Received: 25 May 2024 | Revised: 7 March 2025 | Accepted: 12 March 2025

DOI: 10.1111/cobi.70070

Conservation Biology

CONTRIBUTED PAPER

Assessing the Corn Belt as an anthropogenic barrier to migrating landbirds in the United States

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Article impact statement: The Midwest Corn Belt in the United States acts as an anthropogenic barrier to migrating landbirds, affecting their flight and stopover patterns.

Funding information
Cornell Atkinson Center for Sustainability, Cornell University; National Institute of Food and Agriculture, Grant/Award Number: DEL-00774; High Meadows Foundation; Division of Environmental Biology, Grant/Award Number: DEB-2146052

Abstract

Migrating landbirds adjust their flight and stopover behaviors to efficiently cross inhospitable geographies, such as the Gulf of Mexico and the Sahara Desert. In addition to these natural barriers, birds may increasingly encounter anthropogenic barriers created by large-scale changes in land use. One such barrier could be the Corn Belt in the Midwest United States, where 76.4% of precolonial vegetation (forest and grassland combined) has been replaced by agricultural and urban areas, primarily corn fields. We used 5 years of data from 47 weather radar stations in the United States to compare the population-level flight patterns of migrating landbirds crossing the Corn Belt and the forested landscapes south and north of it in spring and autumn. We also examined the impacts of the Corn Belt relative to the Gulf of Mexico on the stopover behavior of migrating birds by comparing changes in the proportion of migrants that stop to rest (stopover-to-passage ratio [SPR]) relative to distance from both barriers. Birds showed increased meridional airspeeds and stronger selection for tailwinds when crossing the Corn Belt compared with forested landscapes. For birds crossing the Gulf of Mexico, the highest proportion of migrants stopped to rest after crossing the Gulf, and SPR decreased sharply as distance from the shoreline increased. We did not find this pattern after migrants crossed the Corn Belt, although the SPR increased in the Corn Belt as birds approached the down-route forest boundary in both seasons. This weaker pattern for stopover propensity after crossing the Corn Belt is likely due to its narrower width, the availability of small forest patches throughout the Corn Belt, and the subset of species affected, compared with the gulf. We recommend restoring stepping stones of forest in the Corn Belt and protecting woodlands along the Gulf Coast to help landbirds successfully negotiate both barriers.

KEYWORDS
Corn Belt, Gulf of Mexico, landbird migration, land-use change, migration barrier, radar ornithology, SPR, stopover-to-passage ratio, wind selection

INTRODUCTION

Many migratory landbirds must traverse large migration barriers in their twice-annual migration journeys. These are inhospitable landscapes to which birds show diverse behavioral adjustments (Rime et al., 2025). Most of the barriers are major natural geographic features, such as large water bodies (e.g., Gulf of Mexico [Yong & Moore, 1997]), deserts (e.g., Sahara Desert [Bairlein, 1988]), and mountain ranges (e.g., Himalayas [Adamík et al., 2016; Gauthreaux, 1971; Ouwehand & Both, 2016; Prins & Namgail, 2017]). They influence in recognizable ways the migratory flight of birds that negotiate them. For instance, whereas most landbirds migrate at night, prolonged migratory flights that extend into the daytime occur among migrants that make long nonstop flights across major barriers (Abbott et al., 2023; Schmaljohann et al., 2007a, 2007b; Sjöberg et al., 2021). Also, birds tend to fly faster when crossing migration barriers, such as the Mediterranean Sea and Sahara Desert (Finlayson et al., 2021; Lopez-Ricaurte et al., 2021; Rime et al., 2023; Strandberg et al., 2009). In addition to accelerating their self-powered flight (Alerstam et al., 2011), birds can also achieve faster speed through selection for tailwind support by adjusting flight timing (Gauthreaux, 1971; Schmaljohann et al., 2007a) and flight altitude (Bruderer et al., 2018; Gauthreaux, 1991; Schmaljohann et al., 2009). In general, barrier-crossing flights are longer, faster, and more likely to be undertaken with wind support than flights over more hospitable landscapes (Rime et al., 2023).

There are 2 alternating phases of bird migration: passage flights and stopovers in between. During long-distance migration, birds make periodic stopovers to rest, refuel, recover physiological functions, and avoid adverse environmental conditions (Mehlman et al., 2005; Schmaljohann et al., 2022). Therefore, in addition to changes in flight behaviors, migratory landbirds also change their stopover behaviors when negotiating barriers. After nonstop flights to transverse inhospitable landscapes, such as open water, birds often land in higher concentrations around the edges of such barriers (e.g., within 20 km of the Gulf of Mexico and the Great Lakes) (Buler & Moore, 2011; Cohen et al., 2021, 2022). In contrast, in the case of the Sahara Desert, most birds follow an intermittent flight strategy by stopping to rest even in areas with no refueling opportunities (Bairlein, 1988; Biebach et al., 2000; Schmaljohann et al., 2007b) because these stopovers serve other functions, such as physiological recovery and avoidance of high temperatures (Schmaljohann et al., 2007b, 2022). Therefore, birds' stopover patterns can differ depending on whether they surmount open water or inland migration barriers.

In the Nearctic–Neotropical landbird migration system, the Gulf of Mexico is the most prominent migration barrier, requiring a 15- to 35-h nonstop flight to traverse more than 1000 km of open water (Abbott et al., 2023; Deppe et al., 2015). Around two thirds of migratory landbird species in North America, totaling billions of individuals, negotiate the Gulf of Mexico each spring and autumn (Deppe et al., 2015; Dokter et al., 2018). Several lines of evidence point to the potentially high cost and even lethal risks of crossing the gulf. Carcasses wash ashore along coastlines (Newton, 2007) and are found in the stomachs of tiger sharks (Drymon et al., 2019), large flocks of migrants have been observed resting on offshore oil platforms (Ronconi et al., 2015), and many migrants retreat or take detours when confronted with the overwater passage (Zenzal et al., 2021). In contrast, fat birds departing for a gulf-crossing flight under favorable wind conditions exhibit high apparent survival (Ward et al., 2018), and many birds are in good energetic condition when they reach the opposite shore (Deppe & Rotenberry, 2008). Hence, the danger of barrier crossing is highly dependent on intrinsic (e.g., body conditions) and extrinsic (e.g., weather) factors associated with migratory flights (Clipp et al., 2020; Deppe et al., 2015; Smolinsky et al., 2013; Ward et al., 2018).

Large-scale anthropogenic land-use change may also create migration barriers. Forest was the primary land-cover type in the eastern United States until rapid cropland and pasture expansion occurred in the Midwest from 1850 to 1920 (Li et al., 2023). This agricultural expansion has dramatically reduced food availability, especially for insectivorous migrants attracted to deciduous trees, such as oaks (*Quercus* spp.) and hackberries (*Celtis* spp.) (Ewert & Hamas, 1996; Mehlman et al., 2005; Packett & Dunning, 2009). In addition, birds may also experience higher predation risks (Stanton et al., 2018) and less favorable microclimate (Vanneste et al., 2020) in agricultural landscapes, which could have comparable effects on the recovery process during stopover (Schmaljohann et al., 2022).

