



# Ecological barriers mediate spatiotemporal shifts of bird communities at a continental scale

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**Species' range shifts and local extinctions caused by climate change lead to community composition changes. At large spatial scales, ecological barriers, such as biome boundaries, coastlines, and elevation, can influence a community's ability to shift in response to climate change. Yet, ecological barriers are rarely considered in climate 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 1980s and their compositional best match in the 2010s and modeled their response to barriers. The ecological barriers affected both the distance and direction of bird community composition shifts, with coastlines and elevation having the strongest influence. Our results underscore the relevance of combining ecological barriers and community shift projections for identifying the forces hindering community adjustments under global change. Notably, due to (macro)ecological barriers, communities are not able to track their climatic niches, which may lead to drastic changes, and potential losses, in community compositions in the future.**

community composition | distribution shift | Jaccard dissimilarity | macroecology | resistance

Climate change puts pressure on individuals, species, and communities, forcing them to adapt, move, or even go extinct (1), thus having potentially severe consequences for biodiversity (2). Species unable to rapidly adapt to new conditions must shift their ranges to track their environmental niches (3, 4). Indeed, shifts toward higher latitudes and altitudes have been widely documented (5, 6). Species-specific variation in such shifts has been associated with functional traits and temperature trends (7). To date, most studies have summarized individual species' range shifts using range margins and centroids as response variables (6, 8), with little consideration of spatiotemporal shifts in community compositions (but see refs. 3 and 9).

Climate change is expected to modify community composition through variation in the rates of species' range shifts (10), through the appearance of climate types (11), as a consequence of local extinctions and/or colonizations (12), and through species' abundance distribution changes (3). Alterations in community composition are relevant in the context of ecosystem functioning under global change: ecological communities are more than the mere sum of their species because interspecific interactions shape communities' functionality (13). Environmentally driven changes in communities' functionality can be quantified as trends in their taxonomic, functional, and phylogenetic diversities (14) or average trait values (3). However, such summary metrics (e.g., richness and beta diversity) may remain unchanged over time even when the community composition changes entirely (7). Specifically, the identities of the species occurring within a community determine the basis for occurrences of pairwise interactions between species at the same or at different trophic levels. In most communities, species can have complementary functional roles, meaning that replacing one species with another cannot ensure the maintenance of the specific interaction links to other species in the community.

Global change can impact ecosystem functioning via community composition without any effect on species richness such that the larger the compositional changes, the stronger the impact on ecosystem functioning (15). Focusing on community composition may improve predictions of global change effects on ecosystem functioning because temporal changes in community compositions (such as biotic homogenization) (16) can affect biodiversity–ecosystem functioning relationships, particularly at fine spatial scales (17). Therefore, studying spatiotemporal changes of community compositions while accounting

## Significance

We used a unique long-term dataset on breeding bird counts covering an entire continent to quantify the influence of ecological barriers on climate change–driven bird community shifts. We show that ecological barriers exert a significant effect on the distance and direction of bird community composition shifts at the continental scale, with coastlines and elevation having the strongest influence. The results underscore the relevance of combining ecological barriers and community shift projections for identifying the forces hindering community adjustments under global change. The implications of this study are of direct relevance to scientists, decision-makers, and conservation practitioners.

The authors declare no competing interest.

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for the identities of the species within them is highly relevant for the maintenance and protection of biodiversity, ecosystem functioning, and ecosystem services under global change.

Given that the magnitude of shifts in individuals, species, and communities varies spatially, temporally, and taxonomically, several factors likely govern such shifts. One such factor may be the location of a community in relation to surrounding ecological barriers (10, 18). Ecological barriers, such as major water bodies or mountain ranges, influence landscape connectivity and species' movement (19). Landscape connectivity can impact many ecological and evolutionary processes, including dispersal, gene flow, and movement in response to global change (20). Barriers may prevent dispersal and range shifts of even highly mobile taxa (21) but to a varying degree. An ecological barrier may also be associated with different regional species pools on either side of the barrier, which may constrain or enhance the potential of local community composition turnover (22). In the past, studies have looked into thermophilization shifts of communities in relation to ecological barriers at regional scales (9), shifts of species in relation to landscape scale barriers (9, 23, 24), or into specific processes, such as seasonal bird migration (25) in relation to ecological barriers at broad scales. However, barriers influence biodiversity shifts also at macroecological scales, which requires studying them in a broader 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 1980s to the 2010s. Specifically, we define community composition shifts across Europe starting from bird communities in the 1980s and quantifying the distance and direction to their most similar community composition in the 2010s (*SI Appendix, Fig. S1*). Our main objective is to quantify how ecological barriers influence the geographic distance and direction of bird community composition shifts across Europe. We ask whether biome boundaries, coastlines, and elevational changes affect the distance and direction of community composition shifts. For biome boundaries and coastlines, we hypothesize that communities have shifted furthest in direction(s) where the barrier is farthest away (i.e., lowest resistance). For elevation, we hypothesize that communities have shifted furthest and in the direction of least elevation change (*Fig. 1*).

## Results

During the last three decades, breeding bird community compositions shifted on average 93 km, equivalent to two grid cells (each grid being 50 × 50 km; *SI Appendix, Fig. S5A*). The shifts were most pronounced toward northern, eastern, or western directions, with only few southerly shifts (*SI Appendix, Fig. S5 B and C*). Out of 2,092 communities, ~33% did not shift at all at the spatial resolution of our study. We also found that the dissimilarity between bird communities in the 1980s and their best-matching counterparts in the 2010s was higher for non-shifting communities compared to shifting ones (mean dissimilarity = 0.198 and 0.190, respectively;  $t = 2.538$ ,  $df = 1,284.6$ ,  $P = 0.011$ ).

