

1 **TITLE:** Large birds travel farther in homogeneous environments

2 **RUNNING TITLE:** Avian movements in homogeneous environments

3

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138 **Keywords:** Movement ecology, spatial behaviour, terrestrial birds, waterbirds, productivity,
139 Enhance Vegetation Index (EVI), landscape complementation.

140

141 **ABSTRACT**

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

148 **Location:** Global

149 **Time Period:** 2003 - 2015

150 **Major taxa studied:** Birds

151 **Methods:** We compiled GPS tracking data for 386 individuals across 36 bird species. We
152 calculated the straight-line distance between GPS locations of each individual at the 1-hour
153 and 10-day timescales. For each individual and timescale, we calculated the median and 0.95
154 quantile of displacement. We used linear mixed-effects models to examine the effect of the
155 spatial arrangement of resources, measured as Enhanced Vegetation Index (EVI)
156 homogeneity, on avian movements while accounting for mean resource availability, body
157 mass, diet, flight type, migratory status and taxonomy and spatial autocorrelation.

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

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

169

170 **1 | INTRODUCTION**

171 Animal movement plays an important role in shaping a wide range of ecological phenomena
172 from species survival to ecosystem functioning and patterns of biodiversity (Nathan *et al.*,
173 2008; Viana *et al.*, 2016). While animals move across the landscape, they interact with
174 individuals of the same or different species (e.g., predator-prey interactions), carry out
175 ecological functions (e.g., seed dispersal) and mediate processes (e.g., disease dynamics and
176 gene flow) (Bauer & Hoyer, 2014). The search for resources is one underlying driver of animal
177 movements (La Sorte *et al.*, 2014; López-López *et al.*, 2014), where resources can be food,
178 water, cover, suitable breeding habitat and access to mates. The link between resource
179 abundance and movement has been found in animal home range patterns, where home range
180 size, or the area used by an animal to reproduce and survive, decreases with increasing density
181 of food resources (Kouba *et al.*, 2017). The spatial arrangement of resources and the
182 proximity of habitats containing vital resources (i.e., landscape complementarity) are also

183 important factors affecting animal movements (Monsarrat *et al.*, 2013; López-López *et al.*,
184 2014). For example, changes in resource distributions can lead to shifts between movement
185 strategies (e.g., range resident vs. nomadic, (Reluga & Shaw, 2015)) and affect the search
186 behaviours of individuals while foraging, including step length and path tortuosity, depending
187 on how heterogeneously distributed the resource patches are (Smith, 1974; Spiegel *et al.*,
188 2017).

189 Examining the link between avian movement and resources is not only important for
190 building a better understanding of the underlying drivers of animal movement (Nathan *et al.*,
191 2008; Kleyheeg *et al.*, 2017), but is also important for understanding how global landscape
192 modification will impact bird movement patterns (Gilbert *et al.*, 2016). Previous research on
193 the link between bird movement and resources have largely focused upon single populations
194 and migratory movements (Kouba *et al.*, 2017; Thorup *et al.*, 2017), with less attention on
195 how non-migratory movements are impacted by resources across multiple species. Here we
196 aim to examine how the distribution of resources affects non-migratory movement patterns at
197 the within day (1 hour) and within season (10 day) scales across 36 avian species and five
198 continents.

199 We predicted shorter movements when resources are heterogeneously distributed (i.e.,
200 low homogeneity) because heterogeneous areas provide a diverse range of habitats (including
201 diverse resources) within a smaller area (Da Silveira *et al.*, 2016). This means that individuals
202 do not need to travel long distances to fulfil complementary resource needs (e.g., foraging vs.
203 reproduction). We also expected a stronger effect of EVI homogeneity at the 1-hour scale
204 (i.e., a steeper slope) because hourly movements are less likely to include longer inter-patch
205 movements found at the 10-day scale. Therefore, changes to the landscape (e.g.,
206 homogenisation) that result in resources being farther apart would result in birds covering
207 longer distances more frequently to find the resources they need.

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

219 In addition to the distribution of resources, we included other covariates that affect
220 avian movements including mean resource availability, body mass, diet, flight type and
221 migratory status. We predicted shorter 1-hour and 10-day movements when food resources
222 are in high abundance (i.e., high EVI) as animals can fulfil their requirements (e.g., food,
223 shelter etc.) within a smaller area (Gilbert *et al.*, 2016). Allometric scaling relationships have
224 shown that animals of greater body size usually fly farther due to energy efficiency, increased
225 flight speeds and increased resource requirements (Alerstam *et al.*, 2007). In addition,
226 differences in the abundance and distribution of food resources across different diet categories
227 should translate into different movement patterns across carnivores, herbivores and omnivores
228 (Alerstam *et al.*, 2007; Tamburello *et al.*, 2015). We controlled for these differences by
229 including diet as a covariate in our analysis. Finally, there are different energetic costs and
230 flight speeds associated with flapping versus soaring flight. Flapping flight is faster, but
231 soaring flight is more energetically efficient, which generally leads to longer flight distances
232 (Hedenstrom, 1993; Watanabe, 2016). For this reason, we included flight type in our analyses

233 with the expectation that soaring birds would fly longer distances over short and long time
234 periods. We also included migratory status (i.e., migratory or non-migratory) as a covariate in
235 our models to account for any potential differences in movement distances across the two
236 strategies (Alerstam *et al.*, 2007).

