

Ecological barriers mediate spatiotemporal shifts of bird communities

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Abstract

Species' range shifts and local extinctions caused by global change lead to community composition changes. At large spatial scales, ecological barriers, such as biome boundaries, coastlines, elevation, and temperature gradients, can influence a community's ability to shift. Yet, ecological barriers are rarely considered in global change studies, potentially hindering predictions of biodiversity shifts. We used data from two consecutive European breeding bird atlases to calculate the geographic distance and direction between communities in the 1980's and their nearest compositional equivalent in the 2010's and modelled their response to barriers. The ecological barriers affected both the distance and direction of bird community composition shifts, with coasts and elevation having the strongest influence. Combining ecological barriers and community shift projections can identify ecological corridors that facilitate shifts of species and communities under global change.

Introduction

Global change puts pressure on individuals, species and communities, forcing them to adapt, move or go extinct¹⁻³, thus having potentially severe consequences for biodiversity⁴. Species unable to rapidly adapt to new conditions must shift their ranges to track their environmental niches⁵⁻⁷. Indeed, shifts towards higher latitudes and altitudes have been widely documented^{1,7,8}. Species-specific variation in such shifts has been associated with functional traits and temperature trends^{9,10}. To date, most studies have summarized individual species' range shifts using range margins and centroids as response variables^{7,11,12}, with little consideration of spatiotemporal shifts in community compositions.

Global change drivers, such as climate change, are expected to modify community composition through variation in the rates of species' range shifts¹³, through the appearance of novel climate types¹⁴, and as a consequence of local extinctions¹⁵ and species' abundance distribution changes⁶. Indeed, ecological communities are more than the mere sum of their species, as interspecific interactions shape the communities' functionality¹⁶. Environmentally driven changes in communities' functionality can be quantified as trends in their taxonomic, functional and phylogenetic diversities¹⁷ or average trait values⁶, but such summary metrics may not fully capture the change in particular compositions of species. Therefore, studying shifts of particular community compositions in space and time is likely highly relevant to the maintenance and protection of biodiversity under global change.

Given that the magnitude of range shifts in individuals, species and communities varies spatially, temporally, and taxonomically, several processes likely govern such shifts. One such process may be the relative location of the focal species or community in relation to potential barriers^{13,18,19}. Ecological barriers, such as major water bodies or mountain ranges, influence species' movement and landscape connectivity^{20,21}. Landscape connectivity can impact many ecological and evolutionary processes, including dispersal, gene flow, and movement in response to environmental change²². Barriers may prevent dispersal and range shifts of even highly mobile species²³, but to a varying degree. Most studies

on ecological barriers have focused on their impact on a specific process, such as seasonal bird migration^{24,25}. Importantly, barriers influence biodiversity shifts at macroecological scales, which requires studying such shifts in a broad spatiotemporal context.

We use a unique continental scale dataset of European breeding bird distributions^{26,27} to assess spatiotemporal shifts in community compositions from the 1980's to 2010's, during which global change impacts on biodiversity have accelerated. Our main objective is to quantify how ecological barriers influence the geographic distance and direction of bird community composition shifts across Europe. More specifically, we ask whether 1) biome boundaries, 2) coastlines, 3) elevation, and 4) temperature change affect community composition shifts. We select these barriers to study both the more resistant, temporally unvaried geo-physical (coastlines and elevation) and the less resistant and temporally varying bio-climatic barriers (biome boundaries and temperature change). Generally, we expect the distance and direction of the community composition shifts to depend on the type of barrier (Fig. 1), as barriers vary in their resistance. For biome boundaries and coastlines, we hypothesize that communities will shift furthest in direction(s) where the barrier resistance is the lowest. For elevation, we hypothesize that communities will shift farthest and in the direction of least elevation change. Finally, for temperature change, we hypothesize that communities will shift farthest and away from directions where temperatures have changed most over the intervening period, and *vice versa*.

We quantified spatiotemporal shifts in European breeding bird community compositions as the geographic distance and direction between bird communities in the 1980's and their best compositional equivalent (based on pairwise Jaccard's dissimilarities) in the 2010's, where for each 50 km x 50 km grid cell, we defined a community as the species pool within a cell per decade. For biome boundaries and coastlines, we quantified, for each grid cell, the distance and direction to the nearest biome boundary or coast (highest resistance). For elevation, we quantified the distance to the grid cell of most different elevation (highest resistance) and direction along the grid cells of most similar average elevation (lowest resistance). For temperature change, we quantified the distance and direction to the grid cell with the most similar temperature between 1980's and 2010's (lowest resistance). We modelled the effects of ecological barriers on community composition shift distances using ordinal regression and modelled shift directions as expressions of northness and eastness to allow linear regressions using generalized least square models.

Results

During the last three decades, breeding bird community compositions shifted on average 93 kilometers (Extended Data Fig. 2a, and Appendix S1: Fig. S3a), with pronounced shifts towards northern, eastern, or western directions, but only few southerly shifts (Extended Data Fig. 2b, and Appendix S1: Fig. S3b). Out of 2092 communities, ~ 33% did not shift at all at the spatial resolution of our study. Among those communities that shifted, the average shift was ~ 138 kilometers. A small proportion (6.7%) of EBBA1 communities had only highly dissimilar (dissimilarity > 0.30) compositional matches available among EBBA2 communities (Appendix S1: Fig. S2), suggesting a loss of community types. These high

dissimilarity values were accounted for in the analyses by including similarity values as model weights (see 'Online Methods').

Community composition shift distance. Nearly all community composition shift distance models followed our hypotheses, with the distance of the community shift being most affected by the proximity of coasts and temperature change (within 450 km radius) (Fig. 2; Extended Data Tables 1 and 2, and Appendix S1: Tables S1 and S2). The overall response showed that communities shifted significantly farther when they were located farther away from the coastline. Similarly, communities were more likely to shift a longer distance when the most similar temperature was farther away. Yet, for communities that did not shift at all or only one grid cell (ordinal classes 0 and 1), the relationships with coastline and temperature distances were negative. That is, the farther the community was from the coastline or from the most similar temperature, the lower its shift probability was (Fig. 2).