A recent analysis of weather radar data showed that migrants consistently concentrate in the large forest tracts bordering the southern edge of the agricultural Midwest (the so-called Corn Belt) during autumn migration (Guo et al., 2023), providing the first evidence that the Corn Belt might constitute a migration barrier and highlighting the possibility that some birds are making nonstop flights over this vast agricultural landscape. Radiotelemetry tracking studies show that *Catharus* thrushes can fly nonstop for up to 600 km in the Corn Belt (Cochran, 1987; Cochran & Wikelski, 2005; Wikelski et al., 2003). However, the high densities of migrants in forest fragments in the Corn Belt (Guo et al., 2023, 2024) suggest that some migrants are making use of the small woodlots scattered across this agricultural landscape to rest, recover, and refuel (Packett & Dunning, 2009; Robinson, 2023). Thus, the potential barrier of the Corn Belt likely differs from well-studied water barriers, such as the Gulf of Mexico in its inhospitality and consequent impacts on migratory behaviors.

The stopover-to-passage ratio (SPR) is a quantitative measure derived from weather radar data that summarizes the collective stopover decisions made by migrating birds at a landscape scale (Cohen et al., 2021, 2022). It measures the proportional biomass of birds that stop in a radar domain relative to the biomass of birds passing through the same airspace, reflecting the population-wise propensity to stop in that area during migration (Cohen et al., 2021, 2022). A high SPR indicates a large proportion of birds stop to rest in a given location relative to the number of birds flying over it.

We quantified SPR and flight parameters (airspeed and tailwind selection) to assess the barrier impacts on migration behaviors based on 5 years of data from 47 weather radar stations across the eastern United States. Guo et al. (2023) hypothesized that the Corn Belt likely constitutes a notable migration barrier, based on the distribution of migrant stopover densities. We tested whether this agricultural landscape also affects other migration behaviors and whether the impacts are comparable to those of birds crossing the Gulf of Mexico. We predicted birds would exhibit lower SPRs and faster airspeed and select for stronger tailwinds when crossing the Corn Belt compared with more forested landscapes. We also predicted that the SPR would be the highest at the down-route boundary after crossing the migration barrier (i.e., the northern boundary in spring and the southern boundary in autumn for the Gulf of Mexico and the Corn Belt), where tired birds stop to rest. Given the narrower width of the Corn Belt compared with the gulf and the availability of forest fragments in this agricultural landscape, we hypothesized that the Corn Belt is a weaker migration barrier than the Gulf of Mexico. Therefore, we predicted sharp decreases in SPR as the distance from the Gulf Coast increases after birds have crossed the Gulf of Mexico and a weak pattern of changes in SPRs as the distance from the Corn Belt increases after birds have crossed the Corn Belt.

METHODS

Midwest Corn Belt and its land-use history

The eastern United States is divided into 3 avifauna biomes based on the similarity of breeding bird communities, habitats, and resource management issues (Rich et al., 2004). Guo et al. (2023) describe the Midwest migration barrier as the portions of the prairie biome between the northern forest and the eastern forest biomes. The prairie biome, as delineated by Rich et al. (2004), extends into the prairies of Montana, and much of it has been converted to cropland. We considered the Corn Belt the prairie biome east of the 96th meridian and north of Arkansas (Appendix S1) because we focused primarily on forest-dwelling landbirds in the eastern United States (Guo et al., 2023). We used historical land-cover data from Li et al. (2023) to assemble the land-use history of the Corn Belt from 1630 to 2020 (Figure 1).

Data sources

We obtained level II data from the next-generation weather radar (NEXRAD) network (Ansari et al., 2018) at a resolution of 250 m in range by 0.5° in azimuth in polar coordinates. Each radar station samples the atmosphere every 4–10 min (Buler et al., 2017). We obtained 2 measurements to quantify the migratory movements of birds: reflectivity, a measure of bird biomass, and radial velocity, a measure of birds' ground speed relative to the radar. To compare the areas directly affected by both the Corn Belt and Gulf of Mexico, we constrained the study area to 47 radar stations located in the longitudinal range of the Corn Belt (between the 96th and 82nd meridian; Appendix S1), which also excludes the far eastern Gulf of Mexico. Radar stations closer to the eastern Gulf of Mexico are more likely to have migrants that cross the Caribbean than migrants that cross the gulf (Abbott et al., 2023). We included data from 1 March to 15 June for spring migration and from 1 August to 15 November for autumn migration, for the years 2015–2019. We also downloaded wind data from the North American Regional Reanalysis model output (Mesinger et al., 2006) to compute wind speed and birds' airspeed (powered flight speed relative to air).

We calculated the deciduous forest cover percentage and proximity to the barrier edge for each radar domain as potential factors affecting SPR. We obtained forest cover data from the 2016 National Land Cover Database (NLCD) (Homer et al., 2020) and calculated the deciduous forest cover percentage within a 37.5-km radius of each radar station. We also calculated the distances to both forest–agriculture boundaries (northern boundary between the northern forest and the Corn Belt and southern boundary between the Corn Belt and the eastern forest) (Appendix S1) and the northern Gulf Coast for all 47 radar stations. Data for this study are available from Figshare (https://doi.org/10.6084/m9.figshare.25329055).

Radar data filtering

We processed reflectivity and radial velocity data at 30-min intervals from sunset to sunrise for each migration night, covering the altitude bins from 0 to 2800 m (at 100-m intervals) above the radar antenna. This captures the majority of nocturnal migration (Bruderer et al., 2018; Farnsworth et al., 2016). Data were filtered to remove precipitation with the MistNet neural network (Lin et al., 2019). We also filtered out data on spring movement that was southbound (in 90–270° from the north sector) and on autumn movement that was northbound (in 270–90°) to exclude insect contamination (Dokter et al., 2018; Horton et al., 2020).

Meridional flight speed and selection for tailwind support

We derived the mean ground vector of flying birds (meters per second) measured by weather radar by fitting a sine function

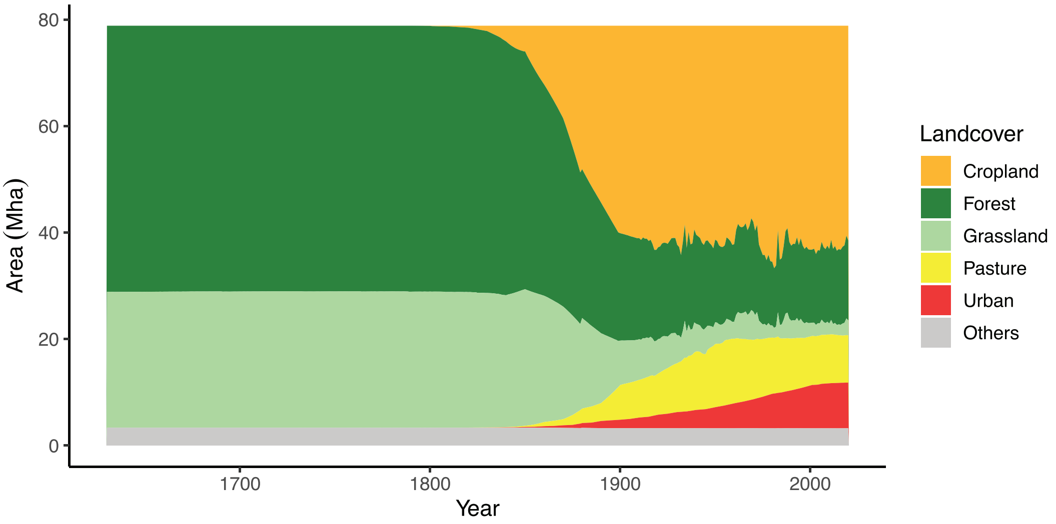

FIGURE 1 Land-cover changes in the Midwest Corn Belt from 1630 to 2020.