237

238 **2 | METHODS**

239 **2.1 | Data**

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

245

246 **2.2 | Movement Metric**

247 Our movement metric was displacement, which is the straight-line distance between two
248 locations. We chose to examine avian movements at the 1-hour and 10-day scales as they
249 enabled us to examine short (i.e., within day) and long-term movements (i.e., within season),
250 and maximised the contrast between scales while preserving sufficient sample sizes at the
251 species and individual levels. To standardise the sampling frequency among studies, we
252 subsampled location data so that intervals between consecutive locations were either 1 hour or
253 10 days. We started the subsampling algorithm from the first location of each individual and
254 the subsampling precision was set to the inter-location interval $\pm 4\%$ (e.g., for the 1-hour scale
255 resulting in inter-location intervals varying between 57 and 62 minutes). There are some
256 individuals that do not have data for both the 1-hour and 10-day scales due to the different
257 tracking regimes of the data, where some individuals have data every 15 minutes, while others

258 only have one location per day. This resulted in some individuals not having the fine-scale
259 data for the 1-hour scale analysis. Some of the individuals were tracked with tags that were
260 switched off for set periods of the day (e.g., nights) to reduce battery use. To avoid any bias in
261 the sampling at the 1-hour time scale, we only included locations that occurred between 6:00
262 am and 6:00 pm local time as this enabled us to include movements between the feeding area
263 and the roost, while avoiding the roosting period when birds are likely to be more settled,
264 particularly in the winter months. This also meant that we only included birds with diurnal
265 movement behaviours. To exclude migratory periods, we only included species that were non-
266 migratory (all seasons) or migratory species outside of the migratory period (i.e., summer and
267 winter movements only). Summer and winter categories were based on month and latitude.
268 Summer included June, July and August (Northern Hemisphere; latitude > 0) or December,
269 January and February (Southern Hemisphere; latitude < 0). Winter included December,
270 January and February (Northern Hemisphere) or June, July and August (Southern
271 Hemisphere). We categorised species as non-migratory (n = 27) or migratory (n = 9) based on
272 Eyres *et al.* (2017) who broadly categorised the movement behaviour of 10 443 bird species
273 as directional migrant (seasonal movements with a specific geographical direction), dispersive
274 migrant (seasonal movements without a specific geographical direction), nomadic (irregular
275 movements, not seasonal or with geographical direction) and resident (sedentary movements).
276 We defined species as migratory if they were classified as “directional migratory” or
277 “dispersive migratory” and non-migratory if classified as “resident”. To ensure that we did
278 not include the beginning or end of migration during the summer or winter for each
279 individual, we calculated the centroid of the densest cluster of points for each season. Clusters
280 were identified based on kernel density estimation, where a cluster is defined by the local
281 maximum of the estimated density function (please see Appendix S2 for R package details).
282 We then calculated a circle centred on the cluster centroid with a radius equal to the

283 maximum displacement distance calculated for that individual and time scale, with a
284 minimum radius size of 30 km for species with very short maximum displacements. We only
285 included locations that occurred within this circle, and we did this for each season separately
286 to avoid tracks that exited and re-entered the circle (see Appendix S3 for a graphical
287 representation of this methodology).

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

297

298 **2.3 | Environment and Life History Data**

299 We annotated each GPS location with the mean Enhanced Vegetation Index (EVI)
300 across 2001 - 2012 and EVI homogeneity across 2001–2005 using publicly available global
301 datasets with 1 km resolution (Appendix S4: Hengl *et al.*, 2015; Tuanmu & Jetz, 2015). The
302 mean EVI data was calculated using monthly MODIS EVI time series data (MOD13A3;
303 Hengl *et al.*, 2015) and the EVI homogeneity data was calculated using the 16-day MODIS
304 EVI time series data (MOD13Q1; Tuanmu & Jetz, 2015). EVI is a modified version of the
305 Normalized Difference Vegetation Index (NDVI), which is designed to deal with structural
306 variations in high biomass regions and is able to decouple the canopy background signal from
307 atmospheric influences (Huete *et al.*, 2002). This means that EVI is more sensitive to