Community composition shift direction. All models of community shift direction followed our hypotheses. That is, communities tended to shift along most similar elevations, away from biome boundaries and coastlines, and towards areas with the most similar temperatures in the EBBA2 period relative to the temperatures of the focal grid cell during the EBBA1 period (Fig. 3, Extended Data Tables 1 and 3, and Appendix S1: Tables S1 and S3). Specifically, community shift eastness was most significantly affected by elevation direction (radius of 150 km) and biome direction, and marginally by coastline direction (Fig. 3a-c; Appendix S1: Table S3). Elevation direction had a positive, biome direction a negative, and coastline direction a marginally negative effect on community shift eastness. The community shift northness was most affected by elevation direction (150 km) and temperature direction (150 km), such that elevation direction had a statistically significant, positive effect, while temperature direction had a marginal positive effect on community shift northness (Fig. 3d-e; Appendix S1: Table S3).

Discussion

In this study, we found that two thirds of the European breeding bird communities experienced spatiotemporal shifts in their composition. Although the directions of community composition shift varied substantially, the shifts were largely directed to north, east, and west, rather than south, corroborating most research findings on directional climate-driven distribution shifts of single species in the northern hemisphere⁵. Following our hypotheses, both geo-physical and bio-climatic barriers consistently, and predictably, influenced community composition shifts, such that bird communities generally shifted in distances and directions to avoid ecological barriers.

Breeding bird community compositions have likely shifted due to the influence of global change drivers on single species distributions¹. Whilst our findings highlight spatiotemporal shifts of communities, ecological communities are undergoing compositional and functional homogenization globally²⁸⁻³⁰. As biotic homogenization proceeds, the dissimilarity decreases among different communities across space^{31,32} but increases between observations of the same community over time²⁸. Indeed, we found cases of high dissimilarities when comparing bird communities in some grid cells in the 1980's to all grid

cells in the 2010's, suggesting that those community compositions observed in the 1980's had no corresponding compositions in the 2010's. Such 'community composition extinctions' can result from losing and/or gaining bird species in the local community, both of which have been observed across Europe³³ and globally³⁴ as a result of environmental change. Importantly, if many communities consistently shift away from certain areas, there may be substantial impacts on interaction network configurations, metacommunity dynamics, and ecosystem functioning over large spatial scales^{23,35}. The lack of compositional matches between bird communities in the 1980's and the 2010's may also reflect the appearance of novel community compositions in the latter that did not occur in the former period, potentially leading to unpredictable alterations in ecosystem functioning³⁶.

Out of the four ecological barriers considered in our study, elevation and coastlines do not change within an ecologically relevant time span, posing constant, geo-physical limitations to community composition shifts. On the other hand, biome boundaries and temperature change are more gradual across space and likely to change within an ecologically relevant time span, thereby posing weaker and potentially adaptable bio-climatic limits to community composition shifts. Together the observed effects of ecological barriers on community composition shifts indicate that species' shifts, and thereby communities that consist of these species, may be mediated through least geo-physical resistance delineated by coastlines and elevation and through most optimal bio-climatic conditions delineated by temperature gradients and biomes. Coastlines was the most important determinant of community composition shift distances, such that the farther away the community was located from the coastline, the farther it shifted. In parallel, bird communities largely moved along directions with the least change in elevation relative to their original location, implying that communities are tightly associated with certain abiotic and biotic conditions along the elevational gradient³⁷. Contrary to community composition shift direction, elevation resistance did not strongly influence community composition shift distance, which may be caused by the fact that in areas of high topographic variation, species may not need to shift far to track their original abiotic and biotic niche^{1,35}. Temperature barriers tended to be associated with longer shifts (and directional shifts towards north) of the bird community compositions when the most similar temperature conditions were also located farther away (and towards north). This aligns with earlier findings that show the importance of the climatic niche in shaping single species' ranges³⁸. Biome boundaries showed differential effects on community composition shift distances and directions, such that the communities located closer to biome boundaries shifted farther, while the communities shifted directionally away from close biome boundaries. Although we did not test differences in edge-contrast of different biomes, it is unlikely that species shift across biome boundaries³⁹ even when the biomes have relatively similar abiotic conditions (e.g., across cold and warm deserts)⁴⁰, as the biotic conditions likely differ considerably among biomes.

Understanding how ecological barriers influence biodiversity shifts at large spatial scales can inform both ecological research and conservation management²³. The environmental drivers influencing ecological communities potentially follow a spatial hierarchy, such that the ecological barriers – including those arising from climate change – likely govern species and community shifts at broader, macroecological

scales, while other processes, such as e.g., species interactions, land use change, and habitat fragmentation, may limit the shift potential at smaller spatial scales³⁵. For example, climate change may mediate shifts of many species through certain areas, but the realized shifts would be limited by anthropogenic landscape modifications³⁵. In addition, different global change pressures, such as climate change, habitat loss and fragmentation, acting separately or in synergy, can favor community shifts in different directions¹⁸. Therefore, including ecological barriers in global change studies could lead to more realistic predictions of species and community shifts by setting the outer bounds of potential shifts⁴¹. These predictions can be further applied to large scale conservation decision making. So far, species with a primarily high latitude or high elevation distribution have been a major concern in the climate change context because their poleward or uphill shifts have natural limits^{42,43}. Our results suggest that similar limitations apply in relation to other ecological barriers, and at the level of entire communities, as the ecological barriers guide the distance and direction of their shifts. In terms of conservation planning and climate change mitigation, understanding the effects of ecological barriers on species' shifts can help identify major shift barriers and inform placement of key corridors that facilitate movement of species between climatically suitable areas.

