

Large birds travel farther in homogeneous environments

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Abstract

Aim: Animal movement is an important determinant of individual survival, population dynamics and ecosystem structure and function. Nonetheless, it is still unclear how local movements are related to resource availability and the spatial arrangement of resources. Using resident bird species and migratory bird species outside the migratory period, we examined how the distribution of resources affects the movement patterns of both large terrestrial birds (e.g., raptors, bustards and hornbills) and waterbirds (e.g., cranes, storks, ducks, geese and flamingos).

Location: Global.

Time period: 2003–2015.

Major taxa studied: Birds.

Methods: We compiled GPS tracking data for 386 individuals across 36 bird species. We calculated the straight-line distance between GPS locations of each individual at the 1-hr and 10-day time-scales. For each individual and time-scale, we calculated the median and 0.95 quantile of displacement. We used linear mixed-effects models to examine the effect of the spatial arrangement of resources, measured as enhanced vegetation index homogeneity, on avian movements, while accounting for mean resource availability, body mass, diet, flight type, migratory status and taxonomy and spatial autocorrelation.

Results: We found a significant effect of resource spatial arrangement at the 1-hr and 10-day time-scales. On average, individual movements were seven times longer in environments with homogeneously distributed resources compared with areas of low resource homogeneity. Contrary to previous work, we found no significant effect of resource availability, diet, flight type, migratory status or body mass on the non-migratory movements of birds.

Main conclusions: We suggest that longer movements in homogeneous environments might reflect the need for different habitat types associated with foraging and reproduction. This highlights the importance of landscape complementarity, where habitat patches within a landscape include a range of different, yet complementary resources. As habitat homogenization increases, it might force birds to travel increasingly longer distances to meet their diverse needs.

KEY WORDS

enhanced vegetation index, landscape complementation, movement ecology, productivity, spatial behaviour, terrestrial birds, waterbirds

1 INTRODUCTION

Animal movement plays an important role in shaping a wide range of ecological phenomena, from species survival to ecosystem functioning and patterns of biodiversity (Nathan et al., 2008; Viana, Santamaría, & Figuerola, 2016). As animals move across the landscape, they interact with individuals of the same or different species (e.g., predator–prey interactions), carry out ecological functions (e.g., seed dispersal) and mediate processes (e.g., disease dynamics and gene flow) (Bauer & Hoye, 2014). The search for resources is one underlying driver of animal movements (La Sorte, Fink,

Hochachka, DeLong, & Kelling, 2014; López-López, García-Ripollés, & Urios, 2014), where resources can be food, water, cover, suitable breeding habitat and access to mates. The link between resource abundance and movement has been found in animal home-range patterns, where home-range size, or the area used by an animal to reproduce and survive, decreases with increasing density of food resources (Kouba et al., 2017). The spatial arrangement of resources and the proximity of habitats containing vital resources (i.e., landscape complementarity) are also important factors affecting animal movements (López-López et al., 2014; Monsarrat et al., 2013). For example, changes in resource distributions can lead to shifts

between movement strategies (e.g., range resident versus nomadic; Reluga & Shaw, 2015) and affect the search behaviours of individuals while foraging, including step length and path tortuosity, depending on how heterogeneously distributed the resource patches are (Smith, 1974; Spiegel, Leu, Bull, & Sih, 2017).

Examining the link between avian movement and resources is important not only for building a better understanding of the underlying drivers of animal movement (Kleyheeg et al., 2017; Nathan et al., 2008), but also for understanding how global landscape modification will impact bird movement patterns (Gilbert et al., 2016). Previous research on the link between bird movement and resources has largely focused upon single populations and migratory movements (Kouba et al., 2017; Thorup et al., 2017), with less attention on how non-migratory movements are impacted by resources across multiple species. Here, we aim to examine how the distribution of resources affects non-migratory movement patterns at the within-day (1 hr) and within-season (10 day) scales across 36 avian species and five continents.

We predicted shorter movements when resources are heterogeneously distributed (i.e., low homogeneity), because heterogeneous areas provide a diverse range of habitats (including diverse resources) within a smaller area (Da Silveira, Niebuhr, Muylaert, Ribeiro, & Pizo, 2016). This means that individuals do not need to travel long distances to fulfil complementary resource needs (e.g., foraging versus reproduction). We also expected a stronger effect of enhanced vegetation index (EVI) homogeneity at the 1-hr scale (i.e., a steeper slope), because hourly movements are less likely to include longer inter-patch movements found at the 10-day scale. Therefore, changes to the landscape (e.g., homogenization) that result in resources being farther apart would result in birds covering longer distances more frequently to find the resources they need.

