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Original Research Article

Impact of future climate change and land-use change on habitat suitability for a long-distance avian migrant under diverse socioeconomic-emission scenarios

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ABSTRACT

Climate change and the alteration of land-use and land-cover (LULC) on a global scale presents a notable threat to biodiversity, with a particular impact on long-distance migratory birds. Nonetheless, our comprehension of how these changes specifically affect these avian migrants remains limited. To address this knowledge gap, species distribution models offer a valuable tool as they allow for projecting habitat suitability and provide insights into a species' ecological responses to changing environmental conditions. In this study, we utilize modelled climate and LULC data spanning from 2015 to 2100, coupled with GPS tracking data and open-source occurrence data of European Nightjars (*Caprimulgus europaeus*), to assess how suitable habitat might be affected by changes in climate and LULC under different emission and socio-economic scenarios. Our models show that climate change alone may expand suitable habitat, particularly under high-emission scenarios, while LULC change generally exerts a constraining effect across annual cycle stages. While some scenarios indicate overall stability in the amount of suitable habitat, our spatially explicit results reveal that these entail substantial redistribution of suitable habitat which may disrupt migration patterns and increase energetic costs. Our findings underscore the importance of explicitly considering spatial and temporal aspects in assessments of global change impacts on migratory species and highlight the need for targeted conservation interventions in critical stopover zones to safeguard the species' future amidst global environmental change.

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1. Introduction

Over the past 300 years, human populations have transformed the terrestrial biosphere by altering land-use and land-cover (LULC) patterns, resulting in the irreversible conversion of wild biomes to intensively utilized anthromes with predominantly novel anthropogenic ecological processes (Ellis, 2011). Ecosystems where the impact of human influence remains low contribute significantly to human well-being (Diaz et al., 2018) by providing ecosystem services (Watson et al., 2018), offsetting the effects of climate change (Martin and Watson, 2016) and maintaining biodiversity (Di Marco et al., 2019). However, as currently around 75 % of the planet's surface is faced with human pressures, the human footprint has become global and keeps increasing rapidly, especially in tropical regions and biodiversity hotspots (Venter et al., 2016).

While the consequences these human pressures entail for biodiversity are difficult to quantify, experts have estimated that about 30 % of species have been globally threatened or driven to extinction since the year 1500 (Isbell et al., 2022). This massive loss of species and the resulting degradation of ecosystems is likely to only further accelerate in the coming years (Johnson et al., 2017). Although there are several causes associated with these declines, LULC change, mainly in the form of rapid expansion and intensifying management of land used for cropping or animal husbandry, has been identified as the most important driver of global biodiversity loss over recent decades (IPBES, 2019; Jaureguiberry et al., 2022). Furthermore, LULC change has the potential to interact with other global change drivers e.g. deforestation and urban expansion, which can contribute to climate change by releasing greenhouse gases and reducing carbon storage. Climate change impacts, such as rising temperatures and extreme weather events can further alter land-use patterns and biodiversity richness (Oliver and Morecroft, 2014; Barati et al., 2023).

As drivers of biodiversity decline and their associated impacts change over time, efficient management of biodiversity requires a forward-looking approach based on scenarios that explore biodiversity changes under future environmental conditions (Sala et al., 2000; Titeux et al., 2016). These scenarios draw upon narratives (storylines) of environmental change that project plausible socio-economic developments or future pathways under specific policy options and strategies (Vuuren et al., 2012; O'Neill et al., 2014). Although LULC change is predominant among the drivers of biodiversity loss, most studies addressing the effects of future environmental changes on biodiversity have focused solely on climate change, or more specifically on changes in temperature (Titeux et al., 2016; Taheri et al., 2021), neglecting other significant potential drivers of species distribution changes (Marshall et al., 2018), but see e.g. Thuiller et al. (2004) and Hof et al. (2018).

Effects of environmental change may vary between species groups (Gibson et al., 2011; Newbold et al., 2020). The conversion of natural ecosystems, or changes in the management of already modified landscapes, does not affect all species uniformly. Some species may tolerate, or even benefit from, these transformations, particularly those that are generalist, synanthropic, or non-native. In contrast, rare or specialist species that depend on intact natural habitats are often the most negatively affected (Sofaer et al., 2020; Davis et al., 2023; Liu et al., 2023). Beyond species-specific ecological traits, the spatial scale at which species operate also shapes their sensitivity to environmental change. Migratory birds, for instance, are considered especially vulnerable due to their dependence on environmental conditions at distinctly separated locations (Newton, 2008; Klaassen et al., 2014; Runge et al., 2014). They have faced widespread population declines over the past decades (Vickery et al., 2014; Studds et al., 2017; Rosenberg et al., 2019). However, addressing these declines is complicated because of incomplete knowledge of migrant non-breeding distributions and migratory routes (Vickery et al., 2014). Recent technological advances allow for tracking individual migrants to provide occurrence data throughout the annual cycle (Kays et al., 2015; Vickery et al., 2023). This fundamental information helps to identify potential threats and drivers of declines and assess their impact for different stages of the annual cycle (Lisovski et al., 2021; Buchan et al., 2023; Davies et al., 2023).

