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Title: Do long-distance migratory birds track their niche through seasons?

Running title: Migratory birds track seasonal niche

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Data accessibility

All data are publicly available; bird range maps at www.birdlife.org, climate data at www.worldclim.org, bird trait data at http://dx.doi.org/10.6084/m9.figshare.c.3306933, bird phylogenetic data at www.birdtree.org, NDVI at http://ecocast.arc.nasa.gov/data/pub/gimms/3g.v0/, and vegetation cover at http://glcf.umd.edu/data/landcover/data.shtml. The species-specific values for niche overlap, niche tracking and traits are contained in Appendix S2.

Abstract

Aim

Seasonal migration by animals is an extensively studied, global phenomenon. Yet, we still lack a general understanding whether migrants track their niche between summer and winter ranges and the mechanisms influencing this behaviour. Here, we assessed the degree of seasonal niche tracking in Holarctic long-distance migratory birds (n=717; excluding very rare species) and evaluate the influence of biogeographic (regional and range characteristics) and ecological (trophic) factors on tracking.

Location

Global.

Taxon

Birds.

Methods

We calculated seasonal niche overlap by means of ordination, and estimated the degree of niche tracking using similarity tests. Niche tracking was evaluated for two different environmental predictor sets: climate and vegetation productivity (reflecting resource selection) versus climate and land cover (reflecting habitat choice). Multivariate phylogenetic regression was used to evaluate effects of biogeographic and ecological traits on niche tracking.

Results

We found significant niche tracking in 65-95 % of species with a higher proportion of species significantly tracking climate and land cover compared to climate and vegetation productivity. Traits explained 12-18% of the variance in niche tracking with strong regional differences, a negative effect of migration distance and positive effects of range size on niche tracking. The effects of niche breadth and trophic traits were less pronounced and varied between environmental predictor sets.

Main conclusions

Our results indicate that at coarse spatial resolution, long-distance migratory species tend to track their niche and select largely similar environments through seasons. Stronger niche tracking of land cover could reflect conservatism in habitat selection across seasons, for example for foraging and roosting. This conservatism towards land cover should be considered when making predictions to future environments. A better understanding of the factors that constrain seasonal range limits will be critical for predicting how migration patterns could respond to future environmental changes.

Keywords: animal migration, environmental niche, functional traits, geographic range, niche breadth, niche tracking, species distribution modelling

Introduction

Animal migration is a fascinating, global phenomenon with billions of individuals travelling between disjunct regions of the world on a regular basis (Fryxell & Sinclair, 1988; Alerstam *et al.*, 2003; Milner-Gulland *et al.*, 2011; Bauer & Hoye, 2014). These movements likely occur because migrants exploit seasonal resource abundance peaks (Fryxell & Sinclair, 1988; Tellería & Pérez-Tris, 2003; Somveille *et al.*, 2015; Gómez *et al.*, 2016). A yet underexplored issue is to what extent migratory animals seek comparable environments throughout the year and thus to what extent they occupy similar niches in their winter and summer ranges (Milner-Gulland *et al.*, 2011). Birds constitute the best-studied group of migratory animals. Several studies suggest that not all migratory birds track their environmental niche between seasons equally well (Boucher-Lalonde *et al.*, 2014; Laube *et al.*, 2015), and some birds have been found to instead switch their environmental niche between seasons (Joseph & Stockwell, 2000; Martínez–Meyer *et al.*, 2004; Nakazawa *et al.*, 2004). Yet, little is known about the relative proportion of *niche tracking* vs. *niche switching* strategies in migratory animals and the species characteristics or seasonal range features that determine these behaviours (Martínez–Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Laube *et al.*, 2015; Gómez *et al.*, 2016). Here, we quantify the degree to which long-distance migratory birds of the Holarctic track their niches between seasons, and we investigate the role of geographic and ecological factors in determining the degree to which species track their niches. This knowledge is critical for predicting how and why species migratory strategies could be influenced by climate change, and for guiding future monitoring and modelling efforts aimed at the conservation of migratory animals.