In this work, we focused on data-rich, large species, including terrestrial birds (e.g., raptors, hornbills and bustards) and waterbirds (e.g., ducks, geese, storks, cranes and flamingos). We used the EVI, which measures vegetation productivity, as a satellite-derived proxy for resources. Satellite-based vegetation indices have been shown to be good proxies for a variety of resources and have been used to predict bird diversity patterns (Tuanmu & Jetz, 2015) and movement (La Sorte et al., 2014). As a measure for the spatial arrangement of resources, we used a recently published metric of EVI homogeneity that estimates the similarity of EVI between adjacent 1-km pixels (Tuanmu & Jetz, 2015). With this measure, any landscape and habitat (e.g., grasslands, forests or agricultural lands) is considered homogeneous if there are no changes or few changes of habitat type at the 1-km scale.

In addition to the distribution of resources, we included other covariates that affect avian movements, including mean resource availability, body mass, diet, flight type and migratory status. We predicted shorter 1-hr and 10-day movements when food resources are in high abundance (i.e., high EVI), because animals can fulfil their requirements (e.g., food and shelter) within a smaller area (Gilbert et al., 2016). Allometric scaling relationships have shown

that animals of greater body size usually fly farther owing to energy efficiency, increased flight speeds and increased resource requirements (Alerstam, Rosén, Bäckman, Ericson, & Hellgren, 2007). In addition, differences in the abundance and distribution of food resources across different diet categories should translate into different movement patterns across carnivores, herbivores and omnivores (Alerstam et al., 2007; Tamburello, Côté, & Dulvy, 2015). We controlled for these differences by including diet as a covariate in our analysis. Finally, there are different energetic costs and flight speeds associated with flapping versus soaring flight. Flapping flight is faster, but soaring flight is more energetically efficient, which generally leads to longer flight distances (Hedenstrom, 1993; Watanabe, 2016). For this reason, we included flight type in our analyses, with the expectation that soaring birds would fly longer distances over short and long time periods. We also included migratory status (i.e., migratory or non-migratory) as a covariate in our models to account for any potential differences in movement distances across the two strategies (Alerstam et al., 2007).

2 METHODS

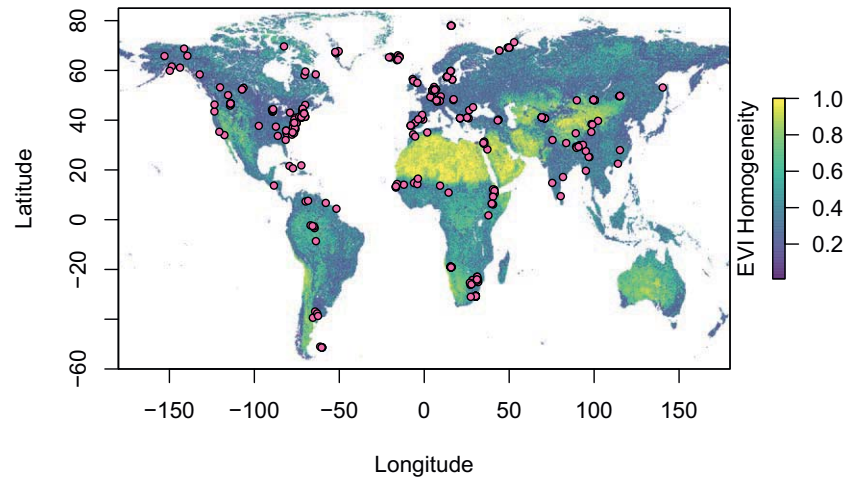
2.1 Data

We compiled GPS tracking data for 36 terrestrial and freshwater bird species between 2003 and 2015, spanning 4,638,594 locations across 386 individuals and five continents (Figure 1). The majority of the data were obtained from *Movebank* (<https://www.movebank.org/>) and the Movebank Data Repository (<https://www.datarepository.movebank.org/>) or were directly contributed by co-authors (see Supporting Information Appendix S1).

