ORIGINAL ARTICLE

The role of atmospheric conditions in the seasonal dynamics of North American migration flyways

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ABSTRACT

Aim Avian migration strategies balance the costs and benefits of annual movements between breeding and wintering grounds. If similar constraints affect a large numbers of species, geographical concentrations of migration routes, or migration flyways, may result. Here we provide the first population-level empirical evaluation of the structure and seasonal dynamics of migration flyways for North American terrestrial birds and their association with atmospheric conditions.

Location Contiguous USA.

Methods We modelled weekly probability of occurrence for 93 migratory species using spatio-temporal exploratory models and eBird occurrence data for the combined period 2004 to 2011. We used hierarchical cluster analysis to identify species with shared migration routes based on normalized spatio-temporal representations of autumn migration. We summarized atmospheric conditions within flyways using nocturnal wind velocity and bearing estimated at three isobaric levels (725, 825 and 925 mbar) for the combined period 2008 to 2011.

Results We identified three migration flyways: an eastern and western flyway whose paths shifted westwards in the spring, and a central flyway whose core boundaries overlapped with the eastern flyway and whose width was more constricted in the autumn. The seasonal shift of the eastern flyway created potentially longer migration journeys in the spring, but this longer route coincides with a low-level jet stream that may enhance migration speeds. Atmospheric conditions appeared to have a more limited role in the seasonal dynamics of the western flyway.

Main conclusions Migration routes for terrestrial species in North America can be organized into three broadly defined migration flyways: a geographically distinct flyway located west of the 103rd meridian and two interrelated flyways located east of the 103rd meridian. Seasonal shifts in flyway locations reflect the influence of looped migration strategies that for the eastern flyway can be explained by the trade-off between minimizing total migration distance while maintaining an association with favourable atmospheric conditions.

Keywords
Citizen science, conservation biogeography, eBird, looped migration, low-level jet stream, migration flyway, North America, seasonal bird migration, wind bearing, wind velocity.

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INTRODUCTION

Evolution has shaped avian migration into a diverse set of strategies that balance the costs and benefits of annual movements between breeding and wintering grounds (Cox, 1985; Pulido, 2007) based on the increased mortality risk of migration (Sillett & Holmes, 2002) and the greater reproductive output on the breeding grounds (Sibly *et al.*, 2012). If similar constraints affect a large numbers of species, geographical concentration of migration routes, or migration flyways, may result. Representations of migration flyways have been used to delineate conservation and management agendas (e.g. USFWS, National Audubon Society) and to structure scientific inferences in biogeographical research, e.g. the ecology and evolution of avian disease (Pearce *et al.*, 2009; Lam *et al.*, 2012) or migration strategies (Williams *et al.*, 2007; Arzel *et al.*, 2009; Piersma, 2011), the determinants of geographical patterns of species richness (Henningsson & Alerstam, 2005), and assessments that consider the implications for migratory species of management practices (Klaassen *et al.*, 2008) or global change (Van Eerden *et al.*, 2005). Within North America, we have historical and qualitative accounts of autumn migration flyways for aquatic birds (Lincoln, 1935), most of which are aggregate, diurnal migrants. For terrestrial birds, which primarily migrate at night, we have historical and qualitative accounts of the location of migration routes as species exit the contiguous USA in the autumn (Cooke, 1915). However, we currently lack knowledge of the migration flyways of terrestrial species in North America. Consequently, the autumn flyways described for aquatic birds (Lincoln, 1935) are currently applied across all species for both spring and autumn migration. Given the current threats faced by North American migratory species and the many gaps in our understanding of their migratory systems (Faaborg *et al.*, 2010), there is critical need for more rigorous empirical estimates of the structure, seasonal dynamics, and determinants of migration flyways.

There is indirect evidence that migration flyways for terrestrial birds in North America are defined by two or possibly three flyways. Breeding distributions of North American birds are geographically separated by the Great Plains in the middle of the continent (Mengel, 1968; Swenson & Howard, 2005), suggesting the presence of two spatially broad flyways. This biogeographical pattern arose through the geographical isolation and differentiation that occurred during the Pleistocene glaciations (Mengel, 1968; Swenson & Howard, 2005; Soltis *et al.*, 2006; Swenson, 2006) in association with the post-glacial evolution of migratory behaviour (Milá *et al.*, 2006). A limited number of species also migrate through the Great Plains itself (Mengel, 1968; La Sorte *et al.*, 2013), suggesting the existence of an additional flyway. However, there have been no direct empirical evaluations of these predictions.

Within migration flyways, individual species do not necessarily follow the same routes during spring and autumn migration. These 'looped migrations' have been identified for many species at the individual level (e.g. Phillips, 1975;

Klaassen *et al.*, 2010; Delmore *et al.*, 2012; Tøttrup *et al.*, 2012; Mellone *et al.*, 2013; Willemoes *et al.*, 2014) and for North American birds at the population level (La Sorte *et al.*, 2013), and are thought to reflect strategies that maximize migration speed by adjusting to seasonally varying atmospheric conditions and stopover habitat quality or availability (Erni *et al.*, 2005; Gauthreaux *et al.*, 2005; Tøttrup *et al.*, 2012; Mellone *et al.*, 2013). Flight speed, for example, can be substantially improved by favourable wind conditions, which in some cases might be of greater relevance than the quantity of energy reserves acquired during stopover (Liechti & Bruderer, 1998). Whereas loop migrations have been described for individual species, loop migration as a general strategy of an entire assemblage of species in a flyway has not been documented.

One leading hypothesis for the choice of migratory routes is that they coincide with seasonal atmospheric currents (Landsberg, 1948) and, in some cases, low-level jet streams (Liechti & Schaller, 1999). For North American migrants, a nocturnal southerly low-level jet stream develops in the spring over the western portion of the Gulf of Mexico and extends north into the Great Plains with a jet maximum occurring between *c.* 600 to 800 m above ground level (AGL) (Bonner, 1968). The Great Plains low-level jet has the potential to facilitate nocturnal trans- and circum-Gulf migration in the spring (Lowery, 1951; Gauthreaux, 1971; Able, 1972; Moore & Kerlinger, 1987).