An animal's capacity to track suitable environments between seasons (i.e. its environmental niche) may be affected by biogeographic factors, such as geographic origin and range size, and by ecological factors, such as body mass and diet specificity, resulting in a number of testable hypotheses. For instance, the region of origin may affect a species' capability to track its niche because broad geographic zones differ in available landmass and spatial arrangement of suitable habitats and climates. This may all translate into different migration distances, or barriers that stop or funnel migration. In addition, the geographic position and size of the breeding and overwintering ranges may affect the distance travelled between those geographic areas (Laube *et al.*, 2015; Gómez *et al.*, 2016). As long-distance migration is energetically costly (Kranstauber *et al.*, 2015), migrants have to balance the benefits of niche tracking against travel distances and movement costs (Laube *et al.*, 2015; Gómez *et al.*, 2016). It may thus be expected that a species' ability to track suitable environments decreases with increasing breeding to overwintering range distances. Correspondingly, we hypothesize reduced niche tracking (or even niche switching) for species breeding in high-latitudes (Gómez *et al.*, 2016), simply because the cold biomes of high latitudes in the Northern hemisphere are further apart from their analogous counterparts in the Southern hemisphere than warmer regions closer to the equator. Furthermore, seasonal niche tracking may increase with environmental niche breadth or range size of the species (Gómez *et al.*, 2016). Also, we expect the degree of niche tracking to be influenced by ecological and behavioural characteristics. For example, as flight is energetically more costly in large birds (Pennycuick, 1969; Hedenström, 1993), we may expect a negative correlation between the degree of niche tracking and species body mass (Watanabe, 2016), at least for migrants employing an active flight mode. Diet specificity may also affect species niche tracking behaviour, as generalists are by definition more flexible than specialist species regarding required resources.

Our objectives were (i) to estimate seasonal niche tracking in long-distance migratory birds of the Holarctic, and (ii) to test which species characteristics (biogeographic and ecological attributes) explain variation in the degree of niche tracking between species. Although migration also occurs in the tropics, we here concentrate on long-distance migrants breeding in the Holarctic (n=717, excluding the very rare species), because these show distinct latitudinal migration patterns and follow comparable resource pulses triggered by northern-hemisphere summer and winter seasons (Newton, 2007). First, we estimated birds' breeding (May-July) and overwintering (November-January) niches using ordinations of environmental data (Broennimann *et al.*, 2012). Second, we calculated niche overlap between seasons and, third, we estimated niche tracking by similarity tests that evaluate whether niche overlap was higher than expected by chance given the environmental conditions. Niche tracking was evaluated for two different predictor sets: climate and vegetation productivity and climate and land cover. We assumed that climate is an important determinant of the broad-scale niche of migratory birds and thus included it in both predictor sets. However, the environmental niche of a species results from a complex combination of multiple components, including also local food resource availability as well as habitat choice for foraging and shelter in addition to climate (Guisan & Thuiller, 2005; Soberón, 2007). Hence, we evaluated whether migrants would track resource availability (approximated by vegetation productivity) and habitat (approximated by proportional land cover) across seasons in combination with climate. Finally, we evaluated our hypothesized relationships between species' degree of niche tracking and biogeographic and ecological factors (Table 1). To account for non-independence between species and their traits, species phylogenetic relatedness was controlled for in all statistical analyses.

Tables

Table 1. Potential biogeographic and ecological factors affecting niche-tracking ability of long-distance migratory birds that were tested in this study. Potential effects of each predictor on species niche-tracking abilities can be positive (+), negative (-), or mixed (+/-).

Category	**Predictors**	**Hypothesised effect**	**Hypotheses**
Region	• Region of origin (i.e. Nearctic, Western and Eastern Palearctic; as categorical variables or as breeding longitude)	+/-	The shape of continents leads to (i) different spatial arrangement of suitable environments resulting in shorter or longer migration distances and, thus, differences in migration costs required for complete niche tracking, or (ii) to differences in the occurrence of migration barriers.
Range position	• Distance between breeding and overwintering ranges	-	Niche tracking ability decreases with migration distance because of increasing energetic and temporal constraints of migration.
	• Breeding latitude	-	Species breeding in colder regions (i.e. high-latitude) need to fly longer distances than species breeding in warmer regions (i.e. low latitudes) to reach comparable biomes in summer and winter, which results in a lower degree of niche tracking.
Range size	• Range size	+	Species with large range sizes have a higher probability of finding comparative environments in opposing seasons.
	• Niche breadth	+	Broad environmental tolerances lead to a higher probability of finding comparative environments in opposing seasons.

Ecological traits	• Body mass	-	Body mass increases energetic cost of migration (particularly in birds employing active flight strategies), resulting in lower degree of niche tracking.
	• Diet	+/-	Diet specificity will increase niche tracking if the resource correlates well with climate and vegetation (e.g. fruits), or will decrease niche tracking if the resource does not correlate well with environment (e.g. vertebrates).