308 differences in heavily vegetated areas (i.e., when vegetation is dense, EVI can differentiate
309 between different vegetation types) due to the correction for atmospheric haze and the land
310 surface beneath the vegetation. The EVI homogeneity metric was originally developed for
311 examining how bird species richness was related to habitat heterogeneity (see Tuanmu & Jetz,
312 2015) and thus provided an ideal and tested dataset to examine how habitat heterogeneity
313 impacts avian movements. EVI homogeneity is a proxy for the spatial distribution of
314 vegetation productivity and reflects fine-grain land-cover heterogeneity. It is calculated based
315 on the similarity of EVI values within a set neighbourhood (see Tuanmu & Jetz, 2015 for
316 additional details). The EVI and EVI homogeneity data are terrestrial-based measures where
317 cells that included water were set as “NA” and water was therefore excluded from our
318 analyses. We assume that EVI captures the resources used by waterbirds based on previous
319 work (Henry *et al.*, 2016), although we note that waterbodies are also an important resource
320 that were not included in our analyses. To examine the average EVI and EVI homogeneity
321 experienced by each individual, we calculated mean values for each individual using the
322 annotated EVI and EVI homogeneity values. We also included species-level traits including
323 body mass from the EltonTraits 1.0 database (Wilman *et al.*, 2014), diet (carnivore (n = 20),
324 herbivore (n = 14) or omnivore (n = 2)), and flight type (soaring and flapping (n = 18) or
325 flapping only (n = 18)). In the case of flight type, soaring species are able to utilise both
326 flapping and soaring flight. Body mass values ranged from 600 g to 9.5 kg and were \log_{10}
327 transformed prior to analyses.

328 Lastly, to attempt to account for the EVI and EVI homogeneity values experienced by
329 individuals while flying, we also ran the models using the weighted mean values of EVI and
330 EVI homogeneity. Weighted mean values were calculated along each displacement segment
331 (i.e. a straight-line distance between two sequential locations), where weights were based on

332 the proportion of the segment that occurred in each pixel. For the final analysis, we averaged
333 these weighted average EVI and EVI homogeneity values for each individual.

334

335 **2.4 | Analyses**

336 Our final database (see Appendix S5 and Appendix S6) included individual median and 0.95
337 quantile displacement values for 1-hour and 10-day displacements, the associated mean
338 values for body mass, EVI, and EVI homogeneity, and diet, flight type and migratory status
339 categories. We only included individuals that had tracking data for a minimum of one week of
340 hourly locations or 60 days of 10-day locations. We ran four linear mixed effects models: two
341 for each time-scale, one with the median and the other with the 0.95 quantile displacement
342 distances as the dependent variable, and body mass, EVI, EVI homogeneity, flight type, and
343 diet as the fixed effects. We included a nested random effect to account for taxonomy (i.e.,
344 Order/Family/Genus/Species). As the tracking data are spatially autocorrelated, we accounted
345 for this correlation in the regression models using a Gaussian function based on the distances
346 between the mean longitude and latitude of each individual. For each model, we checked the
347 residuals for normality (i.e., Q-Q plots). We examined the collinearity among variables and
348 found that all correlation coefficients among the predictor variables were $|r| \leq 0.53$ which is
349 below the common cut-off value of 0.7 (Dormann *et al.*, 2013). We also checked for
350 multicollinearity using variance inflation factors (VIFs) and found that all VIFs were < 2.0 ,
351 which is below the commonly-accepted cut-off value of 4.0 (Zuur *et al.*, 2010). We examined
352 the goodness of fit for each model using the marginal R^2 (variance explained by the fixed
353 effects) and conditional R^2 (variance explained by both fixed and random factors) values for
354 each model (Nakagawa & Schielzeth, 2013). We calculated the model predictions using the
355 mean value of the continuous predictors (e.g., mass and EVI) and varying the covariate of
356 interest (e.g., EVI homogeneity). We chose to make predictions for carnivorous soaring

357 migrants as this is the predominant combination in our data. We tested for differences
358 between the slope estimates for EVI homogeneity for the 1-hour models, the 10-day models
359 and between the 1-hour and 10-day models. We did this using the difference between EVI
360 homogeneity coefficient estimates and the associated confidence intervals calculated via error
361 propagation based on Clark (2007) (see Chapter 5.6.2 and appendix D.5.3). EVI homogeneity
362 slope estimates were deemed not significant when the 95% confidence intervals overlapped
363 zero. All analyses were performed in R version 3.4.3 (R Core Team, 2017) and details on the
364 R packages used in the analyses can be found in Supporting Information Appendix S2.