Here, we use weekly estimates of species' probabilities of occurrence derived from spatio-temporal exploratory models (STEM; Fink *et al.*, 2010) and occurrence information from the eBird citizen-science database (Sullivan *et al.*, 2014) for the combined period 2004 to 2011 to test for the presence of geographically distinct migration flyways within the contiguous USA. Once identified, we then test for a favourable spatial congruence between the seasonal location of the migration flyways and seasonal atmospheric conditions. Because of the nature of the eBird database, we conduct these tests at the population-level where we estimate geographical patterns of migration based on summaries that integrate observations across individuals within an entire migratory population (La Sorte *et al.*, 2013). Specifically, we first estimate the location of migration flyways within the contiguous USA using weekly population-level estimates of species' probabilities of occurrence for the combined period 2004 to 2011. We then summarize within each flyway the geographical associations with high-altitude nocturnal winds (velocity and bearing) estimated at three isobaric levels (725, 825 and 925 mbar) for the combined period 2008 to 2011. Finally, we contrast these observed seasonal associations with expected associations given no geographical shift in flyway location. We predict that the geographical locations of migration flyways will change seasonally to coincide with seasonal changes in atmospheric conditions, which in total should enhance migration speeds for migratory populations through improved tailwind support and reduced headwind resistance.

MATERIALS AND METHODS

Data compilation and preparation

We compiled avian occurrences within the contiguous USA for a total of 447 species from the eBird database (Sullivan *et al.*, 2014). We modelled weekly probabilities of occurrence for each species using spatio-temporal exploratory models (STEM; Fink *et al.*, 2010). In STEM, we used complete eBird checklists that were collected under the 'travelling count' and 'stationary count' protocols from 1 January 2004 to 31 December 2011. We restricted data to those with transect distances ≤ 8.1 km, start times to daylight hours between 05:00 and 08:00 h, and the total search times to < 3 hours. STEM uses a multi-scale strategy to differentiate between local and global-scale spatio-temporal structure, which is achieved by creating a randomized ensemble of overlapping local models, each applied across a restricted geographical and temporal extent (Fink *et al.*, 2010). STEM learns the associations between observed patterns of bird occurrence (eBird data) and local land-cover characteristics (Fry *et al.*, 2011). These models are then used to make estimates of each species' distribution throughout the year based on local land-cover characteristics. For each species, a separate model was fitted and species' probabilities of occurrence, corrected for variation in detection rates, were estimated across the contiguous USA with one daily estimate calculated per week for all 52 weeks of a calendar year. STEM estimates of probability of occurrence were rendered at 130,751 geographically stratified random (SRD) points distributed at a density of about one per 30 km × 30 km within the contiguous USA.

Spatio-temporal migration summary

Using the same procedure described in La Sorte *et al.* (2013), we identified the first week of spring migration and the last week of autumn migration for each species using patterns of change in the weekly frequencies of SRD points with probabilities of occurrence > 0. The median week between these two dates was used to identify the middle of the breeding season. Spring and autumn migration occurs over several weeks and population-level migration speeds in the spring tend to be faster than those in the autumn (La Sorte *et al.*, 2013). However, the duration of spring and autumn migration are considerably shorter than the length of the breeding season; thus each migration event is fully represented in relation to the median date. For each week, we converted STEM probabilities of occurrence to binary presence/absence maps based on the 80% quantile of the distribution of probabilities of occurrence > 0. In order to differentiate between predicted presence and absence at all locations, probabilities of occurrence at SRD points that were greater than the 80% quantile had their probabilities set to one; all remaining probabilities were set to zero. If the 80% quantile was < 0.0175, our minimum probability threshold, the threshold was set to 0.0175. These thresholds were

selected because they removed SRD points with extremely low probabilities of occurrence, provided spatial representations of probabilities of occurrence that did not over- or under-represent species' occurrences for each week, and did this in a consistent fashion across species.

We normalized weeks for the combination of weekly binary presence/absence maps for each species and migration season to the range [0, 1] so that the starts and ends of each season could be compared across all species based on a standard spatio-temporal representation of the full migration event. This procedure resulted in two seasonal migration maps for each species, hereafter termed 'normalized migration maps' (NMMs; see Fig. S1 in Appendix S1 in Supporting Information). For spring migration, this procedure resulted in a map with values ranging from one, the first week of spring migration, to zero, the middle of the breeding season. For autumn migration, this procedure resulted in a map with values ranging from zero, the middle of the breeding season, to one, the last week of autumn migration. This approach generated a consistent spatio-temporal summary of spring and autumn migration events, with greater weight (values approaching one) given to weeks when populations were more likely to be in full migration.

From the 447 species, we selected 93 diurnal terrestrial species for analysis based on several criteria (see Appendix S2 for details). Based on visual inspections of species' frequency of occurrence plots and NMMs, we selected species with: (1) clearly defined beginning of spring and end of autumn migration; (2) NMMs contained geographically continuous weekly representations of migration movements for both seasons (Fig. S1); (3) the northern limit of each species' distribution during the breeding season extending at least halfway into the study area (*c.* 40° N latitude); and (4) complete or nearly complete departure from the study area during the non-breeding season.

Hierarchical cluster analysis

We applied hierarchical cluster analysis to the NMMs to identify flyway clusters: groups of species that shared geographically similar migration routes. To allow for comparisons between seasons and to replicate past North American assessments that only examined autumn migration (Cooke, 1915; Lincoln, 1935), we used the hierarchical cluster analysis to identify autumn flyway clusters of species. Our procedure involved first converting each species' autumn NMMs to a vector of length 130,751 (i.e. the total number of 30 km × 30 km SRD points in the study area), which contained values in the range [0, 1]. We then calculated the Euclidean distance between all unique pairwise combinations of vectors. A hierarchical cluster analysis was then applied to the resulting distance matrix using the unweighted pair-group method with arithmetic averages (UPGMA).