Our study highlights the role of ecological barriers for species and communities under global change. Although our results on the ecological barrier effects on biodiversity shifts are general, it is likely that the relevance of a particular barrier depends on the ecosystem and taxonomic group in question. For example, precipitation change may be a relevant bio-climatic barrier for plant community composition shifts in arid ecosystems⁴⁴. Here, we provide the first evidence of observed rather than predicted shifts of entire communities across large spatiotemporal scales as a function of constant geo-physical and more dynamic bio-climatic ecological barriers, which substantially advances previous research exploring the impacts of ecological barriers as determinants of single species' range shifts^{23,35}. Our approach in studying spatiotemporal shifts under global change is especially useful as it accounts for the composition of entire communities instead of summarizing the communities into richness and beta diversity measures that may remain unchanged over time even when the community composition changes entirely^{10,28}. We suggest that ecological barrier data combined with species' traits can provide complementary information for why species and communities shift slower than expected, for example, based on climate predictors alone^{6,33,45}. Moreover, we suggest that by quantification of community composition shifts with abundance data, it is possible to observe community composition changes that influence the community's functionality via ecological interactions before any species goes locally extinct. Finally, we suggest that time series of ecological barriers and community composition shifts could be combined to study more realistic velocities of community reshuffling and biodiversity shifts in general^{14,46}. Understanding biodiversity shifts under global change is key to predict future ecosystem functioning and integrity, and design effective management and adaptation strategies. Our study adds to the current knowledge by unveiling, for the first time at a continental scale, that shifting communities are strongly, and predictably, affected by a range of ecological barriers. This underscores the importance of moving beyond simple climate change measures when studying community shifts.

Online Methods

Data

European Breeding Bird Atlas (EBBA) data. To study community composition shifts at a continental scale, we obtained data of breeding bird occurrences in two study periods from European Breeding Bird Atlases 1 and 2 (hereafter, EBBA1 and EBBA2)^{26,27}. Breeding birds in EBBA1 were surveyed within 50 x 50 kilometer grid cells mainly during 1981–1989, whereas in EBBA2 birds were surveyed within the same and additional grid cells mainly during 2013–2017 (see Extended Data Fig. 1, and Appendix S1: Fig. S1 for comparison of data coverage). To prevent artificial limitations of community composition shifts in eastern Europe, i.e., to allow community composition shifts to all compass directions for grid cells in the EBBA1 data, we included EBBA2 grid cells beyond the extent of EBBA1 grid cells. All grid cells were assigned WGS84 coordinates according to their centroids. All species with observed possible, probable, and confirmed breeding records were compiled into grid cell-specific lists *sensu*^{27,47}, leading to a presence-absence matrix of species' occurrences in the two study periods. Given the spatial resolution of the data, we assumed that the birds observed within a grid cell co-occurred spatially and temporally to form an ecological community. The surveys were conducted by volunteer birdwatchers and professional ornithologists, organized by national coordinators, and internationally coordinated by the European Bird Census Council. We considered the EBBA1 grid cells as the focal grid cells that were compared to EBBA2 grid cells.

To ensure sufficient data coverage within grid cells, we excluded EBBA1 grid cells of poor sampling coverage as described in Keller et al.²⁷. To ensure a reasonable potential for matching of compositions between EBBA1 and EBBA2 bird communities, we also excluded EBBA1 and EBBA2 grid cells with ≤ 10 species. In addition, we excluded three EBBA1 grid cells on small and remote islands because their community composition shifts would have necessarily been biased towards longer distances in the absence of nearby grid cells. In total, we excluded 201 grid cells that did not meet the selection criteria. We included 2092 focal EBBA1 grid cells to be used as study units and 4843 EBBA2 grid cells to compare EBBA1 grid cells to (see Extended Data Fig. 1, and Appendix S1: Fig. S1 for spatial extents). In total, the bird communities in EBBA1 included 439 species and the bird communities in EBBA2 with the broader spatial coverage included 580 species (for full lists of species, see Appendix S2). We followed the taxonomy of EBBA2²⁷, but merged four species pairs because they were considered as single species in EBBA1 and had unclear distribution zones across atlases: *Phylloscopus collybita* and *P. ibericus*, *Lanius meridionalis* and *L. excubitor*, *Picus sharpei* and *P. viridis*, and *Sylvia subalpina* and *S. cantillans*.

Environmental data. To quantify ecological barriers of biome boundaries and coastlines, we obtained a geographic information layer defining the six major biomes within the study area⁴⁸ (Appendix S1: section S1.2.1). Coastlines were defined from world vector data (R packages *rnaturalearth* and *naturalearthdata*,⁴⁹) within and adjacent to the study area (Appendix S1: section S1.2.3). To quantify ecological barriers related to elevation, we used Digital Elevation Models DEM (m a.s.l.) at 30 arc seconds

resolution⁵⁰ and averaged the elevation values for each grid cell (Appendix S1: section S1.2.4). Finally, to quantify barriers related to temperature change, we obtained the monthly averaged air temperature (K) at two meters above ground for the entire year and for each grid cell at 0.1° resolution⁵¹. We averaged the temperatures across all months and years in EBBA1 period (1981–1989) and in EBBA2 period (2013–2017) in each grid cell. For the 171 grid cells that lacked temperature data (Appendix S1: section S1.2.5, Fig. S14), we used a Kriging interpolation to obtain the mean temperatures⁵².

Quantification of community composition shift

We quantified spatiotemporal shifts of biodiversity by accounting for the composition of entire communities because summary measures, such as species richness, may remain unchanged over time even when the species composition changes¹⁰. To quantify the spatiotemporal shift in breeding bird community composition, we first calculated pairwise Jaccard's dissimilarity index (i.e., 1 - similarity; Appendix S1: Equation S1)⁵³ among all grid cell pairs between EBBA1 and EBBA2 using the 'vegan' R package⁵⁴. Jaccard's dissimilarity quantifies the degree of difference in the compositions of two communities with presence-absence data. Next, we selected the best matching EBBA2 comparison grid cell for each focal EBBA1 grid cell – following the concept of climate reshuffling in space and time^{14,46} (Fig. 4). We did this by first identifying the five least dissimilar, i.e., the most similar EBBA2 grid cells for each focal EBBA1 grid cell. Out of these five EBBA2 grid cells, we selected as the best match the grid cell that either had the lowest dissimilarity value (N = 1798) or a maximum of 3.5% increase in dissimilarity value compared to the lowest dissimilarity value and was located closest to the focal EBBA1 grid cell (N = 294). We used this two-step approach to prevent overestimating the community composition shift distance in cases where another highly similar composition occurred close to the focal EBBA1 grid cell. The best match could be any of the grid cells that were surveyed during EBBA2, including the focal grid cell itself or a grid cell that was not surveyed during EBBA1.