365

366 **3 | RESULTS**

367 We found a significant positive relationship between displacement and EVI
368 homogeneity at both the 1-hour and 10-day time scales (Table 1, Fig. 2 and 3). The results
369 were similar for the weighted mean EVI and EVI homogeneity analyses (Appendix S7). On
370 average, displacements were up to 7 times longer in areas with high EVI homogeneity (Fig.
371 2), such as desert regions (the maximum EVI homogeneity value was 0.85). For example,
372 model predictions for 1-hour median displacements for carnivorous soaring individuals were
373 1.02 km (\pm SE 1.63 km, range = 0.62 – 1.65 km, $n = 168$) in areas of high EVI homogeneity
374 vs. 0.14 km (\pm SE 1.47 km, range = 0.10 – 0.21 km, $n = 168$) in areas of low EVI
375 homogeneity (Fig. 2a). 1-hour long-distance displacements for carnivorous soaring
376 individuals were 10.20 km (\pm SE 1.57 km, range = 6.48 – 16.07 km, $n = 168$) in areas of high
377 EVI homogeneity vs. 2.40 km (\pm SE 1.45 km, range = 1.66 – 3.48 km, $n = 168$) in areas of
378 low EVI homogeneity (Fig. 2a).

379 There was no significant difference between the slope coefficients between the 1-hour
380 and 10-day displacements for both the median and long-distance models (Appendix S8).

381 Contrary to our predictions, these results suggest that movements at both time scales were
382 equally sensitive to decreasing homogeneity.

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

389

390 **4 | DISCUSSION**

391 We have shown that EVI homogeneity is a key factor associated with avian movements,
392 where movements were on average seven times longer in areas of high EVI homogeneity
393 (e.g., deserts) compared with areas of low EVI homogeneity (e.g., mixed broadleaved and
394 needle-leaved forests). The increase in displacement with increasing homogeneity is likely a
395 reflection of the different habitat types (including microhabitat heterogeneity) required for
396 survival (e.g., food resources or tree cover for predator avoidance) and reproduction (e.g.,
397 nesting sites). Some bird species (e.g., upland sandpiper, *Bartramia longicauda*) have larger
398 home range sizes in homogeneous environments such as pastures or grasslands because the
399 structure of these habitats does not meet all of the bird's biological requirements, so that they
400 increase their ranging behaviour until their requirements are met (Stanton *et al.*, 2014;
401 Sandercock *et al.*, 2015). Therefore, landscape complementation, where a single landscape
402 includes habitat patches with different, but complementary resources within close proximity is
403 likely an important feature for shaping avian movements (Mueller *et al.*, 2009). The link
404 between movement and EVI homogeneity may also suggest that it is important to maintain
405 landscape complementarity in human-modified areas that have shifted from heterogeneous to

406 homogeneous landscapes (e.g., croplands), which may reduce the distances covered by
407 individual birds and in turn the potential negative effects of these longer travel distances (e.g.,
408 increased energetic costs).

409 Interestingly, we did not find a significant effect of the mean abundance of resources
410 contrary to our predictions and previous research on single populations of birds (Dodge *et al.*,
411 2014; Stanton *et al.*, 2014). This difference could be due to previous studies focusing on long
412 distance movements such as migration, or not including the effect of spatial arrangement of
413 resources, or both. We can rule out the possibility of spatial arrangement of resources
414 masking the effect of EVI, as we ran our models excluding EVI homogeneity and still found
415 no significant effect of EVI (Appendix S9). While vegetation indices such as EVI have been
416 shown to underlie bird behaviour (La Sorte *et al.*, 2013) and diversity patterns (Tuanmu &
417 Jetz, 2015), it may also be the case that mean EVI is not the best proxy of resources used by
418 birds, particularly on a small scale (e.g., daily movements). It is assumed that vegetation
419 indices provide information across several diet categories however, they may perform poorly
420 for non-herbivore species, specifically those that rely on scavenging. We also ran our models
421 with an interaction term between mean EVI and diet to test for differences in the response to
422 EVI across diet categories (Appendix S10). The interaction term was only significant for the
423 long-distance 10-day displacements, suggesting that we were unable to detect differences
424 between diet categories for hourly movements using EVI at a 1 km resolution. We also note
425 that we did not account for the seasonal variation in resource availability, which may impact
426 avian movements. Our study focused on terrestrial resources that are likely to capture some of
427 the resources used by waterbirds (e.g., crops), but future studies should investigate the role of
428 aquatic resources on water bird movements. Overall, productivity measures such as EVI are
429 currently the best proxy for food resources available and our results indicate that EVI

430 homogeneity is a potentially useful proxy of the spatial arrangement of resources, and has an
431 important role in shaping avian foraging movements.

