine-scale distribution patterns linked to habitat suitability (Guo et al. 2023), barrier crossing (mountain, water body), and rain fronts. This constitutes a necessary step towards resolving localized high-density aggregations on the ground, such as those occurring during migration fallouts. Applying the flow model developed in this study to higher resolution radar data can provide insights into these questions.

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### Author contributions

**Raphaël Nussbaumer**: Conceptualization (equal); Formal analysis (lead); Funding acquisition (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Benjamin M. Van Doren**: Conceptualization (supporting); Writing – review and editing (supporting). **Wesley M. Hochachka**: Conceptualization (supporting); Writing – review and editing (supporting). **Andrew Farnsworth**: Conceptualization (supporting); Writing – review and editing (supporting). **Frank A. La Sorte**: Conceptualization (supporting); Writing – review and editing (supporting). **Alison Johnston**: Conceptualization (supporting); Writing – review and editing (supporting). **Adriaan M. Dokter**: Conceptualization (equal); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

### Transparent peer review

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### Data availability statement

Data and code are available from https://doi.org/10.5281/zenodo.11310910 (Nussbaumer 2024a) for the interpolation and flow model and https://doi.org/10.5281/zenodo.11311087 (Nussbaumer 2024b) for the rest of the analysis analysis.

### Supporting information

The Supporting information associated with this article is available with the online version.

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