Methods

Species and environmental data

Information on summer breeding and wintering ranges were derived from a global dataset of the world's bird species distributions (BirdLife International & NatureServe, 2014). We checked all synonyms, matched species names with phylogenetic and trait data sets (Jetz *et al.*, 2012; Wilman *et al.*, 2014), and excluded species whose taxonomic classification changed recently in one of the above databases. We applied a number of filtering steps to identify long-distance migrants of the Holarctic: (1) species had distinct summer breeding and wintering ranges; (2) the summer breeding range centroid was North of 30°N; and (3) the minimum latitudinal distance between summer and winter range centroids was 10° (ca. 1100 km). (4) We gridded the summer and winter range polygons at a 0.5° resolution, and considered only those species that had at least 40 presences in their summer and 40 presences in their winter ranges. A species was considered as present if its range polygon covered the centre of the gridded cell. Using these filtering steps, we selected n=717 extant long-distance Holarctic migratory birds for subsequent analyses (Fig. 1). Environmental niches of Nearctic and Palearctic breeding birds were analysed separately to control for biogeographic history (329 Nearctic migrants breeding west of 18°W, and 388 Palearctic migrants).

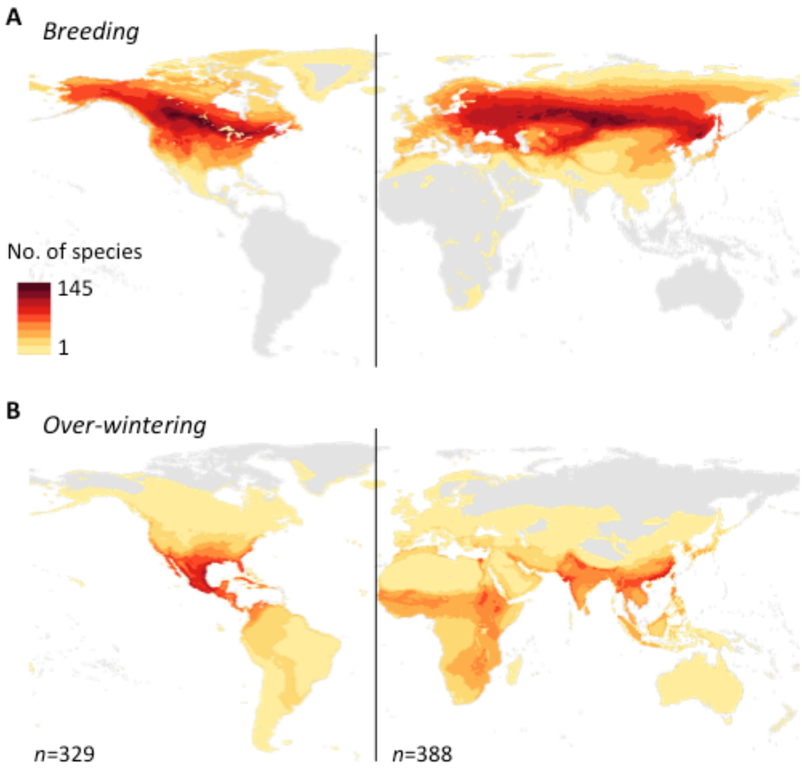

Figure 1. Species richness of Holarctic long-distance avian migrants in summer breeding (A) and wintering (B) ranges. The solid line marks the divide (LON 18° W) between Nearctic (n=329) and Palearctic breeders (n=388).

We considered two different environmental predictor sets to analyse niche tracking, (i) climate + NDVI and (ii) climate + land cover. Climate at 0.5° resolution was represented by mean temperature and total precipitation during the summer breeding (May-July) and wintering season (November-January) and was derived from WorldClim over the period 1960-1990 (Hijmans *et al.*, 2005). Similarly, we calculated the mean normalized differenced vegetation index (NDVI) separately for each season (1982-2000; GIMMS AVHRR Global NDVI; Pinzon & Tucker, 2014). Proportional land cover at 0.5° resolution was calculated from the 1km UMD Land Cover Classification (Hansen *et al.*, 2000) and was constant throughout the year. We aggregated the original land cover classes into seven broad categories (proportional cover of water, forest, shrubland, grassland, cropland, bare ground, urban per 0.5° grid cell; SI Appendix, Table S1) for our analyses. We verified the appropriateness of the predictor sets for describing summer and winter ranges using statistical species distribution models (Guisan & Zimmermann, 2000), which showed good to excellent predictive performance (area under the receiver operating characteristic curve AUC > 0.7 (Hosmer & Lemeshow, 2000) for all species) in repeated (n=3) 70:30 split-sample tests for both seasons and both predictor sets (mean

AUC ± SD for climate + NDVI: summer 0.96±0.03, winter 0.98±0.02; climate + land cover: summer 0.92±0.02, winter 0.92±0.02).