We summarized the results from the hierarchical cluster analysis using two procedures. First, we estimated nodal support using multiscale bootstrap resampling (Shimodaira,

2002, 2004). The bootstrap procedure used 10,000 bootstrap samples with 1000 applied to each of 10 scaling constants (Shimodaira, 2002, 2004). We reported both the approximately unbiased *P*-values and the bootstrap probability *P*-values. Second, we applied an adaptive branch pruning technique to identify the prominent flyway clusters in each of the 10,000 bootstrap dendrograms (Langfelder *et al.*, 2008). This technique represents a more flexible alternative to the constant or static height approach by detecting clusters based on the structure of the branches within the dendrogram. We used the 'Dynamic Hybrid' method with a minimum cluster size of 10 species and the deepSplit option set to zero. To extract the most prominent flyway clusters from 10,000 dendrograms, we first determined the frequency among the dendrograms of each division between clusters. We then determined the frequency of clusters that occurred as either whole units or contained smaller subunits that were not identified outside the cluster. This approach allowed us to identify which clusters of species occurred most frequently among the 10,000 dendrograms, which we then identified as flyway clusters.

We summarized the geographical location of each autumn flyway cluster by averaging the NMMs for species in each cluster. We similarly identified the location of the spring flyways by averaging the spring NMMs for species identified in each autumn flyway cluster. The difference between the average autumn NMM and average spring NMM was used to estimate how the locations of flyways changed between seasons.

For our analysis relating seasonal flyway location to seasonal atmospheric conditions, we identified the seasonal geographical core region of each flyway, which we define as the geographical region where species in each flyway were more likely to be in full migration. This was implemented by first removing all SRD points from the average seasonal NMMs whose values were below that NMM's 95% quantile. The core regions therefore represent the top 5% of the NMMs with values approaching one. We applied alpha convex hulls with an alpha parameter of 10 to delineate the boundary of the seasonal flyway core regions (Edelsbrunner *et al.*, 1983). The two seasonal core regions for each flyway were then divided into three core components based on their geographical intersection. The first component contained the spring core region alone, the second component the autumn core region alone, and the third component the region where the spring and autumn core regions overlapped or intersected.

To summarize the locations of species' breeding and winter ranges and the shortest geographical route between the two regions, we used NatureServe Western Hemisphere range maps (Ridgely *et al.*, 2007). Breeding and winter range map polygons were first converted to 12,452-km^2 hexagons using an equal-area icosahedron (Sahr *et al.*, 2003). Centroids were then calculated for breeding and winter ranges by averaging the latitude and longitude of the hexagon centres located in each range, and the shortest route was estimated using the great-circle or orthodromic distance between the centroids.

Atmospheric conditions

Because the majority of terrestrial migratory birds in North America are nocturnal migrants, we summarized nocturnal atmospheric conditions (wind velocity and bearing of origin summarized from sunset to sunrise) within the three flyway core components (spring alone, autumn alone, and their intersection) using average nocturnal upper-level winds at three isobaric levels (725, 825 and 925 mbar) over a 4-year period (2008 to 2011). The three isobaric levels represent altitudes of *c.* 2734, 1700 and 762 m above ground level (AGL), respectively. We chose the 925 mbar isobaric level because, based on estimates from a variety of regions, the median altitude of nocturnal migrating birds is *c.* 800 m AGL (Bruderer *et al.*, 1995; Klaassen & Biebach, 2000; Zehnder *et al.*, 2001; Dokter *et al.*, 2011; Kemp *et al.*, 2013). Based on estimates from within our study area, the median altitude of trans-Gulf migrants as they arrive on the northern coast of the Gulf of Mexico in the spring (Gauthreaux, 1971) and as they depart New England in the autumn is *c.* 800 m AGL with a maximum of *c.* 3000 m AGL (Williams & Williams, 1978). We included the 725 and 825 mbar isobaric levels to account for higher altitude migrants and to more fully represent atmospheric conditions within the higher elevation regions of western North America (see Fig. S2 in Appendix S1).

For our analysis of atmospheric conditions we used gridded atmospheric data from the North American Regional Reanalysis (NARR; dataset number ds608.0) stored at the Research Data Archive, which is maintained by the Computational and Information Systems Laboratory at the National Center for Atmospheric Research. Ten gridded NARR 3-hourly datasets were used to generate nocturnal wind averages. This included east–west and north–south wind components for each of the three isobaric levels, the geopotential height for each isobaric level, and the geopotential height of the ground surface. The 10 NARR source data layers are spatially organized using the National Centers for Environmental Prediction Grid 221 (Regional North American Grid – Lambert Conformal) grid arrangement (*c.* 32 km resolution). An 11th dataset, sunrise–sunset times for each day of the year, was generated for each grid cell in the Grid 221 inventory. The analysis consisted of converting the 3-hourly east–west and north–south wind components for each grid cell at each isobaric level to a composite nocturnal wind velocity and bearing of origin for which the isobaric geopotential height of the grid cell was less than its surface geopotential height. This procedure removed data that was below ground level (Fig. S2).