2.2 Movement metric

Our movement metric was displacement, which is the straight-line distance between two locations. We chose to examine avian movements at the 1-hr and 10-day scales because they enabled us to examine short- (i.e., within-day) and long-term (i.e., within-season) movements and maximized the contrast between scales while preserving sufficient sample sizes at the species and individual levels. To standardize the sampling frequency among studies, we subsampled location data so that intervals between consecutive locations were either 1 hr or 10 days. We started the subsampling algorithm from the first location of each individual, and the subsampling precision was set to the inter-location interval $\pm 4\%$ (e.g., for the 1-hr scale, resulting in inter-location intervals varying between 57 and 62 min). There were some individuals that did not have data for both the 1-hr and 10-day scales owing to the different tracking regimes of the data, where some individuals had data every 15 min, whereas others had only one location per day. This resulted in some individuals not having the fine-scale data for the 1-hr scale analysis. Some of the individuals were tracked with tags that were switched off for set periods of the day (e.g., nights) to reduce battery use. To avoid any bias in the sampling at the 1-hr time-scale, we included only

FIGURE 1 Global patterns of enhanced vegetation index (EVI) homogeneity spanning from low (dark blue) to high (yellow). Note. The pink circles represent the average longitude and latitude position for each of the 386 individuals across 36 species included in the study [Colour figure can be viewed at wileyonlinelibrary.com]



locations that occurred between 06:00 a.m. and 6:00 p.m. local time, because this enabled us to include movements between the feeding area and the roost, while avoiding the roosting period when birds are likely to be more settled, particularly in the winter months. This also meant that we included only birds with diurnal movement behaviours. To exclude migratory periods, we included only species that were non-migratory (all seasons) or migratory species outside the migratory period (i.e., summer and winter movements only). Summer and winter categories were based on month and latitude. Summer included June, July and August (Northern Hemisphere; latitude > 0) or December, January and February (Southern Hemisphere; latitude < 0). Winter included December, January and February (Northern Hemisphere) or June, July and August (Southern Hemisphere). We categorized species as non-migratory ($n = 27$) or migratory ($n = 9$) based on Eyres, Böhning-Gaese, and Fritz (2017), who broadly categorized the movement behaviour of 10,443 bird species as directional migrant (seasonal movements with a specific geographical direction), dispersive migrant (seasonal movements without a specific geographical direction), nomadic (irregular movements, not seasonal or with geographical direction) and resident (sedentary movements). We defined species as migratory if they were classified as 'directional migratory' or 'dispersive migratory' and non-migratory if classified as 'resident'. To ensure that we did not include the beginning or end of migration during the summer or winter for each individual, we calculated the centroid of the densest cluster of points for each season. Clusters were identified based on kernel density estimation, where a cluster is defined by the local maximum of the estimated density function (see Supporting Information Appendix S2 for R package details). We then calculated a circle centred on the cluster centroid with a radius equal to the maximal displacement distance calculated for that individual and time-scale, with a minimal radius size of 30 km for species with very short maximal displacements. We included only locations that occurred within this circle, and we did this for each season separately to avoid tracks that exited and re-entered the circle (see Supporting Information Appendix S3 for a graphical representation of this methodology).

For the remaining 1-hr and 10-day displacement data, we calculated the geodesic distance between the subsampled locations. We removed outliers based on maximal movement speeds (> 23 m/s; Alerstam et al., 2007) and removed any stationary locations (i.e., displacements < 10 m, based on average GPS error). We removed stationary locations because we wanted to focus on periods when individuals were moving rather than during stationary periods, such as roosting or nesting. We then calculated two response variables for each individual: the median displacement distance and the 0.95 quantile displacement distance (i.e., long-distance movements). We \log_{10} -transformed the displacement values to meet the normality assumption of the distribution of residuals from the linear mixed-effects models.

2.3 Environment and life history data

We annotated each GPS location with the mean EVI across 2001–2012 and EVI homogeneity across 2001–2005 using publicly available global datasets with 1-km resolution (Supporting Information Appendix S4: Hengl, Kilibarda, Carvalho-Ribeiro, & Reuter, 2015; Tuanmu & Jetz, 2015). The mean EVI data were calculated using monthly MODIS EVI time-series data (MOD13A3; Hengl et al., 2015), and the EVI homogeneity data were calculated using the 16-day MODIS EVI time-series data (MOD13Q1; Tuanmu & Jetz, 2015). The EVI is a modified version of the normalized difference vegetation index (NDVI), which is designed to deal with structural variations in high-biomass regions and is able to decouple the canopy background signal from atmospheric influences (Huete et al., 2002). This means that EVI is more sensitive to differences in heavily vegetated areas (i.e., when vegetation is dense, EVI can differentiate between different vegetation types) owing to the correction for atmospheric haze and the land surface beneath the vegetation. The EVI homogeneity metric was originally developed for examining how bird species richness was related to habitat heterogeneity (see Tuanmu & Jetz, 2015) and thus provided an ideal and tested dataset to examine how habitat heterogeneity impacts