to the radial velocity by radial azimuth (Buler & Diehl, 2009). We then matched the corresponding wind vector to the specific altitude bin and time. Given the overall direction of bird migration movement and the orientation of both migration barriers, we compared only the v component (meridional speed in the north–south direction) of the ground and wind vectors to determine the airspeeds directly contributing to barrier crossing: due north in spring and due south in autumn. For each altitude bin and time of the filtered data, we calculated the meridional airspeed (meters per second) (i.e., the powered flight speed in the north–south direction of birds in the air) by subtracting the meridional wind vector from the meridional ground vector. We then calculated the seasonal meridional airspeed (Appendix S1) as the biomass-weighted mean across altitude bins (from radar ground level to 2800 m above at 100-m intervals) and time (from sunset to sunrise at 30-min intervals throughout the migration season) as measured by weather radar.

To compute the seasonal selection for tailwind in the north–south direction (meters per second), we calculated the difference between biomass-weighted meridional wind speed (i.e., the experienced wind speed in the north–south direction weighted by biomass across altitude bins over time) (Appendix S2) and the available meridional wind speed (i.e., the available wind speed in the north–south direction with a standard height distribution and uniform temporal distribution of birds) (Appendix S3). The standard height distribution of birds was calculated by averaging the biomass of flying birds at each altitude bin across all 47 radar stations throughout the migration season. The calculated differences (experienced meridional wind speed − available meridional wind speed [Appendix S4]) represented birds' behavioral adjustments in flight height and migration timing to select for tailwind support during migration at the population level (Bruderer et al., 2018; Schmaljohann et al., 2009).

Stopover-to-passage ratio

We used the area within a 37.5-km radius of each radar station to derive corresponding measures of bird stopover and passage biomass (Cohen et al., 2021, 2022). This captures the altitude bins at which most migration occurs (Buler et al., 2017).

For seasonal passage biomass (in units of total cross-section area of birds [square centimeters]), we integrated the filtered data at 30-min intervals from sunset to sunrise for each migration night, covering the altitude bins from 0 to 2800 m above radar antenna height. For radar stations above the mean ground level, we extrapolated the reflectivity measured at the antenna height level down to the mean ground level to capture the low-altitude migration. This extrapolation is based on the assumption of a uniform reflectivity distribution below the radar antenna to the same level as measured at antenna height (Dokter et al., 2018). We first calculated the nightly passage rate (square centimeters per kilometer per night) by integrating the product of reflectivity (square centimeters per cubic kilometers) and bird groundspeed (kilometers per hour) across all altitude bins (kilometers) in the sampling time window (hours per night). We then multiplied the nightly passage rate (square centimeters per kilometer per night) by the 75 km transect length to get the nightly passage biomass (square centimeters per night). Given the variation in sampling nights (mean = 103 nights [SD 4]) due to radar downtimes, the total seasonal passage biomass (square centimeters) was calculated by multiplying the average nightly passage biomass by 107 nights, the duration of each migration season.

We calculated seasonal stopover biomass for each radar domain based on published fine-scale seasonal stopover density (square centimeters per hectare) data (Guo et al., 2024), which were derived as bird density measured at peak exodus each night (when migrants take flight from the places where they stopped over during the day). For the stopover data, nights with precipitation were excluded using the MistNet neural network (Lin et al., 2019), and nights with insect or waterfowl movements were also removed based on flight speed (Larkin, 1991) and spatial patterns (Guo et al., 2024; O'Neal et al., 2010). We summed the stopover density (square centimeters per hectare) across the land area (hectares) within a 37.5-km radius of that radar to get the aggregated stopover biomass (square centimeters). Because the stopover density was measured only as a snapshot of nightly peak exodus in Guo et al. (2024), birds that took off after the sampling time were not included in their nightly stopover biomass estimates. Therefore, we divided the instantaneous stopover biomass by 0.1, which is the estimated proportion of birds aloft at peak exodus each night based on radio telemetry (Buler et al., 2017), to estimate the total seasonal stopover biomass and SPR (Cohen et al., 2021, 2022). Although the accurate proportional estimate of birds sampled at exodus could be refined with more radiotelemetry studies (Cohen et al., 2021), the SPR is comparable across sites given the consistency in bird exodus timing across multiple studies (Cooper et al., 2023).

The seasonal SPR of each radar domain ($n = 47$) was calculated as a percentage by dividing the total stopover biomass (square centimeters) by the passage biomass (square centimeters) for spring and autumn in each year ($n = 5$ years). Theoretical values of SPR should range from 0% to 100%. However, the KMQT radar in Marquette, Michigan, had a spring SPR value exceeding 100% (Figure 3), likely due to measurement errors (Cohen et al., 2021, 2022).

Comparison of migratory behaviors

To test for the expectation that birds adjust their stopover and flight behaviors when crossing the Corn Belt, we used analysis of variance (ANOVA) and generalized least square (GLS) models with post hoc Tukey tests to compare SPR, airspeed, and tailwind selection across avifaunal biomes. We also built linear models (LMs) to assess how deciduous forest cover and distances from the barriers affect the SPRs in each biome. Given the maximum recorded distance of 600 km for nonstop nocturnal flights of Swainson's thrush (*Catharus ustulatus* Nuttal, 1840) and hermit thrush (*Catharus guttatus* Pallas, 1811) in the Corn Belt (Cochran, 1987; Wikelski et al., 2003), we included radar stations within 600 km of either side of the barriers (Corn Belt and the Gulf of Mexico) when assessing the distance effect. We used Moran's I tests to identify potential spatial autocorrelation by fitting the model residuals with the distance matrix between radar stations with the spdep package in R (Bivand et al., 2017). We then accounted for spatial autocorrelation by compensating with the correlation structure (exponential, Gaussian, linear, or spherical) that best fits the model residual in GLS with the nlme package in R (Pinheiro et al., 2023). We chose the best model based on the Akaike information criterion (AIC) with the MuMIn package in R (Barton & Barton, 2015). We transformed the dependent variables when necessary to meet the normality and homoscedasticity assumptions of model residuals. All analyses were done in R 4.4.2. (R Core Team, 2024).

Sensitivity analyses

Given the orientation of both barriers, we compared birds' meridional airspeed and selection of wind in the north–south directions that directly contribute to barrier crossing. However, zonal wind in the east–west direction could also affect migrating birds because they might need to spend extra energy on compensating for wind drift. Therefore, we ran additional analyses comparing the full airspeed (including both meridional and zonal components) and experienced zonal winds (biomass-weighted mean) across avifaunal biomes with ANOVA or GLS with post hoc Tukey tests. In addition, because weather radar measures the average speed of all individuals flying in various directions, flocks of migratory birds whose constituent members are moving in different directions will show lower apparent speed (Nilsson et al., 2018). To quantify such variation in the flight direction of birds flying above each radar domain, we calculated the standard deviation of the radial velocity sine model fit residuals as an index of variation in flight directions. We then compared the variation in flight directions across avifaunal biomes through ANOVA or GLS with post hoc Tukey tests.