Using the pairwise dissimilarity values, we quantified community composition shift distances and directions. First, we quantified the distance of the community composition shift in kilometers as the distance between the centroid of each focal EBBA1 grid cell and the centroid of its best matching EBBA2 comparison grid cell using the R package 'raster' (function 'pointDistance'⁵⁵). Second, we quantified the direction of the community shift as the bearing (0–360°) between the same pairs of EBBA1 and EBBA2 grid cells using the R package 'geosphere' (function 'bearing'⁵⁶).

In a sensitivity analysis we explored whether coastal communities are more likely to stay in the coastal areas rather than to move inland. This was conducted by bootstrapping analyses where each coastal community was allowed to move randomly to available grids within a 155 km radius (3 grids to cardinal directions). Next, we checked whether the simulated shift happened to a coastal or inland grid and then calculated the frequency distribution of coastal communities that shifted along coastal grids vs moved inland. These distributions were compared to observed changes between EBBA1 and EBBA2. Bootstrapping analyses showed that communities of coastal grids were highly significantly more likely to shift to coastal grids compared to simulated random shifts ($P < 0.001$; Appendix S1: section S3.1).

We accounted for the stochasticity in the selection of the best matching comparison grid cell in two ways. First, we repeated the selection of the best matching comparison grid cell using subsets of species, such that we excluded 1) rare species with a total of < 3 occurrences in EBBA1 and EBBA2 and 2) rare species with < 3 occurrences and all non-native species (for lists of species, see Appendix S2). We did this because in presence-absence data, all species influence the dissimilarity value regardless of their abundance. Thus, the rarest species may disproportionately influence the dissimilarity calculation as they occur in low densities and/or in a restricted number of grid cells. In addition, we also ran sensitivity analyses by excluding all bird species classified as marine or coastal (Appendix S2) to test whether the inland communities respond differently to our set of ecological barrier predictors in comparison to the full data that included coastal species. We did not find substantial differences in barrier effects on community shift direction between full and subset datasets but found that barrier effects on shift distances were mainly influenced by the inclusion of non-native species (Appendix S1: section S3.2). We accounted for the potential sensitivity of the results to the varying dissimilarity value between the focal EBBA1 and the best matching EBBA2 comparison grid cell by including the complement of dissimilarity value as a weight in all statistical models (1 - dissimilarity). Hence, the grid cells with only poor compositional matches available were given less weight in the modelled relationships. We also explored whether the inclusion of weights influenced model estimates by excluding weights from final models, finding no difference between models including and excluding weights (Appendix S1: section S3.3).

Quantification of ecological barriers

We explored the influence of continuous predictors (elevation and temperature change) at multiple spatial scales, because the scale at which the landscape affects populations is often predictor- and species-specific^{57,58}. For the continuous predictor variables, we restricted the analyses of shift distance and direction to two or three ecologically meaningful buffer areas around the focal EBBA1 grid cells. That is, for both elevation and temperature change we estimated: 1) minimum shift potential within three grid cells (150 km radius, corresponding to the average shifted distance among communities that did shift from EBBA1 to EBBA2), and 2) minimum shift potential within six grid cells (300 km). In addition, for the temperature barrier, we estimated minimum shift potential within nine grid cells (450 km; only for temperature barrier). We included this broader scale for temperature because across Europe, temperatures have generally shifted over three-folds faster than species communities^{6,33}.

Table 1
Description of predictor variables.

Name	Description
biome distance	distance to the nearest terrestrial biome boundary
biome direction	direction to the nearest terrestrial biome boundary
coastline distance	distance to the nearest coastline
coastline direction	direction to the nearest coastline
elevation distance 150/300	distance to most different elevation within 150 and 300 km buffers
elevation direction 150/300	direction along most similar average elevation within 150 and 300 km buffers
temperature distance 150/300/450	distance to most similar temperature between EBBA1 and EBBA2 within 150, 300 and 450 km buffers
temperature direction 150/300/450	direction to most similar temperature between EBBA1 and EBBA2 within 150, 300 km and 450 km buffers

Terrestrial biome boundaries. To quantify barriers formed by terrestrial biome boundaries – that is, zones where the land changes from one biome type to another – we excluded coastlines in order to differentiate between terrestrial biome and coastline boundaries. Although the biome boundary barrier partly coincides with other ecological barriers, it represents the combination of several biotic conditions, such as vegetation structure and productivity⁵⁹, that cannot be attributed to the other ecological barriers quantified here. We calculated a distance matrix between all focal EBBA1 grid cell centroids and evenly sampled points along the boundary of the terrestrial biome to which the focal EBBA1 grid cell belonged (function ‘dism’; R package ‘geosphere’). We then extracted the minimum distance in kilometers from each focal EBBA1 grid cell to the nearest biome boundary point (predictor ‘biome distance’) and calculated the direction to this same point (‘biome direction’, Appendix S1: section S1.2.1).

Coastlines. To quantify the barrier formed by coastlines (of seas, but not of large inland lakes), we calculated a distance matrix between all focal EBBA1 grid cell centroids and evenly sampled points along the coastlines. We then extracted the minimum distance in kilometers from each focal EBBA1 grid cell to the nearest coastline point and calculated the direction to this same point (‘coastline distance’ and ‘coastline direction’, Appendix S1: section S1.2.3).