avian movements. The EVI homogeneity is a proxy for the spatial distribution of vegetation productivity and reflects fine-grain land-cover heterogeneity. It is calculated based on the similarity of EVI values within a set neighbourhood (for additional details, see Tuanmu & Jetz, 2015). The EVI and EVI homogeneity data are terrestrial-based measures, where cells that included water were set as 'NA' and water was, therefore, excluded from our analyses. We assume that EVI captures the resources used by waterbirds based on previous work (Henry, Ament, & Cumming, 2016), although we note that waterbodies are also an important resource that were not included in our analyses. To examine the average EVI and EVI homogeneity experienced by each individual, we calculated mean values for each individual using the annotated EVI and EVI homogeneity values. We also included species-level traits, including body mass from the EltonTraits 1.0 database (Wilman et al., 2014), diet [carnivore ($n = 20$), herbivore ($n = 14$) or omnivore ($n = 2$)] and flight type [soaring and flapping ($n = 18$) or flapping only ($n = 18$)]. In the case of flight type, soaring species are able to use both flapping and soaring flight. Body mass values ranged from 600 g to 9.5 kg and were \log_{10} -transformed before analyses.

Lastly, to attempt to account for the EVI and EVI homogeneity values experienced by individuals while flying, we also ran the models using the weighted mean values of EVI and EVI homogeneity. Weighted mean values were calculated along each displacement segment (i.e., a straight-line distance between two sequential locations), where weights were based on the proportion of the segment that occurred in each pixel. For the final analysis, we averaged these weighted average EVI and EVI homogeneity values for each individual.

2.4 Analyses

Our final database (see Supporting Information Appendices S5 and S6) included individual median and 0.95 quantile displacement values for 1-hr and 10-day displacements, the associated mean values for body mass, EVI and EVI homogeneity, and diet, flight type and migratory status categories. We included only individuals that had tracking data for a minimum of 1 week of hourly locations or 60 days of 10-day locations. We ran four linear mixed-effects models: two for each time-scale, one with the median and the other with the 0.95 quantile displacement distances as the dependent variable, and body mass, EVI, EVI homogeneity, flight type and diet as the fixed effects. We included a nested random effect to account for taxonomy (i.e., order/family/genus/species). Given that the tracking data are spatially autocorrelated, we accounted for this correlation in the regression models using a Gaussian function based on the distances between the mean longitude and latitude of each individual. For each model, we checked the residuals for normality (i.e., Q-Q plots). We examined the collinearity among variables and found that all correlation coefficients among the predictor variables were $|r| \leq .53$, which is below the common cut-off value of 0.7 (Dormann et al., 2013). We also checked for multicollinearity using variance inflation factors (VIFs) and found that all VIFs were

< 2.0, which is below the commonly accepted cut-off value of 4.0 (Zuur, Ieno, & Elphick, 2010). We examined the goodness-of-fit for each model using the marginal R^2 (variance explained by the fixed effects) and conditional R^2 (variance explained by both fixed and random factors) values for each model (Nakagawa & Schielzeth, 2013). We calculated the model predictions using the mean value of the continuous predictors (e.g., mass and EVI) and varying the covariate of interest (e.g., EVI homogeneity). We chose to make predictions for carnivorous soaring migrants because this is the predominant combination in our data. We tested for differences between the slope estimates for EVI homogeneity for the 1-hr models, the 10-day models and between the 1-hr and 10-day models. We did this using the difference between EVI homogeneity coefficient estimates and the associated confidence intervals calculated via error propagation based on Clark (2007: see chapter 5.6.2 and appendix D.5.3). The EVI homogeneity slope estimates were deemed not significant when the 95% confidence intervals overlapped zero. All analyses were performed in R v.3.4.3 (R Core Team, 2017), and details on the R packages used in the analyses can be found in the Supporting Information (Appendix S2).