The latitudinal differences among avifaunal biomes might also confound the comparisons of airspeed and selection for tailwinds across avifauna biomes. We therefore ran additional sensitivity analyses comparing airspeed and tailwind selection across latitudes in each biome to test for such confounding effects.

Different regions may have different migratory species assemblages, which could affect average flight speeds. Especially problematic would be the inclusion of nocturnally flying waterfowl in the passage data (Horton et al., 2018) because waterfowl tend to fly faster than most landbirds (Alerstam et al., 2007; Bruderer & Boldt, 2001; Pennycuick et al., 2013). For the stopover data, nights with waterfowl contamination have been manually excluded by Guo et al. (2024) based on their distinct takeoff patterns in the radar images (O'Neal et al., 2010). Hence, flight parameters derived from the passage data are subject to greater waterfowl contamination. From screening millions of radar images, we observed that waterfowl migrate earlier than landbirds in the spring and later in the autumn. Therefore, we ran sensitivity analyses to compare the flight parameters across avifaunal biomes with more constrained time windows (15 April to 15 June for spring migration and 1 August to 15 October for autumn migration) because most waterfowl would have departed from stopover sites in the contiguous United States by 15 April during spring migration and would not start migrating until 15 October during autumn migration (personal observations) (Haas et al., 2022; Horton et al., 2018).

RESULTS

Land-use history in the Midwest Corn Belt

Our analysis of historical and contemporary land-cover maps showed that from 1630 to 2020, the Corn Belt experienced a substantial decrease in forest cover (from 63.4% to 19.0%) and

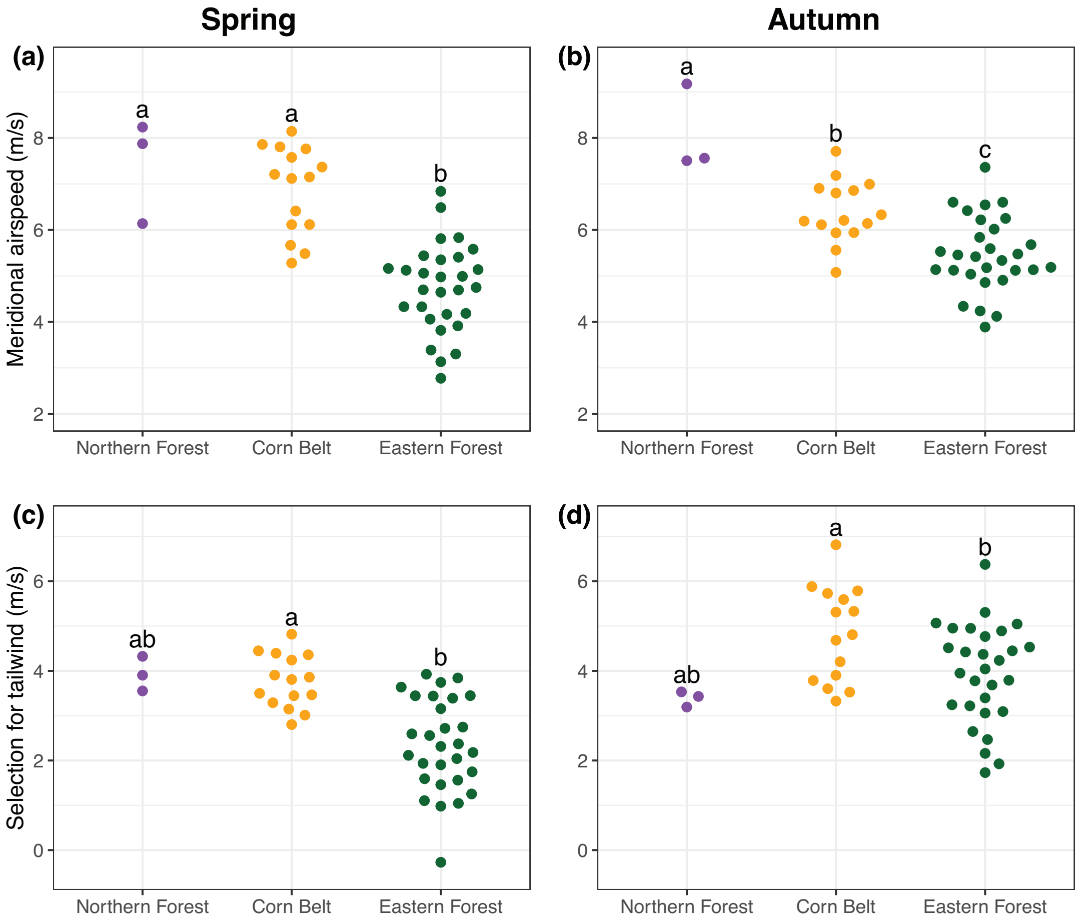

FIGURE 2 Comparison of mean flight parameters averaged from 2015 to 2019 in the northern forest, Corn Belt, and eastern forest of the United States during spring and autumn bird migrations: (a) meridional airspeed in spring, (b) meridional airspeed in autumn, (c) selection for tailwind support in spring, and (d) selection for tailwind support in autumn (nonmatching letters in each panel, significant difference based on Tukey test at 5% significance level). All vectors are plotted as absolute values, which are positive for spring migration from south to north and negative for autumn migration from north to south (Appendices S1–S4), except for the negative selection for tailwind in spring for the KHGX radar (Appendix S4).

grassland cover (from 32.4% to 3.6%) (Figure 1). Cropland is now the dominant land cover (51.1%). Pasture and urban areas now each constitute 11.2% and 10.9% of contemporary land cover in this biome.

Comparison of flight and stopover patterns across avifauna biomes

We predicted faster meridional airspeeds (hereafter airspeeds) across a migration barrier, and we found strong evidence of this when comparing birds migrating through the Corn Belt ($n = 15$) (spring: mean = 6.9 m/s [SD 0.9]; autumn: mean = 6.4 m/s [0.7]) versus the eastern forest ($n = 29$) (spring: mean = 4.7 m/s [1.0]; autumn: mean = 5.5 m/s [0.8]) in both seasons (ANOVA: $p_{\text{spring}} < 0.001$, $p_{\text{autumn}} = 0.002$) (Figure 2a,b; Appendix S1). However, comparing birds traversing the Corn Belt versus the northern forest ($n = 3$, spring: mean = 7.4 m/s [1.1]; autumn: mean = 8.1 m/s [0.9]), there was no evidence that the mean airspeeds differed in spring (ANOVA: $p = 0.65$) (Figure 2a) but strong evidence of higher airspeed in the northern forest compared with the Corn Belt in autumn (ANOVA: $p = 0.004$) (Figure 2b). In each biome, there was only moderate evidence that airspeed increased as latitude increased in the Corn Belt in both seasons, but no evidence for such patterns in other biomes of either season (Appendix S5a,b).