To assess how nocturnal winds changed seasonally within each flyway, we extracted the gridded wind velocities and bearings for each night from 2008 to 2011 that were contained within the three core components of each flyway. These values were then averaged across grid cells within each core component for each night. Wind speed was log$_{10}$ transformed before averaging. Average wind bearing was calculated using the circular mean. We used generalized additive mixed

models (GAMMs) with year as random effect (Wood, 2006) to examine annual trends in average nocturnal wind velocity and bearing within each flyway core component. Specifically, GAMM was applied to the average gridded wind velocity and bearing values that only occurred in the spring component, values that only occurred in the autumn component, and values that occurred in their intersection. This approach allowed us to assess how wind speed and direction were defined in each flyway across the full annual cycle, thus providing the opportunity to assess conditions that would be encountered during spring migration if species used the autumn flyway, and conditions during autumn migration encountered if species used the spring flyway. Functionally, we were modelling the null expectation given no geographical seasonality in the location of the migration flyways. Evidence that changes in the geographical location of the flyways result in enhanced migration speeds through improved tailwind assistance and reduced headwind resistance would provide support for the alternative hypothesis that atmospheric conditions do determine locations of flyways.

We conducted all analysis using R, version 3.0.1 (R Core Team, 2014). Multiscale bootstrap resampling was conducted using the pvclust library and the adaptive branch pruning technique using the dynamicTreeCut library. The alpha convex hulls were calculated using the alphahull library. Daily sunrise and sunset values were estimated using the maptools library. Circular means were calculated using the circular library. GAMM was implemented using the gamm4 library.

RESULTS

Consistent with the prediction of three migration flyways, three groups of species were identified in our cluster analysis whose flyways we term Eastern ($n = 45$ species), Central ($n = 17$), and Western ($n = 31$; Fig. 1, and Fig. S3 in Appendix S1). The Western flyway received full support as a distinct entity in our analysis whereas the Eastern and Central flyways were less well differentiated, occurring either in combination or containing sub-clusters (Fig. 1). More specifically, across iterations of our cluster analysis, the Western flyway was identified in 100% of the clusters (Fig. 1). The Central flyway was identified as one cluster (70%) or in combination with the Eastern flyway (30%; Fig. 1). The Eastern flyway was identified as one cluster (23%), in combination with the Central flyway (30%), or as contained two sub-clusters (47%; Fig. 1). Thus, the Western flyway was the most strongly supported as an independent flyway in our analysis, followed by the Central and the Eastern flyways that presented evidence for shared characteristics as well as evidence for additional spatio-temporal structure.

To estimate the autumn and spring locations of the flyways, we averaged their autumn (Fig. 2a,d,g) and spring NMMs (Fig. 2b,e,h) and calculated their difference (Fig. 2c,f,i). For the Eastern flyway, this analysis indicated that migration was circum-Gulf (of Mexico) to trans-Gulf in the spring,

and trans-Gulf to trans-Atlantic to the Caribbean and South America in the autumn (Fig. 2c). For the Central flyway, migration was geographically more extensive in the spring but became more concentrated within the middle of the continent in the autumn (Fig. 2f). Lastly, for the Western flyway, migration was strongest along the Pacific coast in the spring and strongest within the Intermountain West in the autumn (Fig. 2i).

To assess the potential role of atmospheric conditions in flyway seasonal dynamics, we examined nocturnal wind velocity and bearing of origin at three altitudes within the intersection of the core regions of each flyway's two seasonal locations estimated using the average NMMs (Fig. 3). The intersection of the core regions mirrored the difference observed between the spring and autumn average NMMs (Fig. 2c,f,i). A primary spatial demarcation between the core areas, where there is minimal overlap, occurs between the Western and Central flyways at roughly 103° W longitude (Fig. 3).

Across altitudes, nocturnal winds originated on average from the south to west with limited seasonal differences within each flyway. Thus, based on the seasonal location of each flyway, migratory birds primarily encountered tailwind support in the spring and headwind resistance in the autumn (Fig. 4). The one exception was the Western flyway for 762 m AGL; however, very little terrestrial surface located within the Western flyway occurs at or below this elevation (Fig. S2).

When considering nocturnal wind velocities, winds tended to be faster on average during spring migration and slower during autumn migration at 762 m AGL for the Eastern and Central flyways (Fig. 5). These differences were especially pronounced for the Eastern flyway, and were evident across all three altitudes. Thus, in agreement with our expectations, the seasonality of the Eastern flyway resulted in stronger tailwind support in the spring and weaker headwind resistance in the autumn (Fig. 5). However, contrary to our expectations, autumn nocturnal wind velocities tended to be faster on average across the three altitudes within the Western flyway, suggesting that species in the Western flyway encountered weaker tailwind support in the spring and stronger headwind resistance in the autumn (Fig. 5).

DISCUSSION

Our results provide population-level evidence that migration routes for terrestrial species in North America can be organized into three broadly defined migration flyways. The Western flyway, occurring west of the 103rd meridian, emerged as the most distinct flyway in our analysis. In contrast, the Central and Eastern flyways were not as well differentiated, indicating that species migrating east of the 103rd meridian are not as consistent as their western counterparts, and migrate within two interrelated components of a larger migration system.