Niche tracking

Our niche tracking analyses were based on the protocols described in Broennimann *et al.* (2012) and provided in R package *ecospat* (Broennimann *et al.*, 2016), which involves three basic steps: (1) calculating density of presences and available environment along niche axes for summer breeding and winter ranges, (2) calculating niche overlap between summer breeding and winter ranges along the niche axes while correcting for overall environmental availability, and (3) calculating niche tracking by testing for significant deviation of niche overlap from random expectation using similarity tests.

For (1), we calculated the density of species' presences and of available environmental factors along the axes of a principal components analysis that summarises the main environmental variation. The original algorithms for niche overlap analyses (Broennimann *et al.*, 2012; Broennimann *et al.*, 2016) included only one- and two-dimensional kernel density estimators, and thus only allowed consideration of two niche axes. Here, we extended those algorithms by a multivariate kernel density smoother to allow consideration of up to four niche axes (codes provided in SI Appendix). We estimated species' niches for two different predictor sets: (i) climate + NDVI, and (ii) climate + land cover. For the first predictor set, all environmental niche axes (three variables) could be included in the kernel estimation, while for the second predictor set (nine variables) only the first four PCA axes could be included. These axes explained 65% and 68% of the environmental variation in Palearctic and Nearctic, respectively (SI Appendix, Figs. S1).

For (2), we calculated niche overlap between summer breeding and winter ranges along the chosen niche axes using Schoener's *D* metric (Schoener, 1968) while correcting for differences in relative availability of environments by dividing the density of presences by the density of the environment from the entire environmental space from summer and winter ranges (Broennimann *et al.*, 2012). *D* varies between 0 (no overlap) and 1 (complete overlap).

For (3), we used similarity tests to quantify niche tracking. This was done by comparing the observed niche overlap metric *D* between summer and winter niches against a simulated niche overlap *D* metric. To calculate the simulated *D*, the entire observed density of presences of one range was shifted randomly in PCA space. This was done by randomly selecting the simulated niche centre (the centre of density of presences) within available environments in the PCA space (Broennimann *et al.*, 2012). We repeated these permutations 200 times (100 permutations where the niche of the summer range was assumed to be the observed niche while the niche of the winter range was shifted, and another 100 permutations, where the niche of the winter range was assumed to be the observed niche while the niche of the summer range was shifted). For each permutation, we recorded simulated D, which was defined as the niche overlap D between simulated and observed niche. Then, over all 200 permutations we calculated the standardized effect size SES_D = (observed D – mean of simulated D)/standard deviation of simulated D. Significant niche switching was identified for SES_D smaller than -1.64 (i.e. the 5% percentile of a Normal distribution, indicating that seasonal niches are more dissimilar than expected by chance), while significant niche tracking was identified for SES_D larger than 1.64 (i.e. the 95% percentile of a Normal distribution, indicating that seasonal niches are more similar than expected by chance).

Throughout the text, we refer to the raw measure D as niche overlap, and to SES_D as niche tracking.

Trait analyses

Trait information were extracted from Wilman *et al.* (2014) and phylogenetic information from Jetz *et al.* (2012). We included the following functional traits: body mass and dominant diet type (invertebrates; vertebrates incl. fish and carrion; fruits and nectar; plants and seeds); all species that could not be assigned to one dominant diet category were classified as omnivores (Wilman *et al.*, 2014). Additionally, we considered breeding longitude and breeding latitude (calculated from summer range centroids), the latitudinal distance between summer and winter range centroids, summer and winter range size, and niche breadth in trait analyses. Niche breadth was quantified following Laube *et al.* (2015), by calculating the Shannon index from environmental occupancy (the density of species occurrences in PCA space divided by the density of available environment; cf. niche tracking analyses above), which takes into account the number of occupied grid cells and the evenness in occupancy. From the literature, we compiled information on flight mode, distinguishing between the broad categories of mainly active (flapping) and mainly passive (soaring) flight (SI Appendix, Table S1).

We used phylogenetic regression to estimate the effect of the biogeographic and ecological traits on niche tracking (Table 1) while controlling for non-independence between species and their traits due to phylogenetic relatedness (Paradis & Claude, 2002) using the R package *phylolm* (Ho & Ane, 2014). For longitude, we included linear and quadratic terms to test for non-linear effects. Parsimonious models were identified using AIC-based stepwise variable selection. Variable importance was calculated based on an algorithm where each variable was permutated randomly (n=99) in order to mimic the absence of the variable in the model (Strobl *et al*., 2007). Then, importance was estimated according to the difference in deviance explained by the models with and without permutation. In the main text, we present trait analyses including all long-distance migrants (n=717). Additionally, we repeated trait analyses including only those migrants employing active flight strategies (n=637), to test for potentially confounding effects of different energetic costs of active vs. passive flight on niche tracking. Results for active flying migrants are presented in the SI appendix.