We found similarly strong evidence for faster full airspeed (including both meridional and zonal components) in the Corn Belt ($n = 15$) (spring: mean = 9.3 m/s [SD 0.7]; autumn: mean = 7.9 m/s [0.6]) than in the eastern forest ($n = 29$) (spring: mean = 7.7 m/s [0.8]; autumn: mean = 6.9 m/s [0.6]) in both seasons (ANOVA: $p < 0.001$) (Appendix S6a,b). The northern forest also had the highest full airspeed ($n = 3$) (spring: mean = 10.4 m/s [0.4]; autumn: mean = 9.3 m/s [0.7]) in both seasons (ANOVA: $p_{\text{spring}} = 0.01$, $p_{\text{autumn}} = 0.002$) (Appendix S6a,b). In addition, there was no evidence that zonal wind speeds differed among the 3 biomes in either season (GLS: $p_{\text{spring}} = 0.15$, $p_{\text{autumn}} = 0.94$) (Appendix S6c,d). Similarly, there was no evidence that the variation in flight direction differed between the Corn Belt and the other 2 biomes in either season (ANOVA: $p_{\text{spring}} = 0.41$, $p_{\text{autumn}} = 0.24$) (Appendix S6e,f), although there was weak evidence for greater variation in flight direction in the eastern forest than in the northern forest in autumn ($p = 0.08$) (Appendix S6f).

We also predicted stronger selections for tailwinds across a migration barrier. We found strong evidence that the selection for tailwinds (Appendix S4) was 65% greater for birds in the Corn Belt compared with the eastern forest in spring (Corn Belt: mean = 3.8 m/s [SD 0.6], $n = 15$; eastern forest: mean = 2.3 m/s [1.0], $n = 29$; GLS: $p = 0.003$) (Figure 2c) and moderate evidence that it was 23% greater than the eastern forest in autumn (Corn Belt: mean = 4.8 m/s [1.1], $n = 15$; eastern forest: mean = 3.9 m/s [1.1], $n = 29$; ANOVA: $p = 0.03$) (Figure 2d). There was little evidence for a greater selection for tailwinds in the Corn Belt than in the northern forest in autumn (mean = 3.4 m/s [0.2], $n = 3$; ANOVA: $p = 0.10$) (Figure 2d) but no evidence for it in spring (mean = 3.9 m/s [0.4], $n = 3$; GLS: $p = 0.99$) (Figure 2c). In each biome, there was strong evidence for tailwind selection increasing with latitude in the eastern forest in spring and little evidence in autumn, but no evidence for such a pattern in other biomes of either season (Appendix S5c,d).

In the sensitivity analyses excluding time windows of peak waterfowl migration, we found similar differences in airspeeds and selection for tailwinds across avifaunal biomes (Appendix S7a–d), ruling out the potential impacts of waterfowl contamination on observed patterns.

Contrary to our prediction of lower SPR in the Corn Belt than the more forested biomes, there was little or no evidence that SPR differed between the Corn Belt ($n = 15$) (spring: mean = 39.8% [SD 10.6]; autumn: mean = 37.3% [9.5]), the eastern forest ($n = 29$) (spring: mean = 45.7% [24.8]; autumn: mean = 43.1% [12.7]), or the northern forest ($n = 3$) (spring: mean = 76.4% [26.3]; autumn: mean = 62.4% [37.9]) in either spring (GLS: $p = 0.10$) (Appendix S8e) or autumn (ANOVA: $p = 0.22$) (Appendix S8f). Instead, the SPR showed substantial variation within each biome (Figure 3).

Changes in SPR with relative distance from 2 barriers

For radar stations located within 600 km north of the Gulf Coast (all in the eastern forest biome) (Figure 3), SPR values were high along the immediate northern Gulf Coast in both seasons. They decreased as distance from the coastline increased (Figure 4). This concentration effect of birds along the northern Gulf Coast was stronger in spring at the down-route boundary after barrier crossing (LM: $n = 25$, $p < 0.001$, adjusted $R^2 = 0.60$) (Figure 4a;Appendix S9) than in autumn before crossing (LM: $n = 25$, $p = 0.003$, adjusted $R^2 = 0.29$) (Figure 4b; Appendix S9). Hence, we focused only on the down-route boundaries (i.e., the side encountered after crossing the barrier) for subsequent comparisons.

There were insufficient data in the northern forest ($n = 3$) to test for the distance effect after birds crossed the Corn Belt in spring (Appendix S10a). In autumn, there was no evidence of the distance effect in the eastern forest after birds crossed the Corn Belt (Appendix S10b).

We found strong evidence that distance and deciduous forest cover affected the SPR in both seasons (Figure 5). Following the meridional direction of migration movement, SPR in the Corn Belt increased as proximity to the down-route boundary in spring increased (i.e., northern boundary; LM: $n = 15$, $p_{\text{distance}} = 0.01$, $p_{\text{log-forest}} = 0.003$, $p_{\text{model}} = 0.001$, adjusted $R^2 = 0.62$) (Figure 5a; Appendix S11) and autumn (i.e., southern boundary; LM: $n = 15$, $p_{\text{distance}} = 0.006$, $p_{\text{log-forest}} = 0.005$, $p_{\text{model}} = 0.001$, adjusted $R^2 = 0.61$) (Figure 5b; Appendix S11). We also found strong evidence that in both seasons SPR increased as deciduous forest cover percentage increased (Figure 5c,d; Appendix S11).

DISCUSSION

Midwest Corn Belt as an anthropogenic migration barrier

Our discovery of faster airspeeds and greater selection for tailwinds for birds flying over the Midwest Corn Belt than the eastern forest (Figure 2) is consistent with the hypothesis proposed by Guo et al. (2023) that the Corn Belt poses a barrier for migrating landbirds. Our analysis of the Corn Belt land-use history showed that, on average, 76.4% of the original vegetation (forest and grassland combined) in the 1630s had been converted (Figure 1), and some states, such as Indiana and Illinois, have experienced even more dramatic habitat declines (Evans et al., 2001; Iverson, 1988). Therefore, birds respond to the Corn Belt as if it were an anthropogenic migration barrier stemming from agricultural expansion.

The faster airspeeds exhibited by migrants above the Corn Belt compared with the eastern forest in both seasons (Figure 2a-b) are similar to the flight behaviors of northern wheatears (*Oenanthe oenanthe* Linné, 1758), European nightjars (*Caprimulgus europaeus* Linné, 1758), and lesser kestrels (*Falco naumanni* Fleischer, 1818) crossing the Mediterranean Sea and the Sahara Desert (Lathouwers et al., 2022; Lopez-Ricaurte et al., 2021; Rime et al., 2023). Similar increases in speed have also been recorded for demoiselle cranes (*Grus virgo* Linné, 1758) crossing the Himalayas (Mi et al., 2022) and white storks (*Ciconia ciconia* Linné, 1758) crossing the Strait of Gibraltar (Blas et al., 2020). In all cases, faster speeds enable these birds to cross barriers in a shorter time.