Our analysis showed that the geographical locations of all three migration flyways varied between migration seasons.
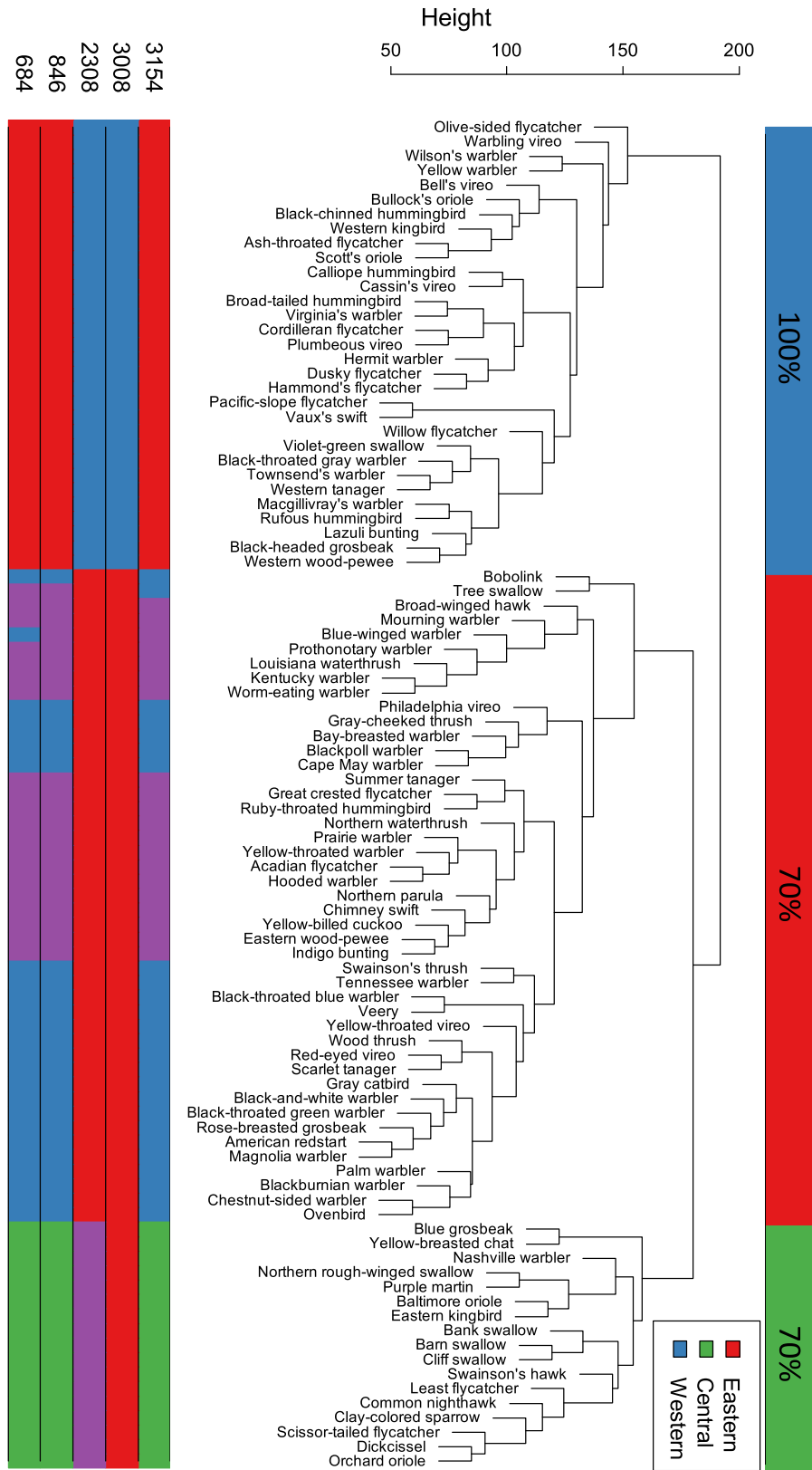
Figure 1 Dendrogram from hierarchical cluster analysis of normalized autumn migration maps for 93 species of North American terrestrial birds (see Appendix S2 for scientific names) with the results of an adaptive branch pruning procedure. The colour bars below the dendrogram show the five unique cluster of species (colours within each colour bar) identified in the adaptive branch pruning procedure and the number of times they occurred within the 10,000 bootstrap samples. The colour bar above the dendrogram show the three most supported clusters and the percentage of samples where the clusters occurred in part or in whole. See Materials and Methods for additional details.
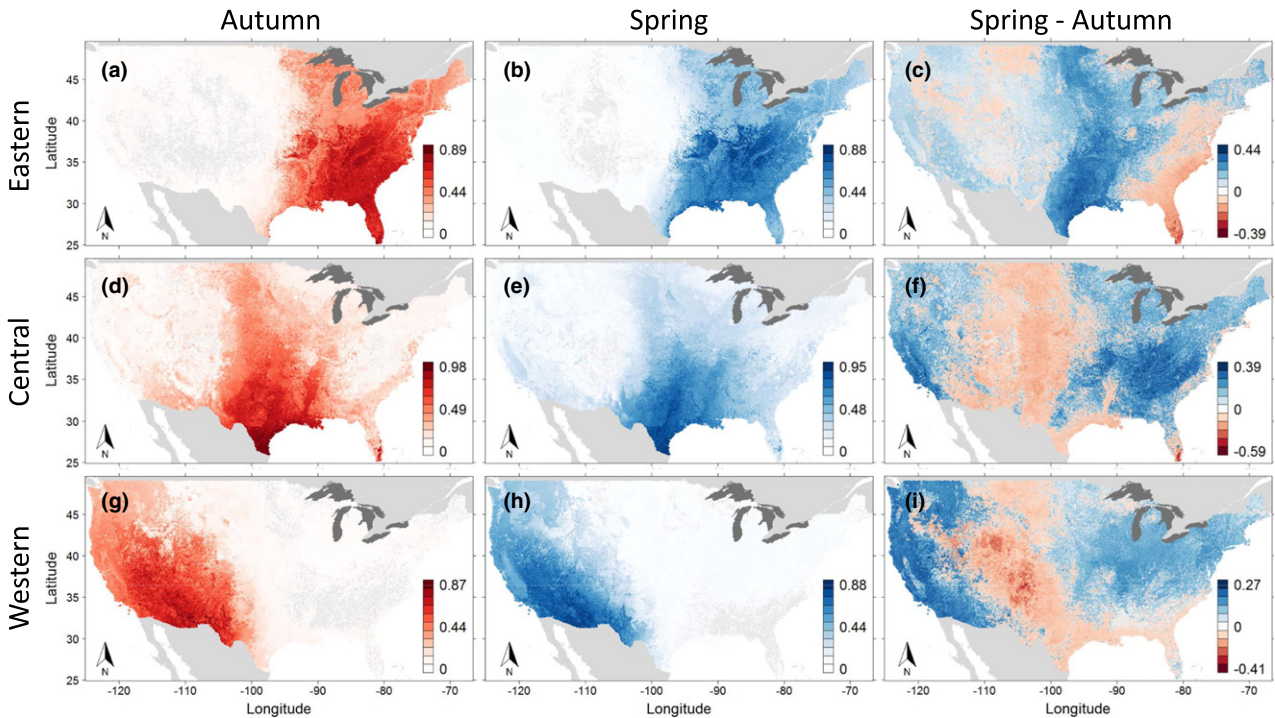
Figure 2 Average normalized migration maps (NMMs) for North American terrestrial bird species identified in the Eastern, Central and Western migration flyways (*n* = 45, 17 and 31 species, respectively) during autumn migration (a, d, g), the same groups of species during spring migration (b, e, h), and the difference between the two (c, f, i). The brighter the colour, the greater the likelihood species are in migration during (red) autumn migration or (blue) spring migration. NMMs are scaled to the range [0, 1], representing an increasing likelihood the species is in migration.