All analyses were conducted using R version 3.2.3 (R Core Team, 2015).

Results

Estimated seasonal niche overlap *D* for climate + NDVI ranged 0.00-0.56 (mean=0.18, sd=0.12), and for climate + land cover ranged 0.00-0.56 (mean=0.21, sd=0.11). Niche overlap *D* estimated for climate + land cover showed significant differences across regions, with Eastern and Western Palearctic migrants (east and west of 65°E) showing larger *D* than Nearctic migrants (west of 18°W). No such differences were apparent for climate + NDVI niche overlap comparison (Fig. 2). Overall, niche overlap for the two different predictor sets (climate + NDVI vs. climate + land cover) was significantly correlated (Pearson correlation coefficient *r*=0.67, t=24.22, p<0.001)(Fig. 3). The amount of niche tracking estimated from similarity tests differed between predictor sets with 65 % of species significantly tracking their climate + NDVI niche, and 95 % of species significantly tracking their climate + land cover niche (Figs. 2-3). We identified no case of significant niche switching. In addition, niche overlap *D* was significantly larger for migrants employing mainly passive flight and also the proportion of niche tracking migrants was slightly larger for migrants employing mainly passive flight (SI Appendix, Fig. S2).

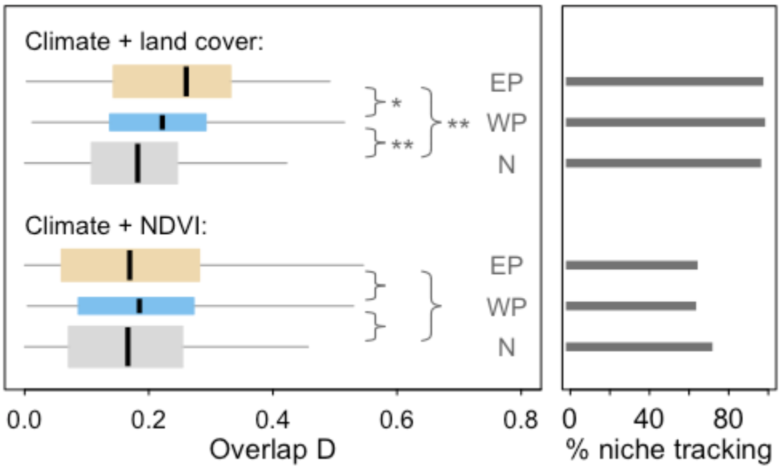

Figure 2. Niche overlap *D* between summer breeding and winter ranges (left) and proportion of species significantly tracking their seasonal niche (right). We distinguish long-distance migratory birds breeding in

Nearctic (N), Western Palearctic (WP) and Eastern Palearctic (EP). Niche overlap *D* was estimated along niche axes obtained from PCA for the two predictor sets climate + NDVI, and climate + land cover; outliers are not displayed. Asterisks indicate significant differences following a two-tailed Wilcoxon rank sum test ($p < 0.01$; * $p < 0.05$). The width of the boxplots is proportional to the species numbers within geographic regions (N *n*=329; WP *n*=132; EP *n*=256). The barplot (right) indicate results from the similarity tests where the niche (in PCA space) during summer is compared to random niches during winter and vice versa.**

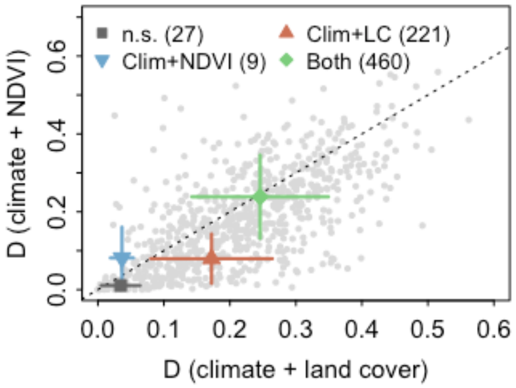

Figure 3. Correlation between estimated niche overlap *D* for the two predictor sets (climate + NDVI, climate + land cover). Grey points show overlap *D* for all species (n=717). Coloured points show the mean *D* (with standard deviation) for species showing no significant niche tracking (darkgrey), species showing significant niche tracking only for climate + NDVI (blue), only for climate + land cover (darkred), and species showing significant niche tracking for both predictor sets (green) with the number of species shown in brackets.