Elevation. To quantify the barrier formed by elevational gradients, we used the grid cell-averaged elevation data to calculate barrier distance and direction variables within the two buffer areas (150 km and 300 km radii; Fig. 1). First, within each buffer area, we quantified the distance to the nearest grid cell in which the elevation difference to the focal EBBA1 grid cell was largest (‘elevation distance’, Appendix S1: section S1.2.4). Second, we quantified the direction of least elevational resistance within the two buffer areas. We created 64 radial lines (every ~ 5°, starting at 0°) around the focal EBBA1 grid cell

centroid (performed in QGIS, plugin 'shape tools', function 'create radial lines') and extracted the average elevation along these 64 lines. Then, we selected the line with the smallest difference in average elevation relative to the focal EBBA1 grid cell elevation and calculated the compass direction of this radial line using the R package 'geosphere' ('elevation direction', Appendix S1: section S1.2.4). If several lines had the same elevation difference, we averaged their direction since they were neighboring lines running along the same DEM raster cells (R package 'circular', function 'mean.circular'⁶⁰).

Temperature change. Climate does not change uniformly in space and time, which can pose an ecological barrier and govern the shifts of species and communities^{23,33}. As species tend to respond more strongly to changes in temperature than to other climatic variables³⁸, we used temperature as a proxy for climate. To quantify the barrier formed by temperature change, we computed the distance and direction from each focal EBBA1 grid cell to the grid cell with the most similar temperature in the EBBA2 period inside the three buffer areas: 150 km, 300 km, and 450 km ('temperature distance' and 'temperature direction', Appendix S1: section S1.2.5).

Modeling community shift as functions of ecological barrier variables

To quantify the effect of ecological barriers on community composition shift, we used the community composition shift distance and direction as response variables in separate models, and the different measures of ecological barriers as predictor variables (Table 1, Fig. 1).

Shift distance models. We analyzed the community shift distance using an ordinal regression model with logit link function (function 'clm' in R package 'ordinal'⁶¹), due to the highly skewed distribution of the distance values. As the response variable, we used the community shift distances that were transformed into eight ordinal classes: 0 = no change, 1 = shift of one grid cell (~ 70 km), 2 = shift of two grid cells (~ 140 km), ..., 8 = shift of > 7 grid cells (\geq 420 km). The used distances accounted for horizontal, vertical, and diagonal shifts in grid cells. As predictor variables, we used the barrier distance variables described in Table 1, which were standardized to a continuous scale. We added similarity values as weights in the models (see 'Quantification of community composition shift'). We included the longitude and latitude of the grid cell centroids as covariates in all models as well as tested for spatial autocorrelation after model fitting (Appendix S1: section S2.1.1). We first tested the hypotheses (Fig. 1) by fitting single-predictor models. For each barrier variable that was measured at several spatial scales, we selected the best scale by comparing the single-predictor models using AIC values *sensu*⁵⁷. Finally, we fitted a full model that included all predictors with (near-)significant effects ($p < 0.1$).

Shift direction models. We excluded 682 communities (grid cells) that did not shift from EBBA1 to EBBA2 and therefore had no value for shift direction, which left 1410 grid cells to be included in the analyses. To model the geographic direction of community shifts with linear regression models, we transformed all circular variables to linear expressions of eastness (shift along the longitudinal axis) and northness (shift along the latitudinal axis). To do so, we first transformed directions from degrees to radians

($direction / 360 * 2 * \pi$) and then calculated the sine and cosine for a measure of eastness (ranging from -1 = west, to +1 = east) and northness (-1 = south, +1 = north), respectively. Consequently, we modelled eastness and northness of community shifts separately, following the same statistical protocol.

Using shift eastness and shift northness as the response variables and barrier direction variables as predictors, we fitted generalized least square models (R package 'nlme'⁶²). We tested for spatial autocorrelation before and after model fitting (Appendix S1: section S2.1.1) and due to observed spatial autocorrelation we included a spatial correlation structure in the models (correlation structure = Gaussian). As in the community shift distance models, we added similarity values as weights in the models and first fitted separate single-predictor models where we matched the eastness (northness) of the response variable with the eastness (northness) of the predictor variable. Again, we selected the best spatial scale of the multiscale barrier variables by comparing single-predictor models. Then, we combined all predictors with marginal effects ($p < 0.1$) in univariate models into a final full model.

Lastly, we explored whether the community shift directions and responses to barrier types varied spatially, i.e., as a function of the biome type or the latitudinal position of EBBA1 communities, finding no strong patterns (Appendix S1: section S3.3).

For all data processing and statistical analyses, we used QGIS⁶³ and R software⁶⁴.

Declarations

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Author contributions

AL, ELM, LB, YX, AS, SH, MV and SM originally formulated the idea, and developed methodology. SH, VK, PV and authors from KA to AL managed, prepared, and provided the raw EBBA data. ELM, LB, MV, YX, and SM performed statistical analyses. ELM and LB led the writing of the manuscript while all authors contributed critically to the drafts and gave their final approval for publication.