3 RESULTS

We found a significant positive relationship between displacement and EVI homogeneity at both the 1-hr and 10-day time-scales (Table 1; Figures 2 and 3). The results were similar for the weighted mean EVI and EVI homogeneity analyses (Supporting Information Appendix S7). On average, displacements were up to seven times longer in areas with high EVI homogeneity (Figure 2), such as desert regions (the maximal EVI homogeneity value was .85). For example, model predictions for 1-hr median displacements for carnivorous soaring individuals were 1.02 km (\pm SE 1.63 km, range = 0.62–1.65 km, $n = 168$) in areas of high EVI homogeneity versus 0.14 km (\pm SE 1.47 km, range = 0.10–0.21 km, $n = 168$) in areas of low EVI homogeneity (Figure 2a). The 1-hr long-distance displacements for carnivorous soaring individuals were 10.20 km (\pm SE 1.57 km, range = 6.48–16.07 km, $n = 168$) in areas of high EVI homogeneity versus 2.40 km (\pm SE 1.45 km, range = 1.66–3.48 km, $n = 168$) in areas of low EVI homogeneity (Figure 2a).

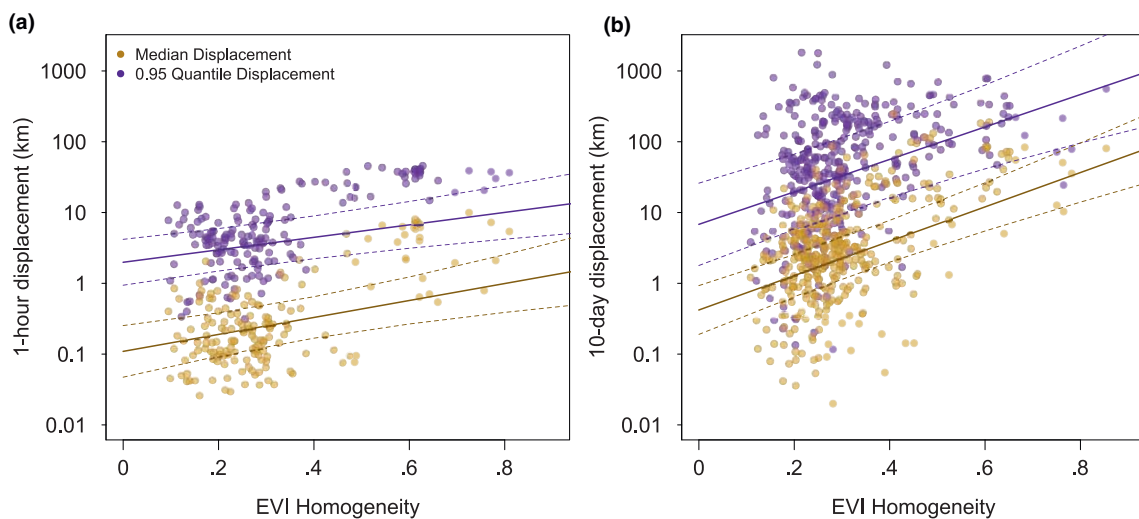
There was no significant difference between the slope coefficients of the 1-hr and 10-day displacements for both the median and long-distance models (Supporting Information Appendix S8). Contrary to our predictions, these results suggest that movements at both time-scales were equally sensitive to decreasing homogeneity.

Our models explained 52–71% of the variation in avian displacements at the 1-hr and 10-day time-scales when accounting for both random and fixed effects, and 10–38% of the variation when accounting for the fixed effects alone (i.e., body mass, mean EVI, EVI homogeneity, diet, flight type and migratory status; Table 1). We did not find any significant effects of mean EVI, body mass, diet, flight type or migratory status on median or long-distance displacements at either time-scale (Table 1; Figure 3).

TABLE 1 Model coefficients, R^2 , p -values and sample sizes of linear mixed-effects models predicting the median and 0.95 quantile of individual displacements for 1- and 10-day time-scales