Faster airspeeds of birds in the Corn Belt and the northern forest could potentially be attributable to larger average body sizes of species migrating farther north (Horton et al., 2018), which would arise if waterfowl constituted a higher proportion of birds flying over the Corn Belt and northern forest relative to the eastern forest. However, our sensitivity analyses showed that the differences in airspeed between avifaunal

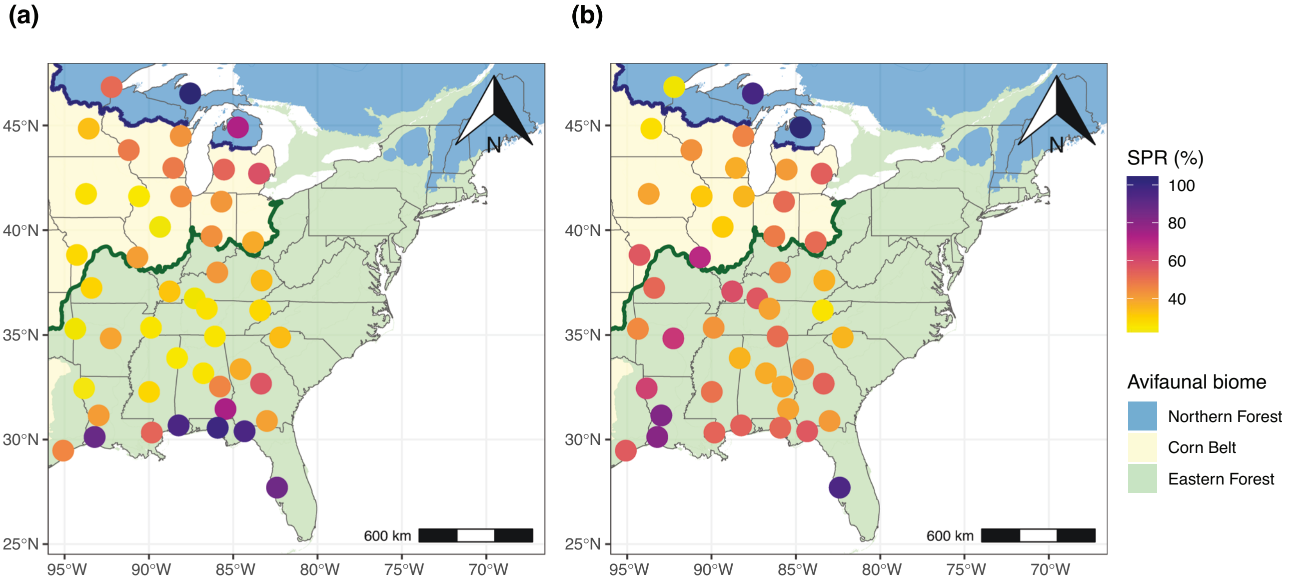

FIGURE 3 Seasonal mean stopover-to-passage ratios (SPRs) averaged from 2015 to 2019 during (a) spring and (b) autumn migrations (dark blue line, northern boundary between the northern forest and the Corn Belt; dark green line, southern boundary between the Corn Belt and the eastern forest). Point size is larger than the 37.5-km sampled radius of each radar domain for better visualization.

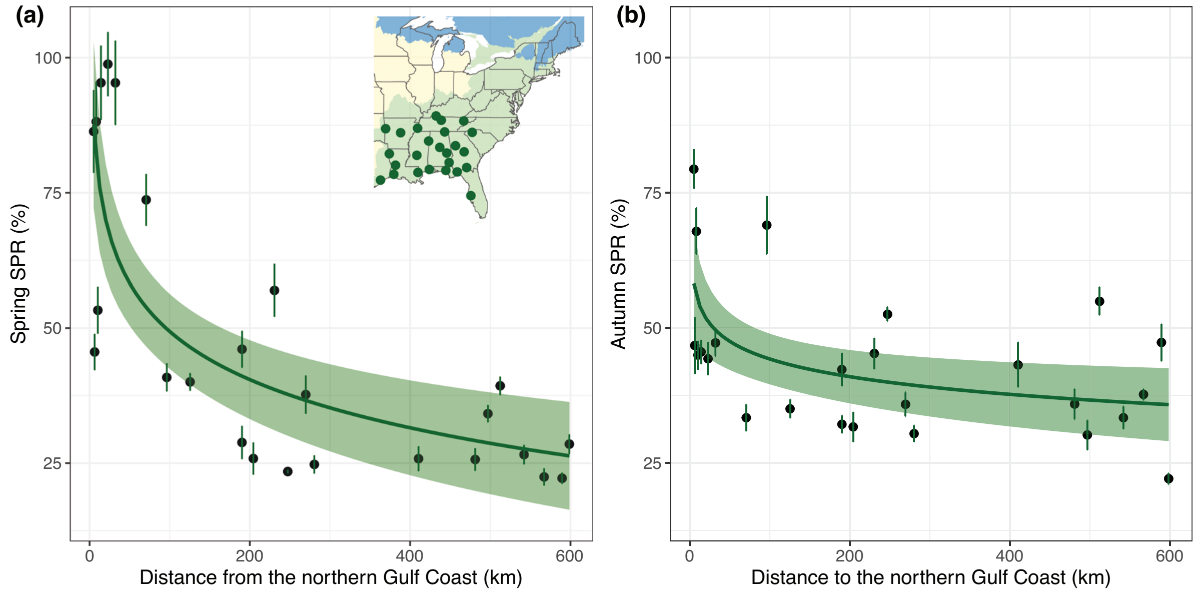

FIGURE 4 Changes in the seasonal stopover-to-passage ratio (SPR) in the eastern forest with distance from or distance to the northern Gulf Coast in (a) spring and (b) autumn migrations (error bars, standard errors of SPR from 2015 to 2019; shading, 95% confidence interval of the linear model). Radar stations located beyond 600 km of the Gulf Coast are not included, as shown in the inset map.

biomes persist even after excluding the prime times for waterfowl migration (Appendix S7a,b). The inclusion of shorebirds in the radar data could also potentially increase the average speed measured. However, given that most migratory shorebirds breed well to the north of our longitudinally restricted study area and pass through in the spring and fall en route to distant wintering areas, their inclusion will not bias the speed comparison toward any particular biome in our study area. Therefore, the airspeed difference between the Corn Belt and the eastern forest was more likely driven by behavioral adjustments for barrier crossing rather than changes in species assemblages.