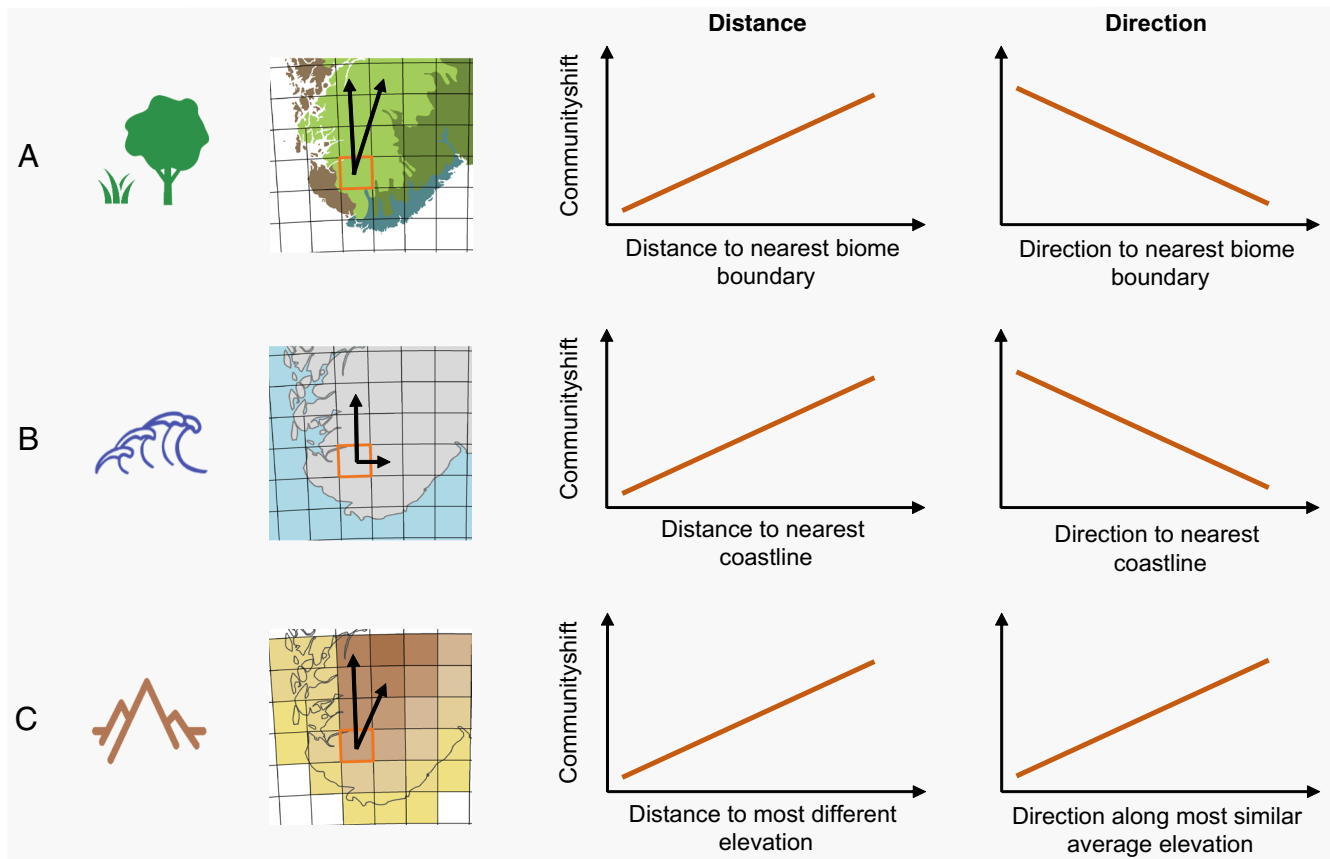
Among those communities that shifted, the average shift was ~138 km, equivalent to three grid cells. A small proportion (6.7%) of bird communities in the 1980s had only highly dissimilar (dissimilarity > 0.30) compositional matches available among bird communities in the 2010s (*Fig. 4B and SI Appendix, Fig. S6*), suggesting an extinction of these community compositions (hereafter "extinct" communities). Such communities without a species composition counterpart in the 2010s were already unique in the 1980s. That is, their average dissimilarity to other bird communities

occurring in the 1980s was higher (0.29) compared to bird communities that had more similar matches in the 2010s (0.14).

The high variation in dissimilarity values measured for each "best match" between the 1980s and the 2010s was accounted for in the modeling by including similarity values as model weights (*Materials and Methods*). We partitioned the spatiotemporal dissimilarities between bird communities in the 1980s and 2010s into the two additive components of species replacement and nestedness. Nestedness occurs when the communities with lower species richness are subsets of the communities with higher species richness, reflecting a nonrandom process of species loss as a consequence of a factor that promotes the disaggregation of communities (28). Contrary to nestedness, replacement of some species by others may occur because of environmental sorting or spatial and historical constraints. We found that the dissimilarities were mainly driven by replacement (mean contribution = 0.94) rather than nestedness (mean contribution = 0.06).

**Community Composition Shift Distance.** The effect sign of nearly all relationships of community shift distance aligned with our hypotheses illustrated in *Fig. 1 (SI Appendix, Table S1)*. The distance of the community composition shift was most affected by the proximity of coastlines: with a variable importance of ~78%, this was the most important factor (*SI Appendix, Table S1*). The overall response showed that communities shifted significantly farther when they were located farther away from the coastlines (*Fig. 2C*). That is, each additional unit increase in distance to the coastline was associated with an 11% increase in community shift distance. The elevation distance, biome distance, and the fixed effect of initial similarity were minimally important for community composition shift distances, with 0.06%, 2%, and 9% relative variable importance, respectively (*Fig. 2D and SI Appendix, Table S1*). Temperature isotherm shift distance significantly influenced how far the community compositions shifted such that with longer temperature isotherm shifts, the longer the community shifts (11% variable importance, *SI Appendix, Table S1*). The degree of nestedness driving spatiotemporal dissimilarities did not influence the observed community composition shift distances ( $r = -0.02$ ).