	1 hr				10 days			
	Median		0.95 quantile		Median		0.95 quantile	
	Estimate (SE)	p	Estimate (SE)	p	Estimate (SE)	p	Estimate (SE)	p
Mass	0.385 (0.265)	.283	0.175 (0.174)	.419	0.155 (0.237)	.532	-0.427 (0.264)	.145
EVI	-0.58 (0.436)	.185	-0.053 (0.328)	.872	-0.225 (0.409)	.582	0.795 (0.484)	.102
EVI_Homogeneity	1.198 (0.323)	< .001	0.881 (0.23)	< .001	2.427 (0.311)	< .001	2.292 (0.434)	< .001
Diet (H)	0.088 (0.33)	.807	-0.065 (0.272)	.827	0.056 (0.302)	.857	0.017 (0.403)	.968
Diet (O)	0.129 (0.56)	.833	-0.654 (0.395)	.196	-0.359 (0.459)	.456	-0.908 (0.553)	.139
FlightT_Soar	0.469 (0.32)	.281	0.195 (0.224)	.476	0.123 (0.315)	.723	-0.202 (0.419)	.663
MigStatus_NM	0.231 (0.148)	.259	0.213 (0.099)	.164	0.252 (0.195)	.232	0.082 (0.206)	.699
R^2 marginal	.376		.360		.261		.102	
R^2 conditional	.696		.706		.518		.566	
Species	19				35			
Individuals	168				356			

Note. Predictor variables included fixed effects for body mass (Mass), enhanced vegetation index (EVI), EVI homogeneity (EVI_Homogeneity), diet (H = herbivore and O = omnivore coefficients), flight type (FlightT; soaring coefficient values shown here) and migratory status (MigStatus_NM; non-migratory coefficient values shown here). The model also included a nested random effect accounting for the taxonomy, and a Gaussian spatial auto-correlation structure. Bold values indicate significance at $p < .05$.

**FIGURE 2** Avian (a) 1-hr and (b) 10-day median (0.5 quantile; yellow) and long-distance (0.95 quantile; purple) displacements with increasing enhanced vegetation index (EVI) homogeneity

Note. Plots include regression lines from the linear mixed-effects models and 95% confidence intervals. An EVI homogeneity value of zero indicates areas of low homogeneity, and values of 0.8 represent areas of high homogeneity at a local scale [Colour figure can be viewed at wileyonlinelibrary.com]

4 DISCUSSION

We have shown that EVI homogeneity is a key factor associated with avian movements, where movements were on average seven times longer in areas of high EVI homogeneity (e.g., deserts) compared with areas of low EVI homogeneity (e.g., mixed broadleaved and needle-leaved forests). The increase in displacement with increasing homogeneity is likely to be a reflection of the different habitat types (including microhabitat heterogeneity) required for survival (e.g.,

food resources or tree cover for predator avoidance) and reproduction (e.g., nesting sites). Some bird species (e.g., upland sandpiper, *Bartramia longicauda*) have larger home-range sizes in homogeneous environments, such as pastures or grasslands, because the structure of these habitats does not meet all of the biological requirements of the bird, meaning that they increase their ranging behaviour until their requirements are met (Sandercock et al., 2015; Stanton, Kesler, & Thompson, 2014). Therefore, landscape complementation, where a single landscape includes habitat patches with different

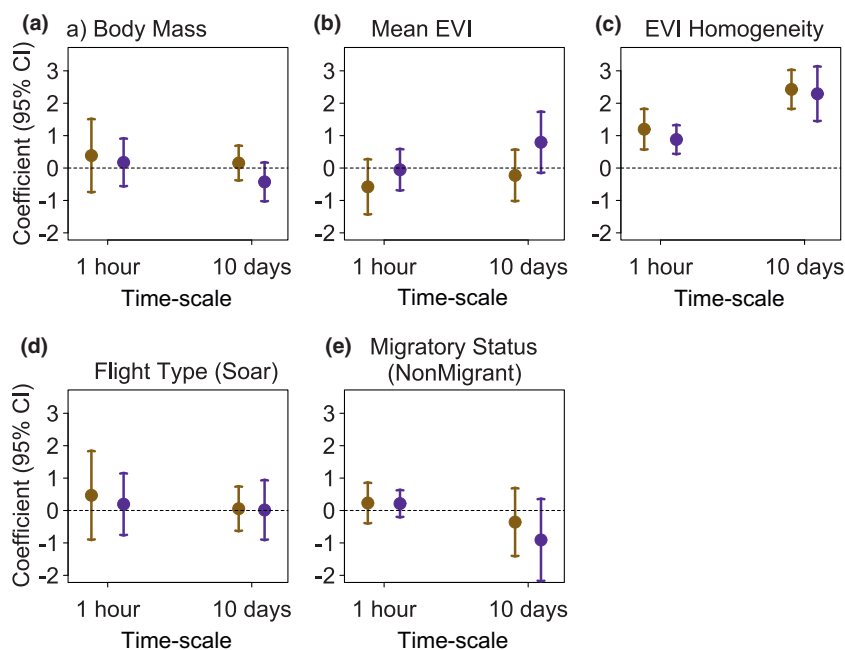


FIGURE 3 Model coefficients (\pm 95% confidence intervals) of linear mixed-effects models predicting avian displacements using: (a) body mass; (b) mean enhanced vegetation index (EVI); (c) EVI homogeneity; (d) flight type (soaring); and (e) migratory status (non-migratory). Note. Models were run for the median (yellow) and long-distance (0.95 quantile; purple) displacements of each individual, calculated across different time-scales. When the error bars cross the horizontal line, the effect is not significant. See Table 1 for details [Colour figure can be viewed at wileyonlinelibrary.com]