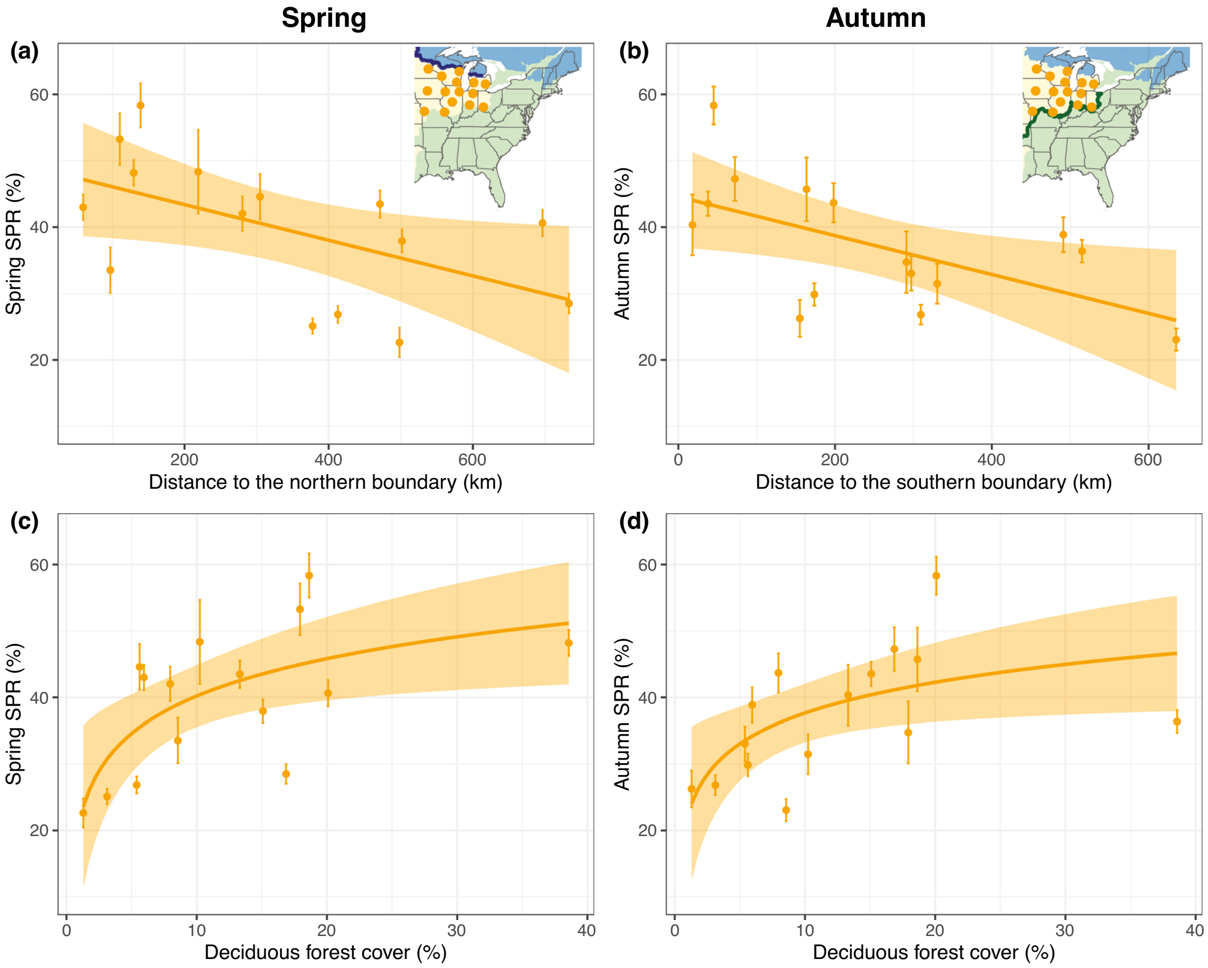

FIGURE 5 Changes in the seasonal stopover-to-passage ratio (SPR) in the Corn Belt with (a, b) distance to the forest–agriculture boundary and (c, d) percentage of deciduous forest cover in each radar domain (error bars, standard errors of SPR from 2015 to 2019; shading, 95% confidence interval of the linear model; dark blue lines, northern boundary between the Corn Belt and the northern forest; dark green line, southern boundary between the Corn Belt and the eastern forest). Birds move toward the forest–agriculture boundaries as distance decreases in (a) spring migration and (b) autumn migration.

The fastest airspeed of birds in the northern forest during autumn migration suggests that other factors may also affect the overall airspeed of migrants. One such possibility could be variation in the directional dispersion of migrants across latitudes. If flights recorded by radar stations at lower latitudes contain migrants bound for more diverse destinations than further north, the average airspeed estimates could be biased low (Horton et al., 2016). Our sensitivity analysis based on the residual variation from the sine model fit of radial velocity showed only weak evidence for higher variation in flight directions in the eastern forest than in the northern forest in autumn (Appendix S7f) but not when compared with the Corn Belt or in spring (Appendix S7e,f), suggesting overall similarity in directional dispersion across biomes. However, this index cannot fully resolve individual variation in flight directions when a radar pulse volume contains multiple birds. Hence, it does not entirely rule out the contribution of directional dispersion to the observed differences in airspeed.

Selection for tailwind support by adjusting migrating timing and flight height is considered a more energy-efficient way for birds to traverse barriers than increasing powered flight speed (Richardson, 1978; Schmaljohann et al., 2009). We found moderate to strong evidence that migrating birds select for better tailwind support when crossing the Corn Belt compared with the eastern forest in both seasons (Figure 2c,d). This remained a robust pattern in our sensitivity analyses, excluding waterfowl migration (Appendix S7c,d). Such preferences for tailwinds have been commonly reported for birds crossing the Gulf of Mexico (Deppe et al., 2015; Gauthreaux, 1971) and the Sahara Desert (Bruderer et al., 2018; Norevik et al., 2021; Schmaljohann et al., 2009). Doing so increases ground speed and reduces travel time, while minimizing energy costs to the bird (Schmaljohann et al., 2009). We computed only meridional tailwind selection in the north–south directions because given the orientation of both the Gulf of Mexico and the Corn Belt, the most time-efficient way to cross these barriers is to take advantage of the meridional wind support, regardless of potential drift caused by zonal wind. However, the increase in tailwind selection with latitude in the eastern forest in spring (Appendix S5c) suggests that other geographic factors might also affect birds' selection for tailwind, at least in that biome.

Contrary to our predictions, however, there was little or no evidence for lower seasonal SPR in the Corn Belt compared with other biomes. Instead, the SPR showed substantial within-group variation in each biome (Figure 3). Part of the variation is driven by distance to the barrier and land-cover features, as discussed in the section below.

Comparing the Corn Belt with the natural barrier at the Gulf of Mexico

Despite the absence of radar stations in the open ocean, the impacts of the Gulf of Mexico on bird migration can be detected by stopover patterns before and after crossing this barrier. In spring, the sharp decrease in SPR for birds migrating farther inland from the immediate vicinity of the Gulf Coast (Figure 4a) suggested that many migrants need to rest and refuel immediately after flying nonstop for >1000 km across the Gulf of Mexico (Deppe et al., 2015). In autumn, the concentration of migrants at the shoreline was weaker, but our data still showed increasing SPR as migrants moved closer to the coastline from inland habitats (Figure 4b). The stronger concentration effects at the Gulf of Mexico in spring than in autumn have been noted in previous studies (Buler & Moore, 2011; Cohen et al., 2021; Guo et al., 2024), suggesting that birds are more likely to fall out and concentrate after crossing the barrier than before crossing it.

Comparatively, the Corn Belt appeared to be a weaker migration barrier than the Gulf of Mexico because we found no evidence of decreasing SPRs after birds crossed the Corn Belt (Appendix S10). However, in the Corn Belt, the SPRs increased as birds approached the down-route boundary (Figure 5a,b). This suggested a tendency of birds flying over this largely inhospitable landscape to stop due to ecological or physiological constraints after crossing significant stretches of it.