**Community Composition Shift Direction.** The effect sign of all relationships of community shift direction aligned with our hypotheses illustrated in *Fig. 1 (SI Appendix, Table S2)*. That is, communities shifted in directions along most similar elevations (positive relationship) but away from biome boundaries and coastlines (negative relationship) (*Fig. 2 and SI Appendix, Table S2*). Specifically, community shift eastness was most significantly affected by elevation (within a radius of 150 km) and biome direction but only marginally by coastline direction, which was reflected in their variable importance with ~38%, 25%, and 6%, respectively (*Fig. 2 E–H and SI Appendix, Table S2*). The community shift northness was most significantly affected by elevation direction (within a radius of 150 km), with a high variable importance of ~73%, while neither biome nor coastline direction had a statistically significant effect on community shift northness (~8% and 3%, respectively, *Fig. 2 I–L and SI Appendix, Table S2*). The fixed effect of temperature isotherm shift did not influence community composition shift eastness or northness and had a low variable importance (2% and 10%, respectively), showing that community composition shift directions do not clearly follow the directions of observed temperature isotherm shifts. The variation in dissimilarity of communities from the 1980s to 2010s negatively influenced the shift direction, with a significant effect along the longitude and a marginal effect



**Fig. 1.** Hypothesized effects of ecological barriers on community composition shift distance and direction. The icons in panels A–C illustrate ecological barriers: biome boundaries, coastlines, and elevation, 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. In panel C, elevation is indicated with a brown–yellow gradient (brown colors: high elevation). 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 a shift along the latitudinal (south–north) or longitudinal (west–east) axis (for details, see *Materials and Methods*).

( $P < 0.1$ ) along the latitude (29% and 6% variable importance, respectively; *SI Appendix, Table S2*).

Overall, the effect sizes of barrier variables and the explained variances of the models were small, suggesting that factors beyond ecological barriers also influence community shift directions and distances (*SI Appendix, Figs. S17 and S18*).

**Climatic Debt.** We found that bird community shift distances lagged temperature isotherm shifts on average by ~210 km. In total, 91% of bird communities had a positive lag (i.e., community compositions shifted less far than the temperature isotherms), indicating a climatic debt. On the other hand, only 9% of bird communities have shifted farther than expected based on temperature isotherm shift (Fig. 3A). The climatic debt of nonshifting communities was significantly higher than that of shifting communities (mean climatic debt shift distance = 287.1 and 168.5 km, respectively;  $t = 19.96$ ,  $df = 1,665.8$ ,  $P < 0.001$ ; Fig. 3B). We also found that the extinct communities tended to have a lower climatic debt (172.6 km) compared to the nonextinct ones (209.7 km;  $t = 2.341$ ,  $df = 152.13$ ,  $P = 0.021$ ; Fig. 3C).

## Discussion

In this study, we found that two-thirds of the European breeding bird communities experienced spatiotemporal shifts in their composition from the 1980s to the 2010s. Following our hypotheses,

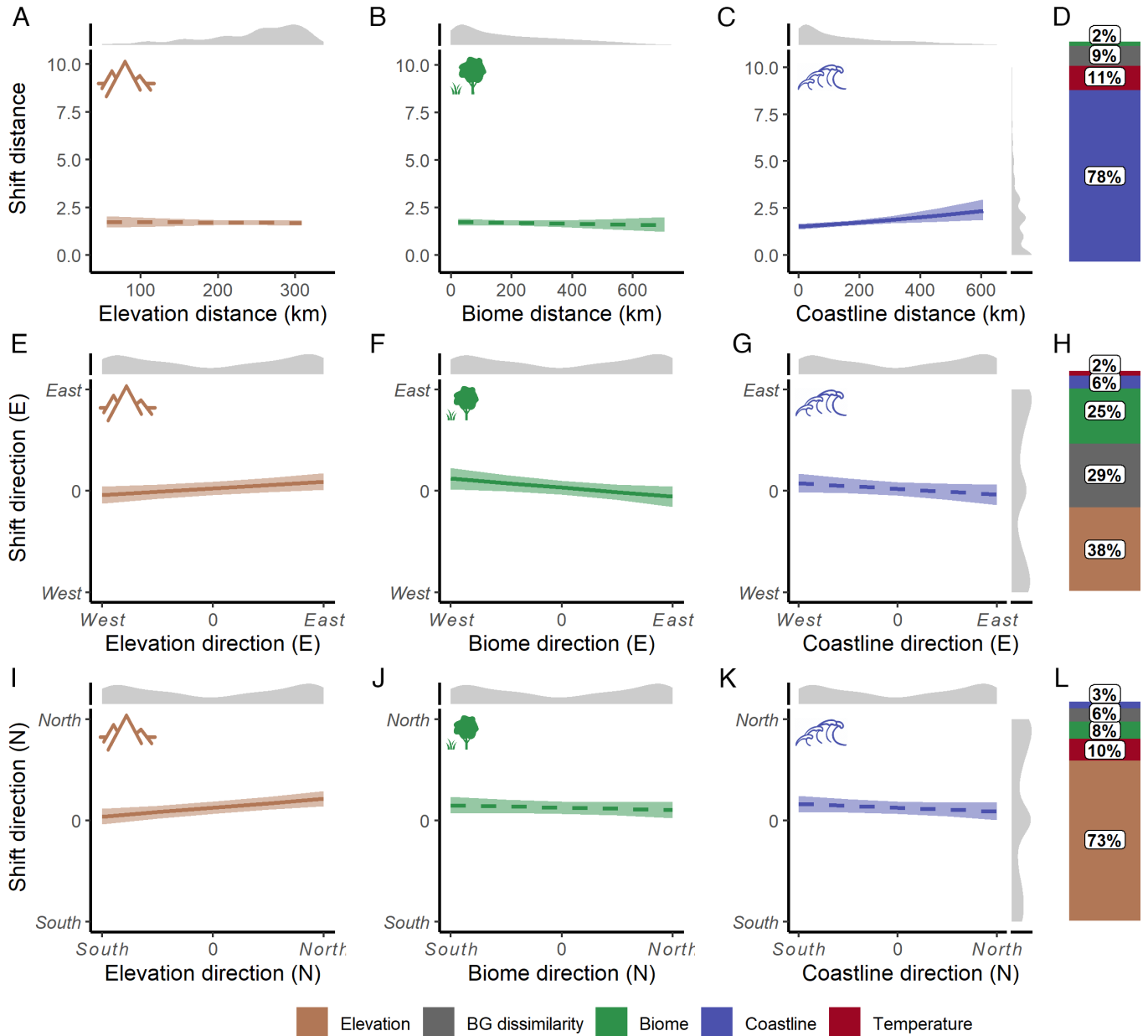
both geophysical and biotic barriers consistently, and predictably, influenced community composition shifts. That is, bird communities generally shifted farther toward directions of low resistance, thereby avoiding ecological barriers. Although the directions of community composition shifts varied substantially, the general tendency of shifts was to north, east, and west, rather than south, corroborating most research findings on directional northeast climate-driven distribution shifts of single species in the northern hemisphere (4). Even if the general pattern of community composition shift directions was toward northeast, the directions of community composition shifts were not significantly correlated with directions of temperature isotherm shifts. This indicates that communities face obstacles such as large-scale ecological barriers (or smaller scale barriers caused by, e.g., land use change or fragmentation) when shifting—even if aiming to track their climatic niche.