432 Also contrary to our predictions, we did not find a significant effect of body mass on
433 displacements. The lack of relationship between displacement and mass could also be a result
434 of the limited range of body mass included in our database, spanning 600 g to 9.5 kg, as well
435 as the low sample size of small birds included in our study. This is due to the limited
436 availability of high-resolution data for terrestrial birds < 250 g, due to the weight of current
437 GPS tracking technologies and the limited battery life for smaller devices (López-López,
438 2016). Based on allometric relationships, birds with smaller body masses (e.g., < 600 g)
439 should travel shorter distances and use a smaller area based on reduced resource requirements,
440 energy efficiency and flight speeds in comparison to larger species (Alerstam *et al.*, 2007). As
441 tracking technologies improve, it will become possible to track smaller species and then re-
442 examine this relationship across a broader range of avian body mass.

443 Lastly, we did not find any significant differences between soaring/flapping flight and
444 flapping only flight. It is possible that flight strategy has a smaller impact on foraging
445 movements compared to migratory movements, where the trade-off between flight distance
446 and energetic costs is greater (Hedenstrom, 1993; Watanabe, 2016). Alternatively, it could be
447 that flight behaviours, such as thermal soaring, were not captured at the temporal resolution of
448 the tracking data used and our restriction to examining 2-dimensional movements (i.e., only
449 longitude and latitude). This means that individuals that use thermal soaring could be
450 covering longer distances that we are not able to detect with our current analysis (Tamburello
451 *et al.*, 2015). Due to the disproportionate increase in flight costs with body mass for flapping
452 flyers, flapping flight is more common in small species (Hedenstrom, 1993), and with the
453 inclusion of these species we might see more divergent displacement behaviours between
454 these flying strategies. It is also possible that the size of the smaller birds in our dataset that

455 are characterised as active fliers (i.e., flapping flight) only use this strategy for short periods
456 as they are still too large to energetically maintain this flight strategy for long periods, thus
457 preventing us from detecting any differences among strategies in our analysis.

458 The random effect (i.e., taxonomy) explained a large portion of the variance in avian
459 movements (~40 - 50%). Previous work has examined species-level differences in movement
460 patterns, including differences in home range size (Haskell *et al.*, 2002) and migration
461 distances/strategies (Alerstam *et al.*, 2003; La Sorte *et al.*, 2013) based on species-level traits
462 (e.g., body size and diet). Some of the variation among individuals within the same species is
463 probably due to sex, where males and females have different movement patterns during brood
464 rearing (Hernández-Pliego *et al.*, 2017). In addition, feather moult (i.e., feathers are shed and
465 regrown) may impact avian movements, including periods of flightlessness (e.g., cranes and
466 waterfowl post-breeding) and reduced aerodynamic performance of the wings (e.g., *Falco*
467 *peregrinus*) (Flint & Meixell, 2017). Variation in moult patterns and their consequences for
468 bird movement between species, populations and individuals were not considered here due to
469 lack of detailed moult data when movement was recorded. Reproduction is another vital part
470 of an individual's life history and often involves a shift in movement patterns due to the
471 distribution of mates, lekking sites or nesting site/food resources availability (Cecere *et al.*,
472 2014; Rösner *et al.*, 2014). Other environmental variables such as wind speed and direction
473 were not included in our analyses, but may also account for some of the unexplained variance
474 of our models (Mellone *et al.*, 2015; Harel *et al.*, 2016).

475 Another potential factor accounting for the within-species variation in avian
476 displacements is related animal personality, where individuals with different personalities are
477 likely to differ in their movement strategies (Patrick *et al.*, 2017; Spiegel *et al.*, 2017). For
478 example, movement patterns are expected to differ according to the boldness of individuals,
479 where bolder individuals may demonstrate more exploratory movements and use more risky

480 environments (Spiegel *et al.*, 2017). This could also be related to age and experience, where
481 individuals with more experience may be less likely to inhabit risky environments and may
482 have already identified where the reliable food patches are, further contributing to intra-
483 specific variation (López-López *et al.*, 2014).

484 A caveat of our analysis is the assumption that our calculation of the EVI and EVI
485 homogeneity values based on endpoints of displacements represent the mean resources or
486 resource homogeneity experienced by the individual while moving. In this context, without
487 high resolution data collected over long durations, it will be difficult to discern what the
488 individual exactly experienced over extended periods. Nevertheless, our results clearly
489 demonstrate a relationship between resources and avian movements because we found similar
490 results using models based only on the end coordinates of displacement segments and models
491 using the weighted mean along the entire straight-line displacement segments (Appendix S7).
492 As higher resolution tracking data becomes more common, future studies can begin to discern
493 foraging behaviours from movement tracks and examine foraging patterns in response to
494 resources at a macroecological scale.