The considered traits explained 12 % and 18 % of the variance in niche tracking (SES_D) for the predictor sets climate + NDVI and climate + land cover, respectively. The importance of biogeographic and ecological traits in predicting niche tracking behaviours varied across traits (Fig. 4). The breeding region was most important for explaining niche tracking of climate + land cover while factors related to range size and range position were most important for explaining niche tracking of climate + NDVI. Among the traits related to range position, migration distance had a consistent negative effect on niche tracking, while breeding latitude had a significant negative effect only for climate + land cover niche tracking. Summer and winter range sizes showed significant positive effects on niche tracking. Niche breadth showed a significant negative effect for climate + NDVI niche tracking. Trophic traits were the least important predictors of climate + NDVI niche tracking with significant positive effects of body mass and frugivorous diet. By contrast, trophic traits had no effect on climate + land cover niche tracking. When considering active flight only, the effects of the considered biogeographic and ecological traits on niche tracking were largely consistent except for the diet traits that had no effect in any of the environmental predictor sets (SI Appendix, Fig. S3).

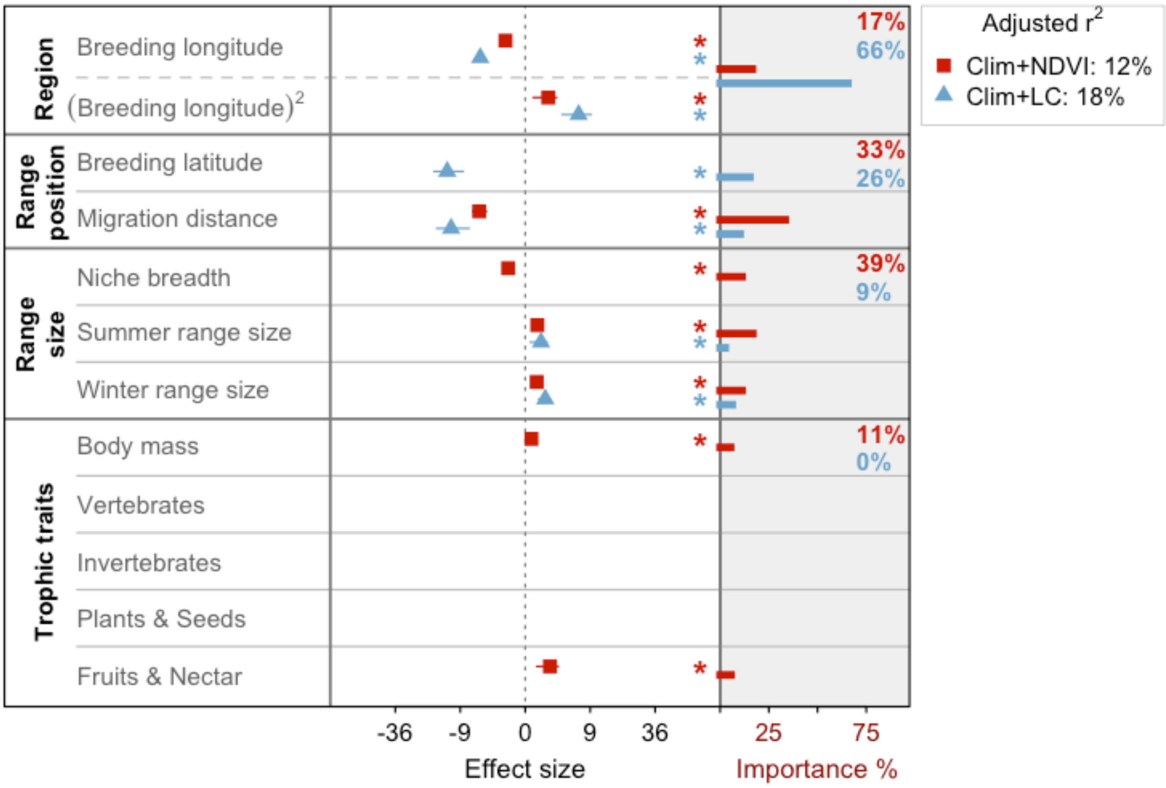

Figure 4. Relationship of species niche tracking with biogeographic and ecological factors. Niche tracking is given by the standardised effect size *SES_D* estimated from niche similarity tests. To explain *SES_D* values from traits, multivariate models were estimated by phylogenetic regression using AIC-based stepwise variable selection (n=717). Asterisks indicate significant coefficients (p<0.05). Bars indicate importance of each variable selected in the final model (note that linear and quadratic terms of longitude are summarised into a single importance value), and given percentages sum the variable importance for the four different categories of biogeographic and ecological factors (cf. Table 1). Overall explained variance is given by the adjusted r^2 of the multivariate model.