Together, the observed effects of ecological barriers on community composition shifts indicate that species' shifts, and their associated communities, may be mediated through areas of least geophysical resistance defined by coastlines and elevation and areas of most optimal biotic conditions defined by biomes. Coastlines were 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 gradient (29). Contrary to shifts in directions, elevation resistance did not strongly influence shifts in distances, potentially because communities do not need to shift far to track their original abiotic and biotic preferences (1, 30) in areas of high topographic variation. Biome boundaries showed different effects on community composition shift distances and directions such that communities shifted directionally away from close biome boundaries along the longitudinal axis, while there was no detectable effect on shift distances.

Typically, coastlines and elevation represent abrupt and spatially well-defined barriers, whereas biome boundaries are more gradual in space, thus posing weaker and potentially more adaptable biotic

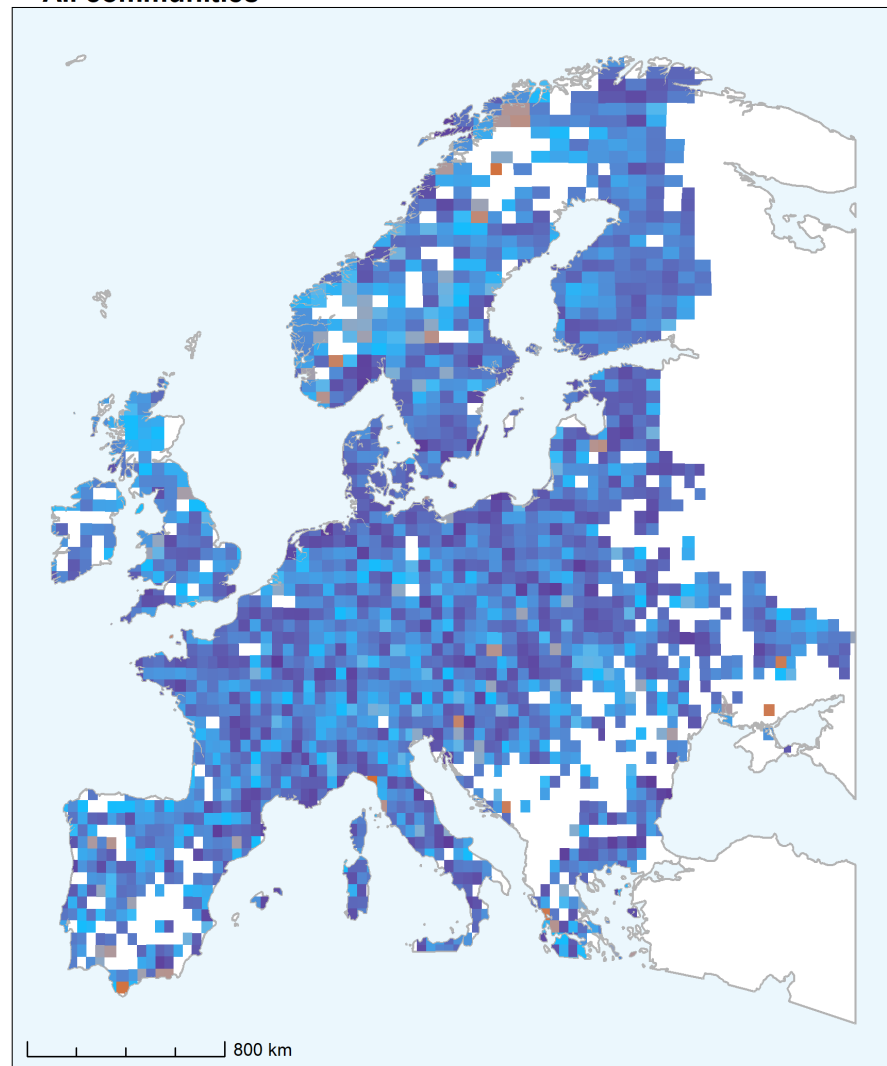
limits to community composition shifts. Although we did not test differences in edge contrast of different biomes, it is unlikely that communities shift across biome boundaries (31) even when the biomes have relatively similar abiotic conditions (e.g., across cold and warm deserts) (32), as the biotic conditions tend to differ considerably among biomes. Yet, given the relatively low effect sizes and variance explained in our models, factors other than the ones tested here must also influence community composition shifts. In addition, the diversity and variation in single species' sensitivities and responses to ecological barriers under global change—which cannot be captured by studying community compositions alone—likely introduce a fair amount of unexplained variation in our analyses. Indeed, previous studies have shown that