495

496 **5 | CONCLUSION**

497 In conclusion, our study is the first to examine the relationship between the
498 distribution of resources and non-migratory avian movement patterns across multiple species
499 and regions. We have demonstrated the importance of resource spatial distribution on shaping
500 movements, highlighting the possible effects of landscape homogenisation, where individuals
501 may need to fly farther to meet their ecological requirements. It is possible that continuing
502 habitat homogenisation (e.g., intensification of agriculture) in landscapes with a naturally high
503 diversity of habitats will have negative impacts on the abundance and diversity of birds

504 (Jerrentrup *et al.*, 2017) due to the loss of complimentary habitats. This may in turn result in
505 greater movement requirements and higher energy expenditure.

506

507 **Table 1.** Model coefficients, r-squared, p values and sample sizes of linear mixed effects
508 models predicting the median and 0.95 quantile of individual displacements for 1 and 10-day
509 time scales. Predictor variables included fixed effects for body mass (Mass), Enhanced
510 Vegetation Index (EVI), EVI homogeneity (EVI_Homogeneity), diet (H = herbivore and O =
511 omnivore coefficients), flight type (FlightT; soaring coefficient values shown here) and
512 migratory status (MigStatus_NM; non-migratory coefficient values shown here). The model
513 also included a nested random effect accounting for the taxonomy, and a Gaussian spatial
514 autocorrelation structure.
515

	1 hour				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)	0.283	0.175 (0.174)	0.419	0.155 (0.237)	0.532	-0.427 (0.264)	0.145
EVI	-0.58 (0.436)	0.185	-0.053 (0.328)	0.872	-0.225 (0.409)	0.582	0.795 (0.484)	0.102
EVI_Homogeneity	1.198 (0.323)	<0.001	0.881 (0.23)	<0.001	2.427 (0.311)	<0.001	2.292 (0.434)	<0.001
Diet (H)	0.088 (0.33)	0.807	-0.065 (0.272)	0.827	0.056 (0.302)	0.857	0.017 (0.403)	0.968
Diet (O)	0.129 (0.56)	0.833	-0.654 (0.395)	0.196	-0.359 (0.459)	0.456	-0.908 (0.553)	0.139
FlightT_Soar	0.469 (0.32)	0.281	0.195 (0.224)	0.476	0.123 (0.315)	0.723	-0.202 (0.419)	0.663
MigStatus_NM	0.231 (0.148)	0.259	0.213 (0.099)	0.164	0.252 (0.195)	0.232	0.082 (0.206)	0.699
R² Marginal	0.376		0.360		0.261		0.102	
R² Conditional	0.696		0.706		0.518		0.566	
Species	19				35			
Individuals	168				356			