Discussion

Every year, billions of animals migrate large distances between their breeding and overwintering ranges. An outstanding question is whether these migratory species select largely similar environments through seasons. Using a cross-continental analysis on all but the very rare long-distance migratory birds breeding in the Holarctic, we demonstrate that most long-distance migrants do significantly track their broad-scale environmental niches through seasons indicating strong niche conservatism at large spatial scales. Our analyses rely on coarse-scale range maps of species and should be interpreted cautiously because of potential range size overestimation especially in winter ranges. Nevertheless, our results indicate that factors related to region, range position and range size seem more important in determining seasonal niche tracking at large spatial scales than ecological factors related to trophic traits. A better understanding of the factors that constrain seasonal range limits will be crucial for improved prediction of how migration patterns could respond to future climate changes as such changes have the potential to affect ecosystem functions worldwide (Bauer & Hoye, 2014).

We explored seasonal niche tracking at broad spatial scales and using two different predictor sets. Overall, our results indicate that long-distance migratory birds largely track their niche through seasons with more than 65 % of the species selecting more similar environments than expected by chance. This is well in line with previous findings on new world warblers that identified significant tracking of climatic niches in 73 % of migrants (Gómez *et al.*, 2016). Other studies had reported niche trackers and niche switchers but are not directly comparable as their niche overlap measures were based on geographic projections (e.g., Martínez–Meyer *et al.*, 2004; Nakazawa *et al.*, 2004) which could be biased by differing spatial structure of environments in the opposing seasons (Broennimann *et al.*, 2012), or because niche tracking and switching was not tested explicitly by similarity tests (e.g., Laube *et al.*, 2015). Here, we estimated stronger niche tracking for climate and land cover compared to climate and vegetation productivity. This indicates that at coarse spatial resolution species tend to select similar environments, but are slightly less conservative in respect to vegetation productivity than to land cover. This seems to imply strong conservatism in important attributes such as in the foraging niche and in other behaviours such as roosting that are better reflected in land cover types than in vegetation productivity. Stronger seasonal niche conservatism for land cover also suggests that land use and land cover are important predictors for projecting species response to global change, while studies focussing on breeding ranges alone mostly found climate to be a more important predictor (Hockey *et al.*, 2011; Howard *et al.*, 2015).

We explored four main hypotheses for how biogeographic and ecological characteristics influence the degree of seasonal niche tracking (Table 1). The considered traits explained 12-18 % of the variation in seasonal niche tracking, indicating that large-scale niche tracking is at least to some extent related to certain species characteristics. Overall, important generalities emerged. First, we found strong support for our hypothesis that geographic origin affects seasonal niche tracking, which was true for both predictor sets although much more pronounced for climate and land cover niche tracking. As we used the standardised effect sizes from similarity tests to assess niche tracking rather than the raw niche overlap values, the results are not biased by availability of environment but must be caused by other geographic features. For example, differences in migration routes could affect niche tracking through migration costs in terms of energy and time (Hedenström, 1993; Wikelski *et al.*, 2003) and atmospheric conditions among others (Sapir *et al.*, 2011; Kranstauber *et al.*, 2015). Additionally, barriers such as oceans, mountains and deserts may limit migration and niche tracking abilities differently between continents, for instance by retaining species in areas of lower habitat suitability and thus reducing the niche tracking abilities.

The trait analyses also corroborated our second hypothesis that increased migration cost due to longer migration distance could reduce niche tracking. Overall, species with large migration distance are less likely to track their climate and vegetation productivity or climate and land cover niche through seasons. Previous studies found either no relationship between migration distance and niche overlap, as was the case for topo-climatic niches of New World warblers (Gómez *et al.*, 2016), or found a negative relationship only when considering land cover niche overlap, as was shown for *Sylvia* warblers (Laube *et al.*, 2015). Our study thus provides new evidence that migratory distance between breeding and over-wintering grounds may strongly affect niche tracking. Breeding latitude, on the other hand, showed mixed results. In line with our initial hypothesis, it had a significant negative effect on climate and land cover niche tracking. By contrast, breeding latitude had no effect on climate and NDVI niche tracking. Thus, more northerly breeding grounds could incur higher migration costs and decrease niche tracking ability in long-distance migrants but, given the inconsistency between predictor sets, this conclusion cannot be generalized.