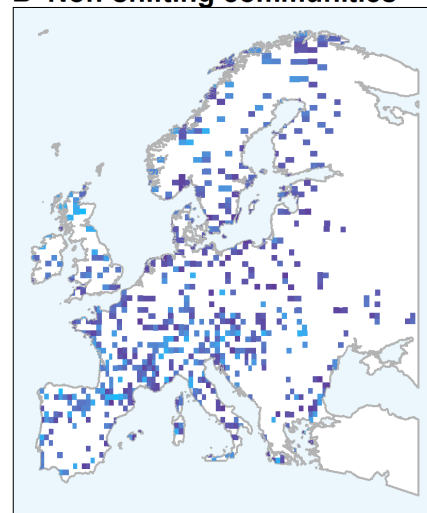
**Fig. 2.** Modeled relationships between ecological barriers and community composition shifts. Predicted linear effects of the three barriers on community composition shift distances (number of grid cells shifted, A–D) and directions (E–L) based on full models. Linear regressions of full model predictions are plotted for all barrier variables by using the term of interest and averaging over other terms in the model. Note that temperature isotherm shift and initial dissimilarity were present as fixed effects in all models. Regression lines are model-based beta estimates, where solid regression lines show significant ( $P < 0.05$ ) and dashed lines ( $P > 0.05$ ) near- or nonsignificant relationships. Shaded areas are the 95% CI, and raw data distributions are illustrated at the top and right-hand side axes. Stacked bar plots D, H, and L illustrate the relative variable importance per model (rounded). Note that directions of response and predictor variables range from  $-1$  to  $1$  as they were sine and cosine transformed to obtain linear expressions along the west–east (E) and south–north (N) axes, respectively.  $N = 2,092$  for A–D (shift distance) and  $N = 1,407$  for E–L (shift direction). BG dissimilarity = initial background dissimilarity.



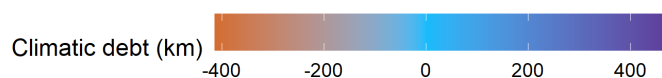
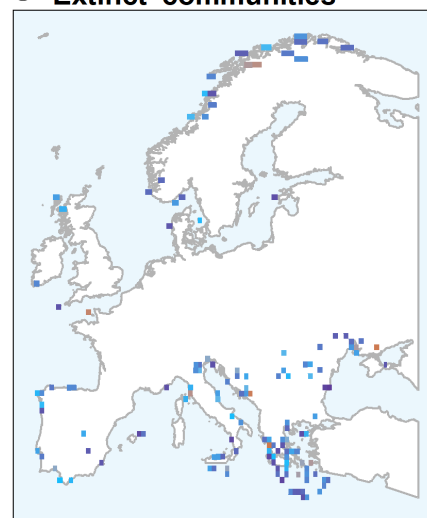
### A All communities



### B Non-shifting communities



### C 'Extinct' communities

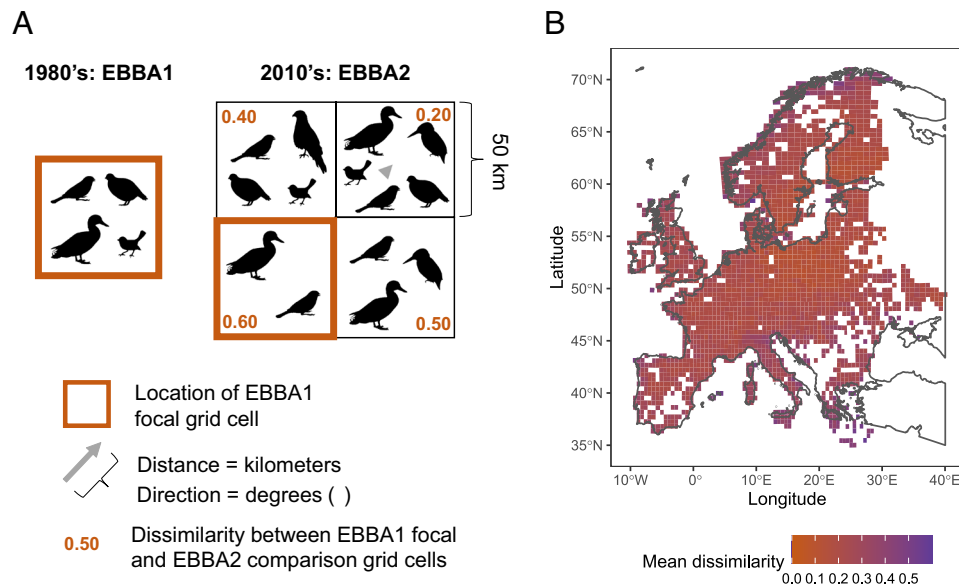


**Fig. 3.** Climatic debt in community composition shift distances of European breeding birds for (A) all 2,092 communities, (B) communities that did not shift ( $N = 681$ ), and (C) communities with poor compositional matches (Jaccard dissimilarity  $> 0.3$ ) suggesting community composition extinctions ( $N = 140$ ). Color gradient in  $50 \times 50$  km grid cells illustrates the observed difference in distances (km) between temperature isotherm and bird community composition shifts between the 1980s and the 2010s across Europe. Negative values indicate that the community composition has shifted further than expected based on climate change, while positive values indicate a climatic debt. Temperature isotherm shift distance is calculated as the distance from each focal grid cell in the 1980s to the grid cell with the most similar temperature in the 2010s inside a buffer area of 450 km.

processes such as habitat loss, fragmentation, habitat diversity, or road density considerably mediate biodiversity shifts (9, 24). Likely, the environmental drivers influencing ecological communities follow a spatial hierarchy such that ecological barriers govern community shifts at macroecological scales, while other processes, such as species' interactions, land use change, and habitat fragmentation, may limit the shift potential at smaller spatial scales (30, 33).