The weaker barrier effect in the Corn Belt compared with the Gulf of Mexico could be due in part to the narrower width (<800 km) of the Corn Belt compared with the gulf (>1000 km). Many birds may be able to continue flying north (spring) or south (autumn) after crossing the Corn Belt, leading to less distinct patterns of SPR changes. The higher-than-expected SPR in the Corn Belt could also be attributed to the inclusion of migratory shorebirds and grassland species in the radar data, groups of birds that make frequent use of agricultural fields during stopover (Stodola et al., 2014; Wilcoxen et al., 2018). Furthermore, even forest-dwelling landbirds that do not forage in agricultural fields can still make stopovers to rest, recover, and avoid adverse weather conditions, similar to birds stopping during the day while crossing the Sahara Desert (Bairlein, 1988; Biebach et al., 2000; Schmaljohann et al., 2007b). Unlike the situation in the Sahara Desert, however, the widely dispersed forest fragments in the Corn Belt likely act as important rest-and-refueling stepping stones for birds unable to complete the journey via continuous flight (Guo et al., 2023, 2024; Liu & Swanson, 2014a, 2014b). The positive correlation between deciduous forest cover and SPR in the Corn Belt also suggests that in this agricultural landscape, birds that cannot cross it in a single, nonstop flight are likely to stop in sites with more deciduous forest cover, highlighting the importance of deciduous forest to landbird migration (Guo et al., 2023, 2024).

Conservation implications and future directions

Most cropland and pasture expansion in the Midwest occurred during 1850–1920, but the growing demand for biofuel and bulk grain in the 2000s has led to additional cropland expansion (Li et al., 2023), which may have led to the intensification of the challenges faced by migratory landbirds while crossing the Corn Belt. Similarly, despite being a natural barrier, the coastal landscape along the Gulf of Mexico has experienced expanded human population growth and urban sprawl (Li et al., 2023), which have led to a diminishment of the sparse coastal woodlots and shrublands that are used by migrating birds, creating a potentially wider barrier for migrants to cross. For instance, Zenzal et al. (2021) reported that 75% of radio-tagged individual landbirds retreated inland or detoured before crossing the Gulf of Mexico in autumn migration, likely due to the lack of good-quality habitats for rest and refueling close to the coastline. It remains unknown what the fitness costs of these additional travel distances associated with crossing the gulf may be. Nonetheless, continuing coastal development (Homer et al., 2020) could pose further difficulties for birds that migrate across the Gulf of Mexico. Guo et al. (2024) highlighted that most stopover hotspots along the Gulf Coast are unprotected or have low protection status. Hence, we see a need for greater conservation efforts to protect the coastal habitats that birds use to rest and refuel, especially after the nonstop flight across the Gulf of Mexico.

The Corn Belt appears to be a weaker migration barrier than the Gulf of Mexico, likely due to its narrower extent, the types of bird species crossing it, and the availability of forested stopover sites in the Corn Belt. However, Guo et al. (2024) also showed that most stopover sites in the Midwest are unprotected and therefore may be vulnerable to land-use changes. More conservation attention is needed to ensure that the remaining forest patches continue to provide rest and refueling sites for migrants negotiating the Corn Belt. The comparatively lower agricultural yield of some farmland in the Midwest (Basso et al., 2019) provides opportunities for habitat restoration initiatives to create more stopover sites in the Corn Belt with minimal impacts on crop output.

The primary limitation of our correlative study is that the spatial difference in airspeed and tailwind selection across avifaunal biomes could be associated with broad geographical patterns independent from land use. Analyses of long-term data will enable more direct assessments of changes in migration behavior in response to land-use changes. Furthermore, the limited radar coverage in the northern forest constrained our ability to assess birds' flight and stopover behaviors in this biome. More field studies at the edge of and farther inside the northern forest would improve understanding of how birds negotiate the Corn Belt. Moreover, we used only radar data from the United States with limited coverage north of the Great Lakes region. Additional radar data from Canada could provide a more holistic assessment of the barrier effects of the Midwest Corn Belt and the Great Lakes on landbird migration in North America.

The main drawback of using radar to track migration is the inability to identify bird species, which poses 2 additional limitations to our study. The first limitation is that the flight and stopover patterns could perhaps be partially attributed to species assemblages of different body sizes and migratory behaviors moving across radar domains and avifauna biomes (e.g., a potentially higher proportion of large, fast-flying birds crossing the Corn Belt than the eastern forest biome). However, given that most eastern North American landbird species are recorded throughout the eastern United States during migration (La Sorte et al., 2014; Lin et al., 2020; Schuster et al., 2019), there is unlikely to be strong taxonomic bias toward certain landbird species in a given area. We accounted for potential waterfowl contamination in our data through a sensitivity analysis that excluded peak waterfowl migration time windows. Moreover, the much smaller total population of shorebirds moving through eastern North America than landbirds (Rosenberg et al., 2019) would suggest that landbirds dominate the radar signals. Hence, the patterns we saw are more likely to reflect population-level behavioral adaptations of migrating landbirds to different landscapes. The second limitation is that different bird species might have different strategies for crossing a given barrier (Deppe et al., 2015), which would not be discernable based on the aggregated radar patterns. Our results on SPR changes in the Corn Belt suggest 2 migration strategies: nonstop flights across the Corn Belt (nonstop migratory strategy) and intermittent flights with stopovers in areas with more forest cover in the Corn Belt (intermittent migratory strategy). We recommend more field studies to assess how different bird species adjust their behaviors to negotiate the Corn Belt.

Furthermore, whether crossing the Corn Belt poses direct fitness consequences remains to be tested, especially given the birds' selection of favorable winds that should assist with migration. Besides, the heterogeneity in land cover and spatial extent of the Corn Belt also suggests that the challenges and impacts of barrier crossing might vary by location. For instance, crossing the eastern side of the Corn Belt (~500 km) would be easier than the western side (~800 km). We encourage more physiology studies comparing the body conditions of birds before, during, and after crossing the Corn Belt to better assess its impacts on migrants.

We found evidence supporting the hypothesis that the Corn Belt acts as an anthropogenic migration barrier for many landbirds. When crossing it, birds fly faster and select for better tailwind support, and their SPR increases as they approach the finish line (i.e., the down-route boundary between the Corn Belt and continuous forests). However, the Corn Belt appeared to be a weaker barrier than the natural barrier at the Gulf of Mexico, likely due to the Corn Belt's narrower width, the possibility of landing, the subset of species affected, and the availability of isolated patches of forest that serve as stopover sites. Given the millions of migratory birds crossing the 2 barriers every year, we believe it is important to protect and create food-rich and safe stopover sites in the Corn Belt and along the Gulf Coast to help landbirds successfully negotiate both barriers.

ACKNOWLEDGMENTS

This project was funded by the High Meadows Foundation (to D.S.W). F.G. was supported by the Cornell Atkinson Center for Sustainability. J.J.B. and J.A.S. were supported by USDA NIFA Hatch (DEL-00774). E.B.C. was supported by the NSF (DEB-2146052). We thank the Princeton Research Computing Center for access to high-performance computing clusters. We also thank H. Schmaljohann, T. Katzner, and 2 anonymous reviewers for their feedback on earlier versions of this manuscript.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Guo, F., Buler, J. J., Dokter, A. M., Horton, K. G., Cohen, E. B., Sheldon, D., Smolinsky, J. A., & Wilcove, D. S. (2025). Assessing the Corn Belt as an anthropogenic barrier to migrating landbirds in the United States. *Conservation Biology*, e70070. https://doi.org/10.1111/cobi.70070