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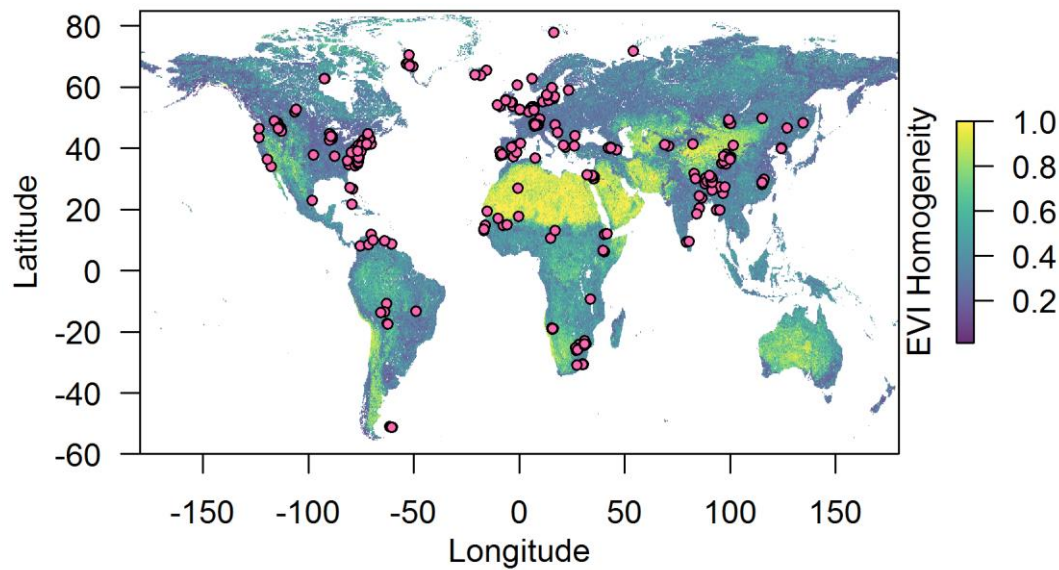
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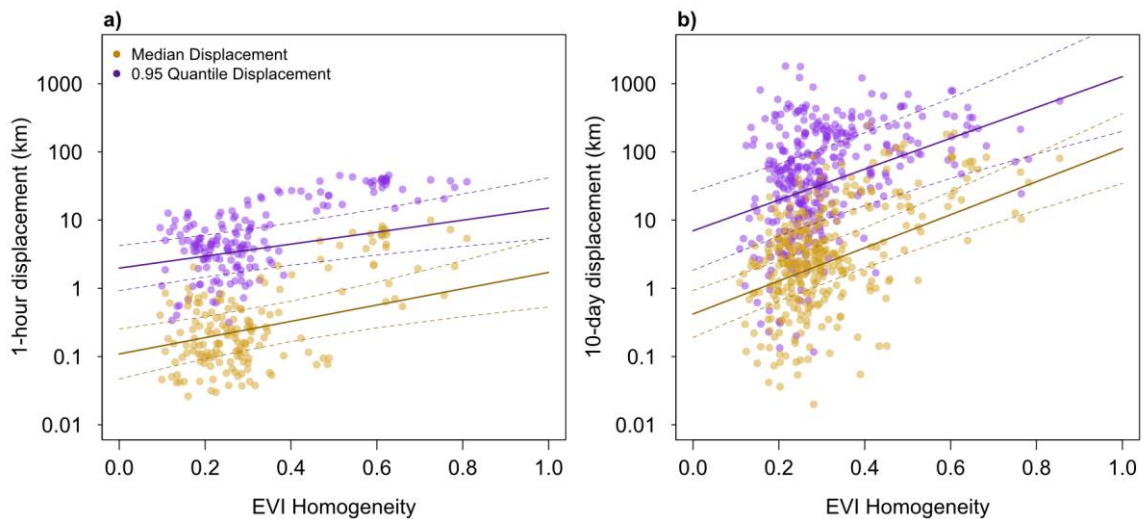
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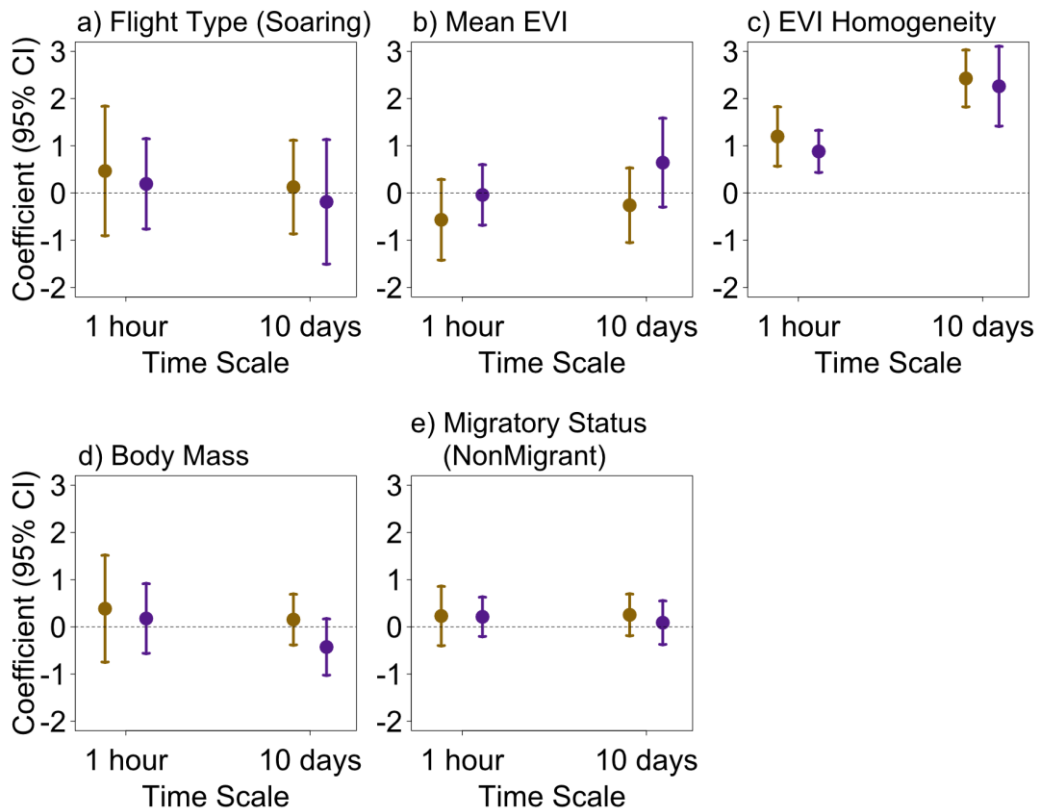
528 **Figure 1** Global patterns of Enhanced Vegetation Index (EVI) homogeneity spanning from
 529 low (dark blue) to high (yellow). The pink points represent the average longitude and latitude
 530 position for each of the 386 individuals across 36 species included in the study.