Community composition shift distances, but not directions, were significantly correlated with temperature isotherm shifts, indicating that breeding bird community compositions have likely shifted due to the influence of climate change drivers on single species distributions (1). However, the shifted distances were consistently shorter than the temperature isotherm shifts, indicating that European bird communities were not able to track their climatic niches (i.e., accumulating climatic debt). In particular, the climatic debt, as well as the dissimilarity between the matching

communities in the 1980s and 2010s, was higher for the non-shifting than the shifting bird communities. This indicates that spatiotemporal shift is a necessary strategy to remain within the climatic niche while maintaining the original community composition as closely as possible under global change. Unlike the nonshifting communities, the extinct communities had a lower climatic debt than the nonextinct communities because they shifted further to track their climatic niche. However, we note that the shift distance of an extinct community is difficult to interpret as the shift is calculated to the location of the best match in the 2010s, to which the dissimilarity is so high that the community has in reality experienced partial or full species composition turnover. In the ecological context, our results mean that an average bird community can now be found  $\sim 100$  km toward northeast compared to where it was located 30 y ago, lagging behind the average temperature isotherm shift by  $\sim 200$  km. Consequently, some bird communities may potentially no longer



**Fig. 4.** Schematic illustration of community composition shift quantification. In panel *A*, the orange numbers indicate Jaccard's dissimilarity index values when comparing community composition of a hypothetical focal EBBA1 grid cell (orange outlines, on the left) to hypothetical EBBA2 comparison grid cells (four squares on the right, including the focal grid cell). The gray arrow points from the focal EBBA1 grid cell to the compositionally 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 observed Jaccard's dissimilarity index values across the extent of EBBA1 grid cells ( $N = 2,092$ ), quantified as the dissimilarity between each focal EBBA1 grid cell and its best-matching EBBA2 grid cell.

co-occur with essential components of the ecosystem, such as their food resources or mutualistic partners, due to asynchronous responses of the different trophic levels to climate change (34).

The observed "community composition extinctions" can result from losing and/or gaining bird species in the local community, of which both cases have been observed across Europe (35) and globally (36) as a result of environmental change. Extinct communities were mainly located along coastlines (*SI Appendix, Fig. S6A*) and were compositionally unique in the 1980s. This suggests that such unique community compositions are particularly in danger of disappearing under climate change and that ecological barriers likely influence their shifting potential in the coastal areas. This conclusion also aligns with earlier findings on biotic homogenization influencing functionally unique specialists at the species level (16). In particular, ecological community compositions have been found to shift toward dominance of highly dispersive habitat generalists (24), potentially degrading the ecological function of such communities due to losses of specialist species (16). 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 (21, 30). The lack of compositional matches between bird communities in the 1980s and the 2010s may also reflect the appearance of novel community compositions over time, potentially leading to unpredictable alterations in ecosystem functioning (37).

Although our results are general, it is likely that the relevance of a particular barrier depends on the ecosystem and taxonomic group in question. For example, fixed day lengths along the latitudinal gradient may be a relevant biotic barrier for community compositions of various taxa in arctic ecosystems (38). Moreover, barrier effects on community shifts may also depend on the general dispersal ability of the taxa in question such that more mobile taxa, like birds, may be less constrained by certain ecological barriers than sessile plants or dispersal-limited animals. We suggest that ecological barrier data combined with species' traits can help to understand why communities shift slower than expected, for

example, based on climatic predictors alone (3, 35, 39). We also encourage carrying out future studies on fine-scale differences in community composition changes, for example, among different habitat types, to assess the variation in species-level responses. That is, instead of delineating communities with spatial units, communities could be defined within different habitat types, which would allow studying their distinct spatiotemporal shifts in response to global change drivers. Additionally, the potential uncertainty in defining spatiotemporal shifts of community compositions per se could be explored, for example, by using stochastically defined correspondence of compositional matches over time or applying a fuzzy set framework to define a "degree of belonging" (40). Moreover, we suggest that by quantifying 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, time series of ecological barriers and community composition shifts could be combined to study more accurate velocities of community reshuffling and biodiversity shifts in general (11, 41). Putting these components together, future work should aim to predict biodiversity shifts in space and time while incorporating ecological barriers into the predictions.

Here, we provide evidence of observed, rather than predicted, shifts of entire communities across large spatiotemporal scales as a function of ecological barriers, substantially advancing previous research exploring the impacts of ecological barriers as determinants of single species' range shifts (21, 30). We assert that including the effects of ecological barriers in global change studies can lead to more realistic predictions of community shifts because they set the outer bounds of potential shifts (42). This in turn can increase the accuracy of community shift predictions and contribute to advancing large-scale ecological research and conservation management (21). Our results have potential to inform conservation policies under climate change, for example, via improved designation of a reserve network for biodiversity shifts, protection along climate change trajectories and ecological corridors, and identification of contemporary climate refugia (24). So far,

conservation of communities with primarily high latitude or high elevation distributions has been a major concern in the climate change context because their poleward or uphill shifts have natural limits (43). Our results suggest that similar limitations apply in relation to other ecological barriers, and at the level of entire communities, as ecological barriers guide the distance and direction of their shifts. Our study adds to the current knowledge by unveiling, at a continental scale, that shifting communities are affected by a range of ecological barriers, likely adding to the observed climatic debt. This underscores the importance of moving beyond simple climate change measures when studying community shift dynamics.

## Materials and Methods

**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) (23, 24). Breeding birds were surveyed within 50 × 50 km grid cells mainly during 1981 to 1989 for EBBA1 and mainly during 2013 to 2017 for EBBA2 (*SI Appendix, Fig. S2*). The surveys were conducted by volunteer birdwatchers and professional ornithologists, organized by national coordinators, and internationally coordinated by the European Bird Census Council. The broad spatial extent of the data allowed us to study biodiversity shifts at large spatial scales, in accordance with earlier studies (9). 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 species with observed possible, probable, and confirmed breeding records were compiled into grid cell-specific lists *sensu* ref. 24, 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. To ensure sufficient data coverage within grid cells, we excluded EBBA1 grid cells of poor sampling coverage as described in ref. 24. To ensure a reasonable potential for comparable 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 toward 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 2,092 focal EBBA1 grid cells to be used as study units and 4,843 EBBA2 grid cells to compare EBBA1 grid cells to (*SI Appendix, Fig. S2*). 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 *SI Appendix, Table S7*). We followed the taxonomy of EBBA2 (24) but merged four species pairs because they were considered as single species in EBBA1 and had unclear distributions across atlases: *Phylloscopus collybita* and *Phylloscopus ibericus*, *Lanius meridionalis* and *Lanius excubitor*, *Picus sharpei* and *Picus viridis*, and *Sylvia subalpina* and *Sylvia cantillans*.