Third, we found support for increased niche tracking in species with larger range sizes but no support for increased niche tracking with wider niche breadth. Large range sizes increased the probability of finding comparable environments in opposing seasons for both predictor sets. Such a positive effect of range size, after controlling for statistical bias through similarity tests, could indicate other biotic controls on seasonal niche tracking. Among the factors that are hypothesized to correlate with range size are traits such as habitat niche, diet niche, life history traits such as fecundity, dispersal ability, body size, historical legacies (related both to geographic and evolutionary factors) and interspecific interactions (Brown *et al.*, 1996; Laube *et al.*, 2013). In our study, we separately assessed the effects of diet, body size, niche breadth, and controlled for phylogenetic history (i.e. using phylogenetic regressions). By contrast, dispersal ability, life history characteristics (fecundity) and interspecific interactions could not be evaluated, but are interesting candidates for future (population-level) analyses of seasonal niche tracking (Gómez *et al.*, 2016). For niche tracking of climate and vegetation productivity, we found an unexpected negative effect of niche breadth. This effect could be related to the calculation of niche breadth, which considers the total annual niche of the species. However, the range of temperature and precipitation values experienced in winter seems to be larger than that experienced in summer while no such effect was found for NDVI (Fig. S4). Thus, the negative effect of niche breadth on niche tracking of climate and vegetation productivity could actually mirror a low seasonal overlap in the temperature niche and precipitation niche.

Last, we only found weak support for our fourth hypothesis related to trophic traits. In contrast to our expectation, we found a positive effect of body mass on niche tracking of climate and vegetation productivity although this effect vanished when considering active flight only. Thus, overall, our analyses suggest that body mass has no significant effect on seasonal niche tracking in long-distance migratory birds. Functional traits related to diet also did not seem to play an important role in niche tracking. We only found a significant positive effect of frugivorous diet on niche tracking of climate and vegetation productivity. This result supports our hypothesis that diet specificity will increase niche tracking if the resource correlates well with climate and vegetation as in fruits, but seems not to be generalizable across environmental predictor sets. Overall, seasonal niche tracking at large spatial scales seems to have little functional signals but is primarily determined by geographic and potentially range size related effects.

These results are contingent on broad-scale environmental niches inferred from range maps. Generally, range maps may not be equally precise in all species, may include a high number of false presences (Hurlbert & Jetz, 2007), and may have better evidential support in the summer than in the winter ranges (Brown *et al.*, 1996), which could potentially bias our analyses. Here, we quantified niche overlap in environmental space using ordination and kernel density estimation, which should reduce the problem of spatial bias in occurrence records (Broennimann *et al.*, 2012; Gómez *et al.*, 2016). Also, we tried to reduce potential bias by controlling for range size effects using similarity tests. For future analyses, it would be desirable to quantify seasonal niche tracking at finer spatial scales and possibly at population-level using occurrence records that become increasingly available, for example through eBird data portal (www.ebird.org). Yet, such citizen science data currently suffer from uneven sampling efforts and size and from potential spatial biases especially in winter ranges.

With increasing loss of biodiversity due to global environmental change, there is a strong need to forecast the species' responses to these changes (Urban *et al.*, 2016; Zurell *et al.*, 2016). This is especially challenging in long-distance avian migrants, as they are affected by environmental conditions in different parts of the world. Our results identify two important questions for migratory bird responses to global change. (i) Which factors limit the range of a species, and how plastic are species seasonal niche requirements? The large proportion of significant niche tracking for climate and vegetation productivity and in particular for climate and land cover indicate that abiotic environmental variables other than climate also may be important for predicting species response to climate change. (ii) How will migration strategies respond to global change? Our results suggest that migration cost plays an important role in determining the degree of niche tracking. Thus, if climate and land use change lead to an increased distance between suitable breeding and overwintering ranges, this could then alter migration strategies. On the one hand, migration may cease altogether with important repercussions on biodiversity patterns and ecosystem functioning (Bauer & Hoye, 2014). On the other hand, migratory species may shift from seasonal niche tracking to seasonal niche switching with unclear effects on the stability and size of their populations, making their response to and survival under global change even less predictable. Long-term observations in migratory population dynamics by means of telemetry and censuses may help to gain a more comprehensive understanding of the complex nature of animal migration (Rotics *et al.*, 2016), seasonal niche tracking, and population development through time. Improving the intensity in surveying distribution and population sizes is especially important in overwintering ranges for improving our capability to forecast and conserve migratory animals in the future.

Supplementary Material

Appendix S1. Supplementary results.

Appendix S2. Species data table.

Biosketch

Damaris Zurell is broadly interested in macroecology and biodiversity modelling. Main topics include environmental change effects on spatio-temporal structuring of species' ranges, populations and communities, and the evolution of life history characteristics, especially in migratory species.

Author contributions

DZ and NEZ conceived the idea. DZ compiled all data and ran the analyses with the aid of LG, prepared the figures and wrote the initial draft of the paper. All authors contributed to interpreting the results and to writing the manuscript.

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