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Figures

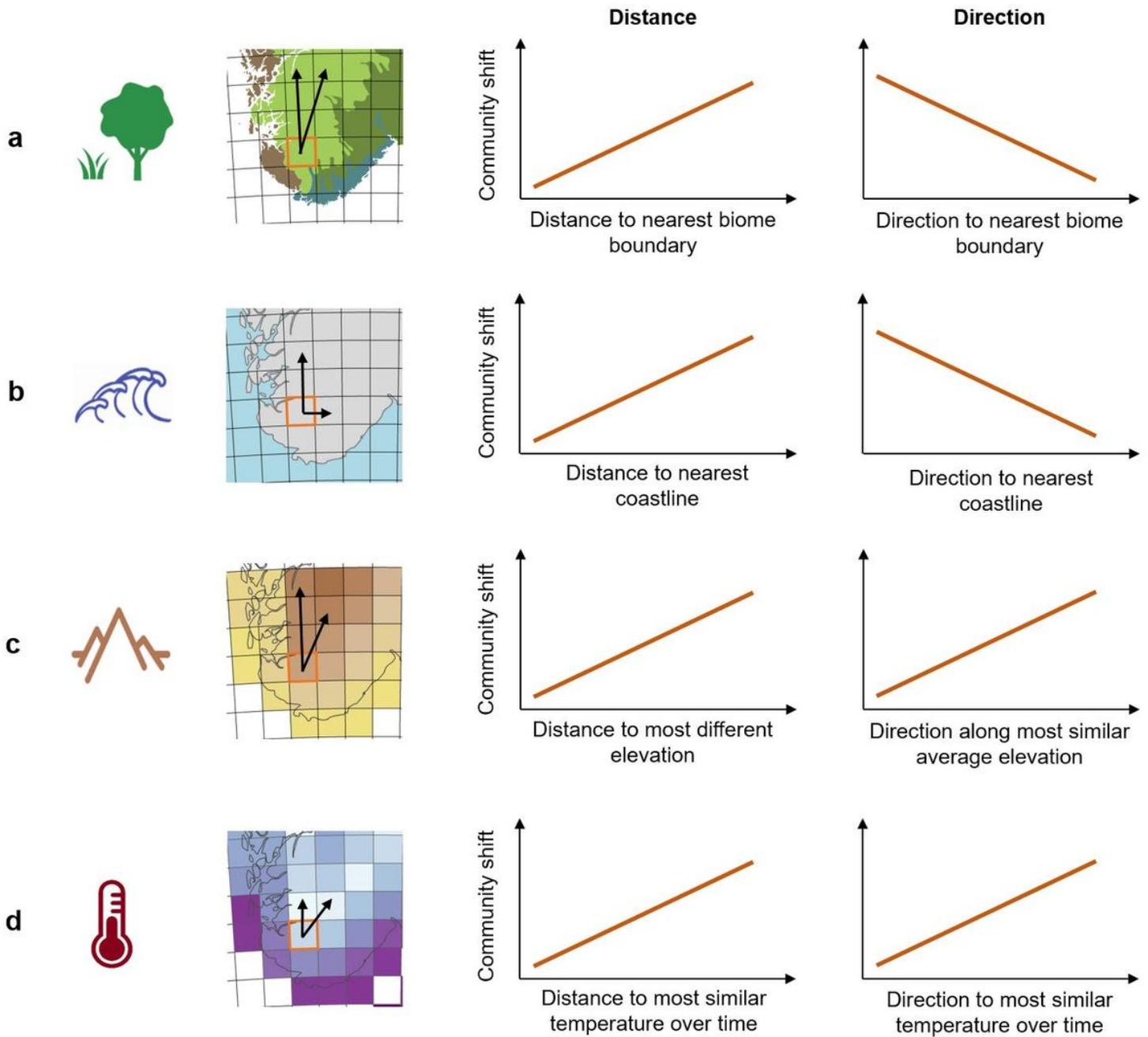


Figure 1

Hypothesized effects of ecological barriers on community composition shift distance and direction. The icons in panels a-d illustrate ecological barriers: biome boundaries, coastlines, elevation, and temperature change, respectively. In each map, the orange-outlined square indicates the hypothetical bird community of interest and the black arrows the hypothetical distances and directions of community composition shift. In panel a, terrestrial biome boundaries are indicated with different colored polygons. In panel b, the coastline is indicated with a black line and sea with blue color. In panel c, elevation is indicated with a brown-yellow gradient (brown colors: high elevation). In panel d, temperature change over time is indicated with a blue-purple gradient (blue colors: small difference in temperatures between the orange grid cell and other grid cells over time). Each graph illustrates the hypothesized effect of a barrier on

community composition shift distance and direction (x-axis). For simplicity of the illustration, the x-axis for direction is represented as a linear term, expressing the northness or eastness of the shift direction (for details, see 'Online Methods').