Thus, the often implicit assumption that migration flyways have the same geographical locations during spring and autumn migration is not tenable. Seasonality was most pronounced for the Western and Eastern flyways, which showed substantial west-to-east shifts between spring and autumn. These patterns likely reflect the influence of shared looped migration strategies, which were previously noted for this system (La Sorte *et al.*, 2013), supporting the conclusion that shared looped migration strategies can be detected in the seasonal locations of some migration flyways.

Seasonality in the location of the Eastern flyway and to a lesser extent of the Central flyway probably reflects the influence of the Great Plains low-level jet stream (Fig. S2). The seasonal shift in the location of the Eastern flyway appears to represent a trade-off between migration distance and maintaining a geographical association with the low-level jet stream. When examining the location of breeding and wintering grounds and the shortest geographical distance between the two (see Fig. S4 in Appendix S1), the location of the spring migration flyway is associated with longer

Figure 3 Flyway geographical core components for spring (S) and autumn (A) migration of North American terrestrial bird species. Red polygons are the Eastern flyway (*n* = 45 species), green the Central flyway (*n* = 17), and blue the Western flyway (*n* = 31). The core components are the top 5% of the average normalized migration maps based on the 95% quantile, with values approaching one indicating a greater likelihood species in the flyways are in migration (see Fig. 2). Alpha convex hulls were used to delineate the boundaries of each core region (see Materials and Methods for details).
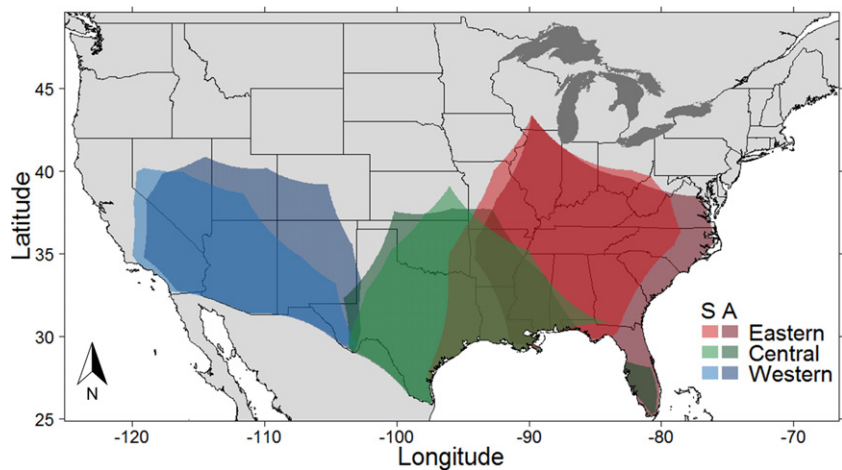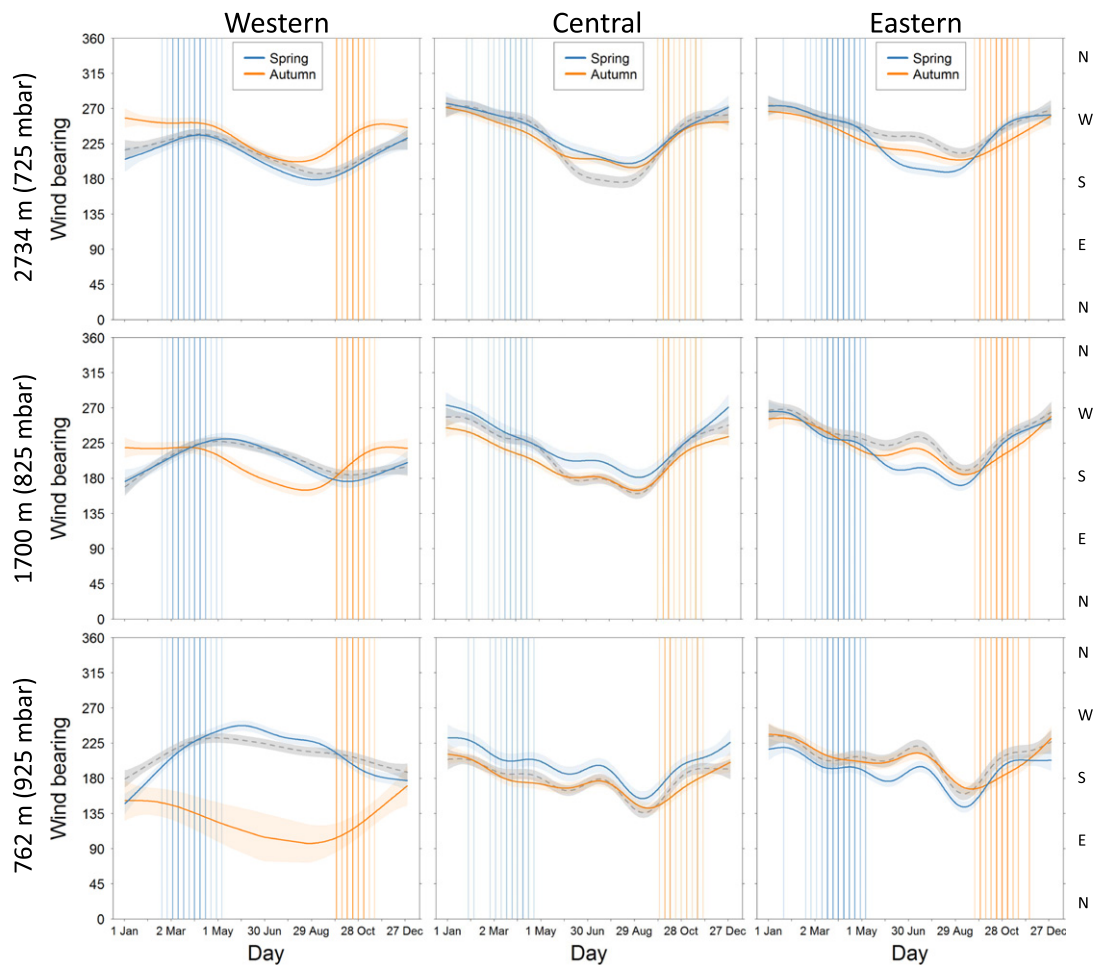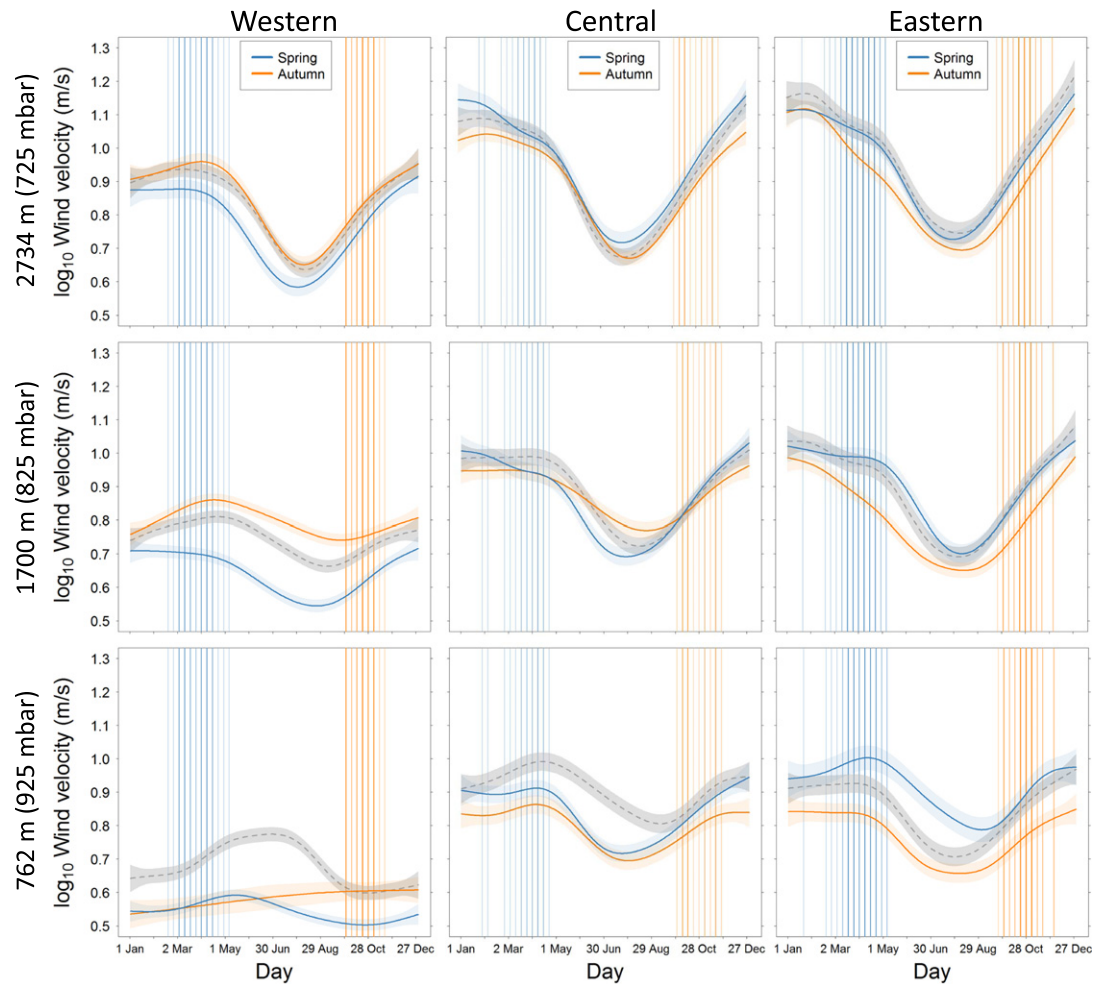