**Quantification of Community Composition Shift.** We acknowledge that a one grid cell can potentially be composed of several different bird communities. However, given the spatial resolution of the data, in this study, we define a community as a group of species within a one grid cell. We quantified spatiotemporal shifts of entire breeding bird community compositions because summary measures, such as species richness, may remain unchanged over time even when the species composition changes (7). To quantify the spatiotemporal shift in community composition, we first calculated pairwise Jaccard's dissimilarity index (*SI Appendix, Eq. S1*, 44) among all grid cell pairs between EBBA1 and EBBA2 using the "betapart" R package (version 1.5.6; 28). Jaccard's dissimilarity quantifies the degree of difference in the compositions of two communities with presence-absence data. We selected Jaccard's dissimilarity index because it is the most widely applied index for quantifying temporal changes in community composition at macroecological scales when using presence-absence data (e.g., refs. 45 and 46). A potential limitation of the index is that it gives a strong emphasis on rare species when using presence-absence data. We therefore tested the effect of rare species on the results by repeating the analyses with subset data

(see *SI Appendix, section S3.1* for details). To assess the underlying mechanisms driving community composition shifts, we also partitioned the spatiotemporal dissimilarities between bird communities in the 1980s and 2010s into components of replacement and nestedness. 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 (11, 41; Fig. 4 and *SI Appendix, Fig. S1*). We decided to use the approach of selecting the EBBA2 grid cell with the lowest dissimilarity (i.e., the most similar community composition) because we aimed to find a compositional equivalent between two time points. In a recent study, Ankori-Karlinsky et al. (46) used a similar logic and approach applying Jaccard's index to explore the compositional turnover of communities in time. They present robust and relevant findings by using North American bird census data and calculating the degree of species community similarity among the survey units (i.e., blocks or routes) of each census and comparing the mean similarity values. For our study, we selected the best-matching EBBA2 grid cell by first identifying the five 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 ( $N = 1,798$ ) 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 chose this threshold as it is the 0.5 quantile across all percent increases when comparing the lowest EBBA2 dissimilarity disregarding the geographic distance and the EBBA2 dissimilarity of the closest among the five best matches (exact value = 3.53%, see also *SI Appendix, Fig. S4*). 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. 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 grid cell (R package "raster," 47). Second, we quantified the direction of the community shift as the bearing (0 to 360°) between the same pairs of EBBA1 and EBBA2 grid cells (R package "geosphere," 48).

To understand how the uniqueness of the focal EBBA1 communities influences the spatiotemporal community composition shifts, we included the "initial EBBA1 dissimilarity" as a control variable in the analyses. We calculated initial dissimilarity as Jaccard dissimilarity between each focal EBBA1 grid cell and its best-matching EBBA1 grid cell (i.e., grids within the same time period; *SI Appendix, Fig. S3B*). To confirm the relevance of our approach, we tested for the difference in spatial (within EBBA1) and spatiotemporal (between EBBA1 and EBBA2) dissimilarity in community composition shift distances. For the spatial shift, we calculated the distance from each EBBA1 grid cell to the EBBA1 grid cell with the most similar community composition. Then, we quantified the difference between the spatial shift distance and the spatiotemporal shift distance and found that the majority of EBBA1 communities that shifted between EBBA1 and EBBA2 shifted further than expected based on the spatial shift distance (*SI Appendix, Fig. S8*).

**Quantification of Temperature Isotherm Shift.** Based on earlier studies, we know that communities shift along temperature isotherms in order to track their climatic niche (9). Temperature isotherm shift, or climate change velocity (49), is broadly used in macroecological studies to explain responses of biodiversity to climate change (9, 21). To quantify a proxy of temperature isotherm shift at the same spatial scale as the EBBA data, 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° resolution (50). We averaged the temperatures across all months and years in EBBA1 (1981 to 1989) and EBBA2 (2013 to 2017) periods in each grid cell. We used the annual mean temperature because it has been found to be the best climate (51) and temperature predictor in earlier studies (21, 23, 52). For the 171 grid cells that lacked temperature data (*SI Appendix, Fig. S15*), we used a Kriging interpolation to obtain mean temperatures (53). To control for the effect of temperature isotherm shift on bird community composition shift distance and direction, 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. We did this inside a buffer area of 450 km, equaling the three-fold distance of observed average community shifts in our data (*SI Appendix, section S1.2.4*)—because across Europe, temperatures have generally shifted over threefold faster than species communities (3, 35).



**Quantification of Ecological Barriers.** To quantify ecological barriers of biome boundaries (i.e., zones where the land changes from one biome type to another), we obtained a geographic information layer defining the six major biomes within the study area (54; *SI Appendix, section S1.2.1*) and excluded coastlines to differentiate between terrestrial biome boundaries and coastlines. Although the biome boundary barrier partly coincides with other ecological barriers, it represents the combination of several biotic conditions, such as vegetation structure and productivity (55), 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 (R package *geosphere*, 48). We then extracted the distance in kilometers from each focal EBBA1 grid cell to the nearest biome boundary point and calculated the direction to this same point (*SI Appendix, section S1.2.1*).

Coastlines were defined from world vector data within and adjacent to the study area (of seas but not of large inland lakes; *SI Appendix, section S1.2.2*) and calculated using a distance matrix between all focal EBBA1 grid cell centroids and evenly sampled points along the coastlines. We then extracted the distance in kilometers from each focal EBBA1 grid cell to the nearest coastline point and calculated the direction to this same point (*SI Appendix, section S1.2.2*).