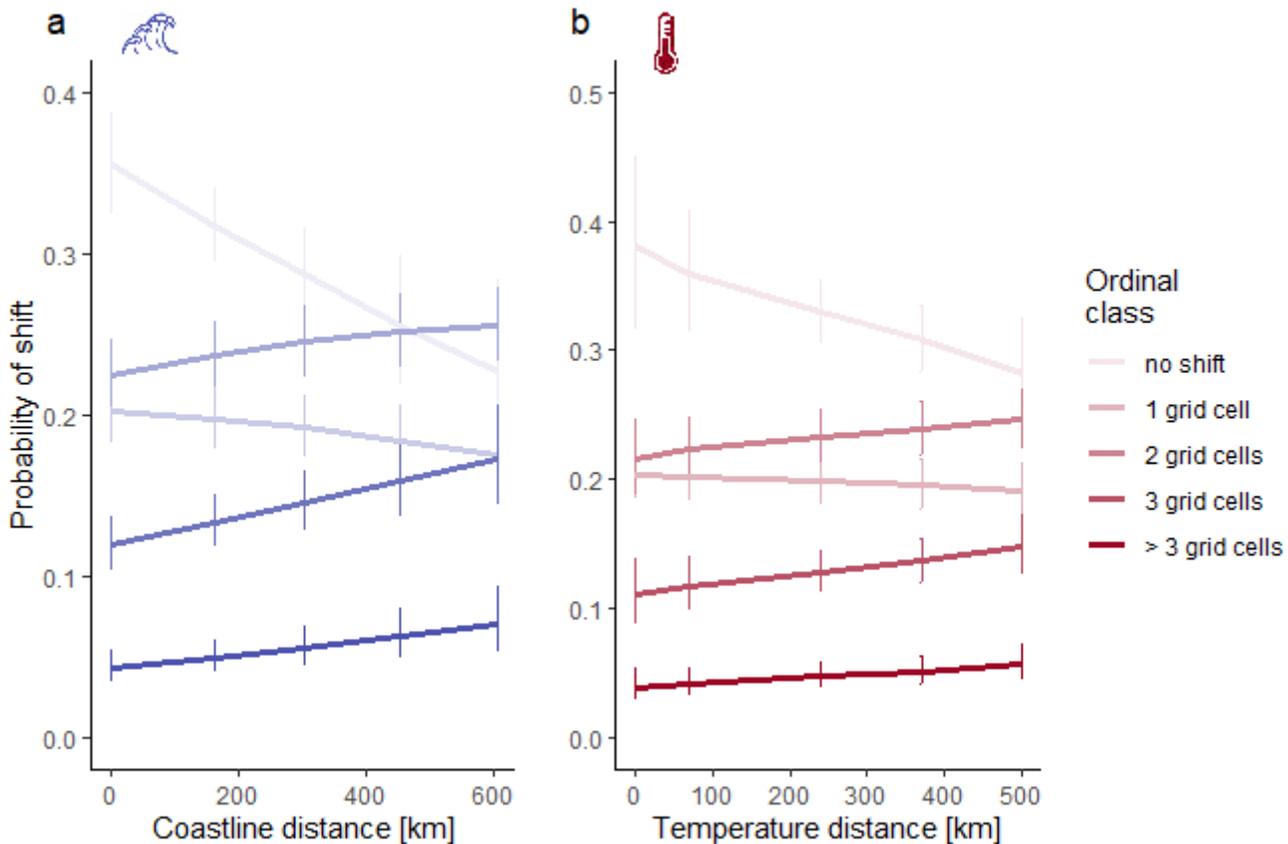


Figure 2

Modelled relationships between ecological barriers and community composition shift distances.

Predicted linear effects of significant predictors on community composition shift distances based on full models, shown for the ordinal classes separately (shift of 1 grid cell equals ~70 kilometer). The overall response across all classes is significantly positive for both predictors which is in line with our hypotheses in Fig. 1. For illustration purposes, the ordinal classes 4-7 were combined in the figure panels since they showed very similar regression patterns. Panel a illustrates the probabilities of community composition shift (y-axis) in relation to the shortest distance to the coastline (x-axis) for each ordinal shift class. Panel b illustrates the shift probabilities in relation to the distance to the most similar temperature measured within a 450 kilometer buffer. Regression lines are model-based beta estimates, error bars represent the 95% confidence intervals. The x-axis shows the back-transformed predictor values in kilometers. Note that the illustrated ordinal model predictions differ from the hypothesized ones in Fig. 1 where we assumed simple linear regressions for visualization purposes.

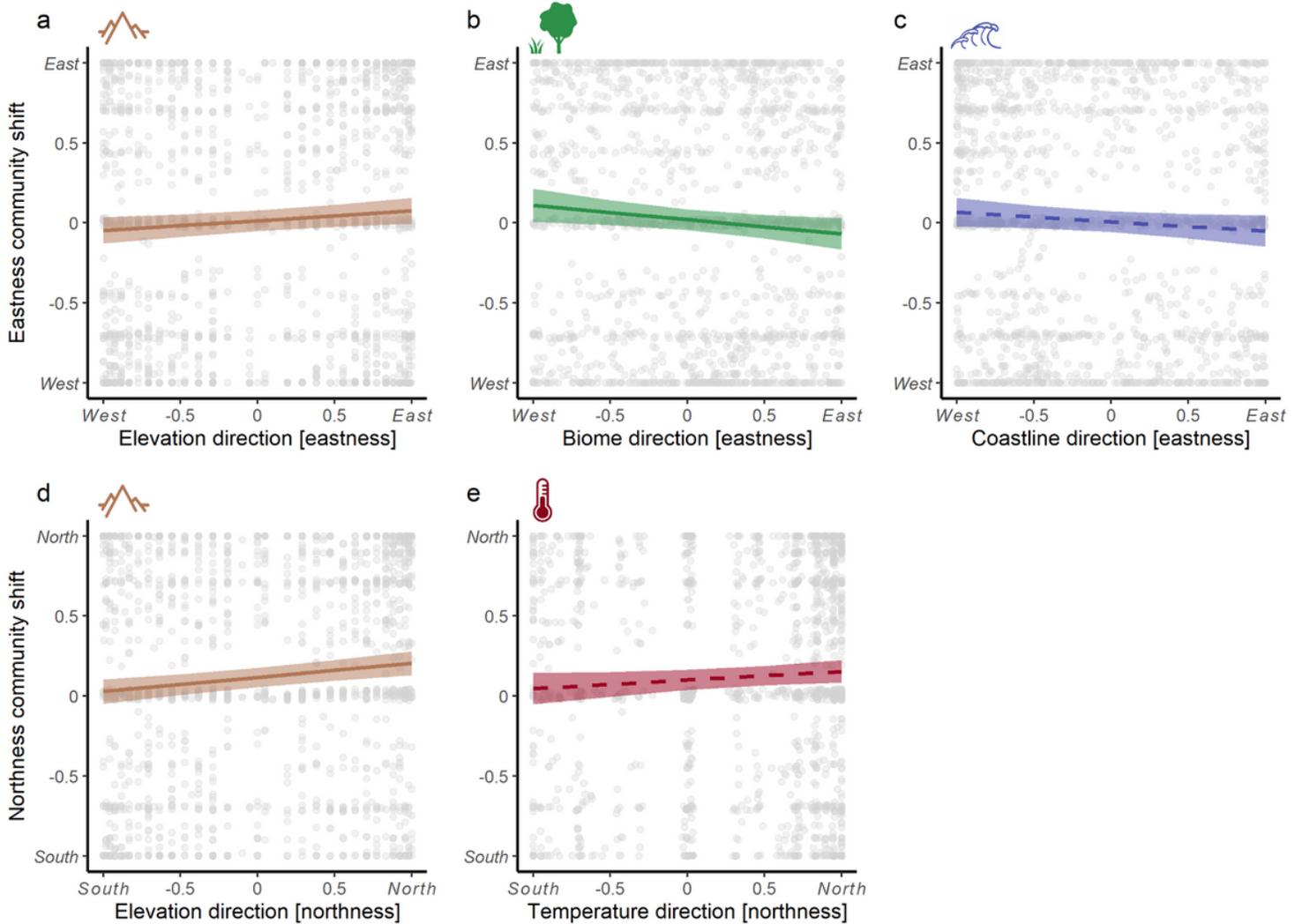


Figure 3

Modelled relationships between ecological barriers and community composition shift directions.