Figure 4 Annual trends in nocturnal wind bearing at three altitudes summarized within three geographical core components of three migration flyways (columns) of North American terrestrial bird species over a 4-year period (2008–11): Eastern flyway (n = 45 species), Central flyway (n = 17), and Western flyway (n = 31). The components included (solid blue) spring, (solid orange) autumn, and (dashed grey) their intersection, and each is fitted using generalized additive mixed models with year as a random effect. The 95% confidence bands are included with each fit. Vertical lines are the first week of spring migration (blue) and last week of autumn migration (orange) estimated for species in each flyway.

migration journeys but, as our findings indicate, also with more favourable tailwinds. The location of the autumn migration flyway, in contrast, is associated with shorter migration journeys but with headwinds that are weaker than would occur if species returned along the spring flyway. In addition, the headwinds in the autumn are mitigated by the occasional passage of cold fronts with north-westerly tailwinds (Able, 1973); an association we were not able to detect in our population-level assessment. A related factor is the use by some species during autumn migration of trans-Atlantic migration routes. The trans-Atlantic strategy has been well documented (Williams & Williams, 1978) and is identified in our findings based on the strong presence along the Atlantic coastline of the Eastern flyway in the autumn (Fig. 3, Fig. S1b). The trans-Atlantic strategy represents shorter migration journeys to wintering grounds in South America (Fig. S4) and our findings reinforce the importance of this strategy for some species in the Eastern flyway.