but complementary resources within close proximity, is likely to be an important feature for shaping avian movements (Mueller, Selva, Pugacewicz, & Prins, 2009). The link between movement and EVI homogeneity might also suggest that it is important to maintain landscape complementarity in human-modified areas that have shifted from heterogeneous to homogeneous landscapes (e.g., croplands), which might reduce the distances covered by individual birds and, in turn, the potential negative effects of these longer travel distances (e.g., increased energetic costs).

Interestingly, we did not find a significant effect of the mean abundance of resources, contrary to our predictions and previous research on single populations of birds (Dodge et al., 2014; Stanton et al., 2014). This difference could be attributable to previous studies focusing on long-distance movements, such as migration, or not including the effect of spatial arrangement of resources, or both. We can rule out the possibility of spatial arrangement of resources masking the effect of EVI, because we ran our models excluding EVI homogeneity and still found no significant effect of EVI (Supporting Information Appendix S9). Although vegetation indices, such as EVI, have been shown to underlie bird behaviour (La Sorte, Fink, Hochachka, DeLong, & Kelling, 2013) and diversity patterns (Tuanmu & Jetz, 2015), it may also be the case that mean EVI is not the best proxy of resources used by birds, particularly on a small scale (e.g., daily movements). It is assumed that vegetation indices provide information across several diet categories; however, they might perform poorly for non-herbivore species, specifically those that rely on scavenging. We also ran our models with an interaction term between mean EVI and diet to test for differences in the response to EVI across diet categories (Supporting Information Appendix S10). The interaction term was significant only for the long-distance 10-day displacements, suggesting that we were unable to detect differences between diet categories for hourly movements using EVI

at a 1-km resolution. We also note that we did not account for the seasonal variation in resource availability, which may impact avian movements. Our study focused on terrestrial resources that are likely to capture some of the resources used by waterbirds (e.g., crops), but future studies should investigate the role of aquatic resources on waterbird movements. Overall, productivity measures, such as EVI, are currently the best proxy for food resources available, and our results indicate that EVI homogeneity is a potentially useful proxy of the spatial arrangement of resources and has an important role in shaping avian foraging movements.

Also contrary to our predictions, we did not find a significant effect of body mass on displacements. The lack of relationship between displacement and mass could also be a result of the limited range of body mass included in our database, spanning 600 g to 9.5 kg, and the low sample size of small birds included in our study. This is because of the limited availability of high-resolution data for terrestrial birds < 250 g, owing to the weight of current GPS tracking technologies and the limited battery life for smaller devices (López-López, 2016). Based on allometric relationships, birds with smaller body masses (e.g., < 600 g) should travel shorter distances and use a smaller area based on reduced resource requirements, energy efficiency and flight speeds in comparison to larger species (Alerstam et al., 2007). As tracking technologies improve, it will become possible to track smaller species and then re-examine this relationship across a broader range of avian body mass.

Lastly, we did not find any significant differences between soaring/flapping flight and flapping-only flight. It is possible that flight strategy has a smaller impact on foraging movements compared with migratory movements, where the trade-off between flight distance and energetic costs is greater (Hedenstrom, 1993; Watanabe, 2016). Alternatively, it could be that flight behaviours, such as thermal soaring, were not captured at the temporal resolution of the tracking

data used and our restriction to examining two-dimensional movements (i.e., only longitude and latitude). This means that individuals that use thermal soaring could be covering longer distances that we are not able to detect with our current analysis (Tamburello et al., 2015). Owing to the disproportionate increase in flight costs with body mass for flapping flyers, flapping flight is more common in small species (Hedenstrom, 1993), and with the inclusion of these species we might see more divergent displacement behaviours between these flying strategies. It is also possible that the size of the smaller birds in our dataset that are characterized as active fliers (i.e., flapping flight) use this strategy for only short periods because they are still too large to maintain this flight strategy energetically for long periods, thus preventing us from detecting any differences among strategies in our analysis.