531



532

533 **Figure 2** Avian (a) 1-hour and (b) 10-day median (0.5 quantile; yellow) and long-distance
 534 (0.95 quantile; purple) displacements with increasing EVI homogeneity. Plots include
 535 regression lines from the linear mixed effects models and 95% confidence intervals. An EVI
 536 homogeneity value of 0 indicates areas of low homogeneity, and values 0.8 represent areas of
 537 high homogeneity at a local scale.



550

551 **Figure 3** Model coefficients (\pm 95% CI) of linear mixed effects models predicting avian
 552 displacements using (a) body mass, (b) mean Enhanced Vegetation Index (EVI), (c) EVI
 553 homogeneity, (d) flight type (soaring), and (e) migratory status (non-migratory). Models were
 554 run for the median (yellow) and long-distance (0.95 quantile; purple) displacements of each
 555 individual calculated across different time scales. When the error bars cross the horizontal line
 556 the effect is not significant. See Table 1 for details.

557

558 DATA ACCESSIBILITY

559 The data used in this study are available at datadryad.org. Most of the animal movement data
 560 originates from and are publically available from www.movebank.org.

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562

563 ACKNOWLEDGEMENTS

564 The authors are grateful for financial and logistical support from the Robert Bosch
 565 Foundation, Goethe International Postdoctoral Programme, People Programme (Marie Curie
 566 Actions) of the European Union's Seventh Framework Programme FP7/2007-2013/ under

567 REA grant agreement no [291776], ‘Juan de la Cierva - Incorporación’ postdoctoral grant,
568 Spanish Ministry of Economy and Competitiveness (IICI-2014-19190), 3M Gives, COWRIE
569 Ltd., U.K. Department for Energy and Climate Change, Environmental Impact Assessment
570 study for Kriegers Flak offshore wind farm funded by Energinet.dk, Hawk Mountain
571 Sanctuary, Irish Research Council GOIPD/2015/81, MAVA Foundation, Green Fund of the
572 Greek Ministry of Environment, Minerva Center for Movement Ecology, NASA Award
573 NNX15AV92A, NSF Division of Biological Infrastructure Award 1564380, German
574 Aerospace Center Award 50JR1601, Netherlands Organization for Scientific Research grant
575 number VIDI 864.10.006, NSF Award ABI-1458748, Penguin Foundation, Australian
576 Research Council, Solway Coast AONB Sustainable Development Fund, Scottish Natural
577 Heritage, BBC, National Trust for Scotland, Heritage Lottery Fund, COWRIE Ltd., DECC,
578 U.K. Department for Energy and Climate Change, NASA's Arctic Boreal Vulnerability
579 Experiment (ABoVE) (#NNX15AV92A), the National Key R&D Program of China
580 (2016YFC0500406), The Bailey Wildlife Foundation, The Nature Conservancy, Biodiversity
581 Research Institute, the Bluestone Foundation and The U.S. Department of Energy (DE-
582 EE0005362), U.S. Army Aberdeen Proving Ground, The Center for Conservation Biology,
583 ArcticNet, Government of Nunavut, Nunavut Wildlife Management Board, Canadian
584 Circumpolar Institute, The MPG Ranch and Whooping Crane Eastern Partnership
585 (www.bringbackthecranes.org). JPS was supported by a post-doctoral scholarships from FCT
586 – Fundação para a Ciência e tecnologia (SFRH/BPD/118635/2016). Thank you to Mitch
587 Weegman, Ed Burrell, John Skilling, Arthur Thirlwell and Carl Mitchell for assistance with
588 catching and data download for the Greenland white-fronted geese, Richard Hesketh for the
589 Svalbard barnacle geese and Alyn Walsh, Maurice Cassidy, Richard Hesketh for the
590 Greenland barnacle geese. Movebank is hosted by the Max Planck Institute for Ornithology
591 and the Movebank Data Repository is hosted by the University of Konstanz.

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593

594 **AUTHOR CONTRIBUTIONS**

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

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744 **BIOSKETCH**

745 Marlee Tucker is a postdoctoral researcher who is interested in large scale patterns in ecology
746 and biogeography, and species vulnerability to changing environments. Marlee’s research
747 encompasses macroecological questions related to allometric scaling, predator-prey
748 interactions and animal movement.

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762 **SUPPLEMENTARY MATERIALS**

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

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

768 **Appendix S3** Example of data selection process for migratory species.

769 **Appendix S4** Environmental data annotation summary.

770 **Appendix S5** Data used in the analyses.

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

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

774 **Appendix S8** Comparison of the EVI Homogeneity slope coefficient estimates.

775 **Appendix S9** Results for models excluding EVI Homogeneity.

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