The Central flyway shared many features with the Eastern flyway but contained seasonal dynamics that spanned a large portion of the continent and occurred primarily outside the core region, whose location changed little from spring to autumn migration. These dynamics likely reflect the combined influence of species whose migration routes are strongly focused on the centre of the continent with little seasonal variation (Fig. S1c) and species whose migration routes are not as centralized and contain greater seasonal variation (Fig. S1d).

The lack of evidence for an atmospheric explanation for the seasonal dynamics in the Western flyway suggests that alternative, non-climatic factors may be more relevant. Relative to the Central and Eastern flyway, the Western flyway is located within the portion of the continent containing the highest elevations and greatest topographic and environmental heterogeneity (Fig. S2). In addition, species in the Western flyway winter primarily in Mexico and Central America,

Figure 5 Annual trends in nocturnal wind velocity at three altitudes summarized within three geographical core components of three migration flyways (columns) of North American terrestrial bird species over a 4-year period (2008–11); Eastern flyway ($n = 45$ species), Central flyway ($n = 17$), and Western flyway ($n = 31$). The components included (solid blue) spring, (solid orange) autumn, and (dashed grey) their intersection, and each is fitted using generalized additive mixed models with year as a random effect. The 95% confidence bands are included with each fit. Vertical lines are the first week of spring migration (blue) and last week of autumn migration (orange) estimated for species in each flyway.

whereas species in the Central and Eastern flyways winter primarily in the Caribbean, Central and South America (Fig. S4) (Mengel, 1968; Hutto, 1985a; Kelly & Hutto, 2005). Thus, migratory journeys tend to be shorter for species in the Western flyway and do not require navigating around or across large water bodies such as the Gulf of Mexico. These differences suggest that migrating species in the Western flyway are not likely to associate with high-altitude winds in a similar fashion as observed with species in the Eastern and Central flyways. For example, nocturnal migrants tend to avoid traversing high-altitude ridges (Liechti *et al.*, 1996) and migrating birds in the west have been observed using riparian and montane habitats during stopover (Carlisle *et al.*, 2004; DeLong *et al.*, 2005). In some cases, migrants have shown seasonality in their use of these stopover habitats, for example along elevational gradients (Austin, 1970; Blake, 1984), which in some cases has been correlated with

changes in insect density (Hutto, 1985b). A related factor is the timing of the flight feather moult. Moulting during autumn migration is more prevalent for species in the western flyway and is often associated with latitudinal or elevational movements to regions where food resources are more abundant in the late summer (Leu & Thompson, 2002; Rohwer *et al.*, 2005). Thus, seasonality in the natural environment along elevational or latitudinal environmental gradients may be more relevant in explaining the seasonal variation in the location of the Western flyway.

CONCLUSIONS

The concept of migration flyway was created to summarize the tremendous geographical variation that occurs across avian migration strategies, and have been used in structuring research and management for large numbers of migratory

species. Our findings provide the most rigorous and comprehensive evidence to date for the existence and locations of flyways used by terrestrial birds in North America. Here we generate the first empirically-based descriptions of spring and autumn migration flyways for terrestrial birds at the population level, and the first evaluation of the potential role that atmospheric conditions might have in their seasonal dynamics. Our findings provide a robust basis for population-level, full life-cycle conservation planning for migratory species, highlighting the value of citizen-science data in conservation biogeography (Devictor *et al.*, 2010). Large-scale conservation policies and goals for migratory birds can now be more appropriately informed through spatio-temporally detailed empirical observations, reducing the reliance on indirect, incomplete or anecdotal information. The development of this biogeographical perspective has particular significance for modeling efforts and mitigation strategies that consider the large-scale ecological implications of global climate change for migratory birds where all aspects of their geographically varied life cycles are likely to be impacted (La Sorte & Jetz, 2010). For example, current climate change projections suggest that the atmospheric conditions migratory species rely upon are likely to be altered, including the Great Plains low-level jet stream examined in this study, whose springtime wind velocities are projected to increase during this century (Cook *et al.*, 2008). Lastly, additional work is needed to provide more comprehensive estimates of migration strategies for both terrestrial and aquatic species in the Western Hemisphere. Work that can narrow the temporal and spatial concordance between atmospheric conditions and migration events at the population-level would be valuable. This would be particularly relevant for species whose migration strategies contain divergent sub-strategies that may occur within or among flyways (e.g. Delmore *et al.*, 2012). These efforts will improve our understanding of the ecology and evolution of migration strategies and will enhance the efficiency and effectiveness of current conservation efforts directed towards maintaining migratory bird populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting figures containing example spring and autumn normalized migration maps (Fig. S1), example nocturnal wind velocities and bearings (Fig. S2), dendrograms from the hierarchical cluster analysis (Fig. S3), and a summary of the geographical distributions of the 93 bird species considered in the analysis (Fig. S4).

Appendix S2 The 93 bird species considered in the analysis and their flyway designations.

BIOSKETCH

Frank A. La Sorte has research interests in the macroecology, biogeography and conservation of plants and birds within the context of global environmental change.

Author contributions: F.A.L. conceived of the study; F.A.L., D.F., W.M.H. and A.F. developed the methods; F.A.L. and D.F. conducted the analyses; F.A.L. wrote the first draft of the manuscript, and all authors contributed suggestions and text to subsequent drafts.

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