Predicted linear effects of significant ($p < 0.05$, solid regression lines) and near significant ($0.05 < p < 0.1$, dashed regression lines) predictors on community composition shift directions based on full models for eastness and northness. Linear regressions of full model predictions are plotted for barrier variables with significant effects on shift directions by absorbing the term of interest and averaging over other terms in the model. Panel a, community composition shift eastness is illustrated in relation to the eastness of the direction along most similar average elevation within 150 km buffer. Panel b, shift eastness is illustrated in relation to the eastness of the nearest terrestrial biome boundary. Panel c, shift eastness is illustrated in relation to the eastness of the nearest coastline. Panel d, shift northness is illustrated in relation to the northness of the direction along most similar average elevation within 150 km buffer. Panel e, shift northness is illustrated in relation to the northness of the direction to the most similar temperature in EBBA2. Regression lines are model-based beta estimates, shaded areas the 95% confidence interval and light gray dots the raw data points (jittered for visualization). Note that directions of response and

predictor variables range from -1 to 1 because they were sine- and cosine-transformed to obtain linear expressions of eastness and northness, respectively.

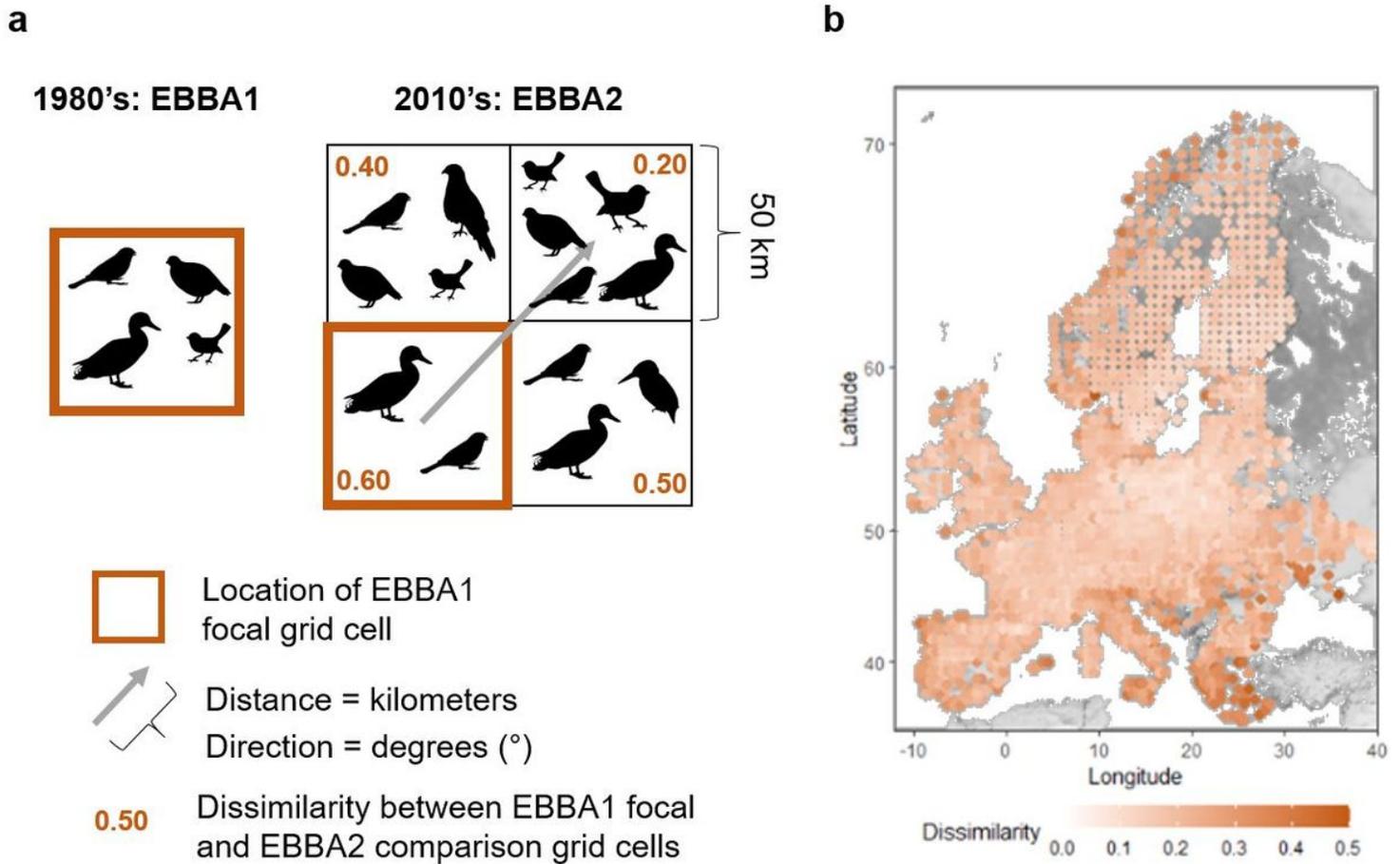


Figure 4

Schematic illustration of community composition shifts. In panel a, the orange numbers indicate Jaccard's dissimilarity index values when comparing the community composition of the focal EBBA1 grid cell (orange outlines, on the left) to all EBBA2 comparison grid cells (four squares on the right, including the focal grid cell). The grey arrow points from the focal EBBA1 grid cell to the best matching EBBA2 grid cell (i.e., smallest dissimilarity value), indicating the spatiotemporal shift of the breeding bird community composition. Panel b illustrates the spatial variation in the Jaccard's dissimilarity index values across the extent of EBBA1 ($N_{\text{grid cells}} = 2092$), quantified as the dissimilarity between a focal EBBA1 grid cell and its best matching comparison EBBA2 grid cell.

Supplementary Files

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- [AppendixS2.xlsx](#)
- [ExtendedData.docx](#)