The random effect (i.e., taxonomy) explained a large portion of the variance in avian movements (c. 40–50%). Previous work has examined species-level differences in movement patterns, including differences in home-range size (Haskell, Ritchie, & Olff, 2002) and migration distances/strategies (Alerstam, Hedenström, & Åkesson, 2003; La Sorte et al., 2013) based on species-level traits (e.g., body size and diet). Some of the variation among individuals within the same species is probably attributable to sex, because males and females have different movement patterns during brood rearing (Hernández-Pliego, Rodríguez, & Bustamante, 2017). In addition, feather moult (i.e., feathers being shed and regrown) may impact avian movements, including periods of flightlessness (e.g., cranes and waterfowl post-breeding) and reduced aerodynamic performance of the wings (e.g., *Falco peregrinus*; Flint & Meixell, 2017). Variation in moult patterns and their consequences for bird movement between species, populations and individuals were not considered here owing to lack of detailed moult data when movement was recorded. Reproduction is another vital part of an individual's life history and often involves a shift in movement patterns owing to the distribution of mates, lekking sites or availability of nesting sites or food resources (Cecere, Gaibani, & Imperio, 2014; Rösner, Brandl, Segelbacher, Lorenc, & Müller, 2014). Other environmental variables, such as wind speed and direction, were not included in our analyses, but might also account for some of the unexplained variance of our models (Harel, Horvitz, & Nathan, 2016; Mellone et al., 2015).

Another potential factor accounting for the within-species variation in avian displacements is related animal personality, where individuals with different personalities are likely to differ in their movement strategies (Patrick, Pinaud, & Weimerskirch, 2017; Spiegel et al., 2017). For example, movement patterns are expected to differ according to the boldness of individuals, because bolder individuals may demonstrate more exploratory movements and use more risky environments (Spiegel et al., 2017). This could also be related to age and experience, because individuals with more experience might be less likely to inhabit risky environments and might already have identified where the reliable food patches are, contributing further to intraspecific variation (López-López et al., 2014).

A caveat of our analysis is the assumption that our calculation of the EVI and EVI homogeneity values based on endpoints of

displacements represent the mean resources or resource homogeneity experienced by the individual while moving. In this context, without high-resolution data collected over long durations, it will be difficult to discern exactly what the individual experienced over extended periods. Nevertheless, our results clearly demonstrate a relationship between resources and avian movements, because we found similar results using models based only on the end coordinates of displacement segments and models using the weighted mean along the entire straight-line displacement segments (Supporting Information Appendix S7). As higher-resolution tracking data become more common, future studies can begin to discern foraging behaviours from movement tracks and examine foraging patterns in response to resources at a macroecological scale.

5 CONCLUSION

In conclusion, our study is the first to examine the relationship between the distribution of resources and non-migratory avian movement patterns across multiple species and regions. We have demonstrated the importance of resource spatial distribution on shaping movements, highlighting the possible effects of landscape homogenization, where individuals may need to fly farther to meet their ecological requirements. It is possible that continuing habitat homogenization (e.g., intensification of agriculture) in landscapes with a naturally high diversity of habitats will have negative impacts on the abundance and diversity of birds (Jerrentrup et al., 2017) owing to the loss of complementary habitats. This might, in turn, result in greater movement requirements and higher energy expenditure.

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AUTHOR CONTRIBUTIONS

M.A.T. and T.M. conceived the manuscript, M.A.T. conducted the analyses, and M.A.T. and T.M. wrote the first manuscript draft. Co-authors contributed datasets and assisted with writing the final version of the manuscript.

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SUPPORTING INFORMATION

Appendix S1 Summary of species and number of individuals per species included in the analyses.

Appendix S2 Details of R packages used in the analyses including the specific function used and its role in the analyses.

Appendix S3 Example of data selection process for migratory species.

Appendix S4 Environmental data annotation summary.

Appendix S5 Data used in the analyses.

Appendix S6 Data distributions of the displacement data used in the analyses.

Appendix S7 Results for the models including the weighted mean EVI and EVI homogeneity values.

Appendix S8 Comparison of the EVI Homogeneity slope coefficient estimates.

Appendix S9 Results for models excluding EVI Homogeneity.

Appendix S10 Results models including an EVI Homogeneity and diet interaction term.