To quantify ecological barriers related to elevation, we used Digital Elevation Models (m a.s.l.) at 30 arc seconds resolution (56) and averaged the elevation values for each grid cell (*SI Appendix, section S1.2.3*). We used the grid cell-averaged elevation data to calculate barrier distance and direction variables. We explored the influence of the continuous predictor of elevation at two different spatial scales by restricting the analyses of shift distance and direction to two ecologically meaningful buffer areas around the focal EBBA1 grid cells. That is, we estimated 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 shift potential within six grid cells (300 km). 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, indicating shift distance potential with the lowest elevational resistance (*SI Appendix, section S1.2.3*). Second, per buffer, we created 64 radial lines (every  $\sim 5^\circ$ , starting at  $0^\circ$ ) around the focal EBBA1 grid cell centroid 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* (48; *SI Appendix, section S1.2.3*).

**Modeling Community Composition Shift as Function of Ecological Barriers.** We used the community composition shift distance and direction as response variables in separate models, the different measures of ecological barriers as predictor variables (Fig. 1), and included temperature isotherm shift and the initial EBBA1 dissimilarity as fixed effects. 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 modeled relationships.

We analyzed the community shift distance using a generalized linear mixed model with penalized quasi-likelihood ("glmmPQL" in R package "MASS," (57), a Poisson structure with log-link function, and a Gaussian spatial correlation structure to account for spatial autocorrelation in the model residuals. As the response variable, we used the community composition shift distances that were transformed into count data, i.e., the number of grid cells shifted. A shift of one grid cell equaled approximately  $\sim 70$  km, two grid cells  $\sim 140$  km, etc., accounting for horizontal, vertical, and diagonal shifts in grid cells. All variables were standardized to a continuous scale. For the elevation predictor, we selected the best spatial scale by comparing single-predictor models of buffer radii 300 km and 450 km. For the full model, we combined all three barrier variables, temperature isotherm shift distance, and initial dissimilarity. We calculated the relative variable importance for the three barrier variables and the fixed effects using the leave-one-out jackknife procedure. That is, we dropped one variable at a time from the full model and calculated the subsequent relative change in conditional  $R^2$ . We used  $R^2$  because glmmPQL models do not allow calculating Akaike Information Criteria (AIC) values, unlike the shift direction generalized least square models (gls) for which we used AIC values as a measure of goodness of fit.

We excluded 685 communities that did not shift from EBBA1 to EBBA2 and therefore had no value for shift direction, which left 1,407 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 modeled eastness and northness of community shifts separately, following the same statistical protocol. We fitted generalized least square models (R package "nlme," 58). Due to observed spatial autocorrelation, we included a Gaussian spatial correlation structure in the models. Again, we selected the best spatial scale of elevation by comparing single-predictor models. Then, we combined all barrier variables and the two additional fixed effects into a full model and calculated relative variable importance again using the leave-one-out jackknife procedure. That is, we dropped one variable at a time from the full model and calculated the subsequent relative change in AIC ( $\Delta AIC$ , %).

To quantify the lag in community composition shifts in relation to temperature isotherm shifts, we calculated the climatic debt (3, 9) in community composition shift distances across the study area. For this, we calculated the difference between the temperature isotherm shift distance and bird community composition shift distance and mapped the values to obtain a spatial understanding of the variation in climatic debt across Europe for all communities together and those that did not shift or had only poor compositional matches (Fig. 3 A–C).

**Sensitivity Analyses.** We accounted for the stochasticity in the selection of the best-matching EBBA2 grid cell in two ways. First, we repeated the selection of the best-matching comparison grid cell using different cutoff values to select the best match and then tested how this influenced the resulting shift distances and direction (*SI Appendix, Fig. S4*) and the observed relationships with the ecological barriers (*SI Appendix, section 3.1*). We combined a set of additional values for the number of EBBA2 grid cells with the most similar community compositions (2, 4, 10, 20 grid cells) and the percentage threshold in dissimilarity increase compared to the grid cell with the lowest dissimilarity among the chosen grid cells from step 1 (1%, 2%, 4%, and 5%). We found that only for the eastness of community shift direction, there were some minor changes in the significance of the observed relationships, while almost none of the effects changed for northness or shift distances, and overall, all relationships were qualitatively similar, i.e., in their effect sign and even their effect size (see *SI Appendix, section 3.1* for detailed results).

Next, 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 (*SI Appendix, section S3.2*). We did this because in presence-absence data, all species influence the dissimilarity value regardless of their abundance. In addition, we also ran sensitivity analyses by excluding all bird species classified as marine or coastal (*SI Appendix, section S3.3*) to test whether the inland communities respond differently to our set of ecological barriers in comparison to the full data that included coastal species. Comparing the model outputs for the full and the subset communities, we found that barrier effects on shift direction and distances were influenced by the inclusion of rare and non-native species (for more details, see *SI Appendix, section S3.2*). We also explored whether coastal communities were more likely to stay in the coastal areas rather than to move inland. For this, we conducted a bootstrapping analysis where each coastal community was allowed to move randomly to available grid cells within  $\sim 105$  km and  $\sim 155$  km radius, respectively—equivalent of two and three grid cells to cardinal directions, respectively. Third, we checked whether the simulated shift happened to a coastal or inland grid cell and calculated the frequency distribution of coastal communities that shifted along coastal grids against those that moved inland. These distributions were compared to observed spatiotemporal shifts between EBBA1 and EBBA2. Bootstrapping analysis showed that coastal communities were significantly more likely to shift to coastal grid cells compared to simulated random shifts ( $P \leq 0.05$ ; *SI Appendix, section S3.3*). Last, we also explored whether the inclusion of weights influenced model estimates by excluding weights from final models, finding no qualitative difference between models including and excluding weights (*SI Appendix, section S3.4*). For all data processing and statistical analyses, we used QGIS (59) and R software (version 4.2.0 vigorous calisthenics; 60).



**Data, Materials, and Software Availability.** Previously published data were used for this work [Raw data on bird occurrences from both breeding bird atlases can be downloaded: EBBA1 on GBIF (<https://www.gbif.org/dataset/c779b049-28f3-4daf-bbf4-0a40830819b6#:~:text=ln>)(61) and EBBA2 (<https://ebba2.info/maps/>)(62). Data and code used for statistical analyses are available on Zenodo (63).

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