Species distribution models (SDMs) can bridge ecological knowledge gaps for poorly understood species by predicting suitable habitats within an area of interest (Guisan and Thuiller, 2005; Coxen et al., 2017). This approach employs predictors which limit a species' known distribution, in terrestrial settings typically climate and sometimes substrate, terrain and land-cover, to determine features associated with locations occupied by a target species (Elith et al., 2006; Elith and Leathwick, 2009; Elith and Franklin, 2017). A model associating known distribution patterns with these predictors can then be used to generate maps estimating the probability of finding that species at other locations based upon similarity in values for the same ecological predictors (Phillips et al., 2006). Occurrence data are generally gathered through direct field observations or open-source distribution databases (Stoetzel et al., 2020; Neice and McRae, 2021; Nzei et al., 2022). Satellite tracking has opened up the possibility of using this approach for modelling distribution of long-distance migrants. Species distribution modelling for long-distance migrants has been focused on temporally explicit climatic models to identify avian migrants' climatic niches and predict seasonal distribution patterns (Gschweng et al., 2012; Engler et al., 2017; Kassara et al., 2017; Williams et al., 2017).

In this study we combine global climate and LULC data with both open-source occurrence data and GPS tracking data of a long-distance Palearctic-Afrotropical migrant, the European Nightjar *Caprimulgus europaeus* (Linnaeus, 1758), hereafter referred to as Nightjar, to construct habitat suitability models for each distinct annual-cycle period. Nightjars are aerial insectivores, hunting for flying insects typically during periods of dusk and dawn (Cleere and Nurney, 1998). They can be considered habitat specialists during the breeding season, typically associated with semi-open landscapes on dry, sandy soils, and exhibit a degree of synanthropy. In Western Europe, its preferred breeding areas are often found in man-made habitats such as heathlands, military training areas, and young conifer plantations, while it forages in extensively managed agricultural landscapes (Sharps et al., 2015; Evens et al., 2017a). Emerging evidence suggests that these relatively strict habitat preferences may be somewhat relaxed during the non-breeding period (Lathouwers et al., 2023). However, due to Nightjars' constrained migration pattern, evident form their dependence upon a discrete wintering area in Central-Africa and reliance upon stopover locations essential for refuelling and successfully crossing ecological barriers (Evens et al., 2017b, Lathouwers et al., 2022a), losses of suitable habitat across the flyway would be expected to result in severe impacts.

Through our approach we aim to quantify suitable habitat across the Western-European - African flyway for each distinct stage of the annual cycle and estimate relative changes in suitable habitat under future climate and LULC change as projected by a combination of Shared Socioeconomic Pathways (SSP) and Representative Concentration Pathway (RCP)-based projections. Shared Socioeconomic Pathways are a set of scenarios designed to explore plausible future developments in global society, demographics, economics, politics, and technology. They were developed to provide a consistent set of narratives indicating how different socio-economic factors could evolve over the 21st century (O'Neill et al., 2014). Representative Concentration Pathways are scenarios that represent different greenhouse gas concentration trajectories and resulting levels of radiative forcing. They were developed to support the assessment of climate change impacts, adaptation, and mitigation (van Vuuren et al., 2011). Combining SSPs with RCPs allows us to explore the interactions between different socio-economic pathways and climate policies, providing a more comprehensive understanding of the potential future impacts of climate change and the possible responses of society to those impacts, in order to help guide future conservation efforts for Nightjars and other long-distance avian migrants.

2. Material and methods

2.1. Occurrence data

We conducted fieldwork in Belgium (51.1° N, 5.5° E; 2015–2022) and the UK (52.5° N, 0.7° E; 2015–2018, 53.1° N,−3.5° E; 2018–2019) where we captured Nightjars in breeding areas using ultra-fine mist nets (Ecotone, 15 ×3 m) and tape lures. We marked each individual with a unique alphanumeric ring and fitted a GPS-logger dorsally between the wings (Lathouwers et al., 2022a). In total, we tagged 117 adult male individuals with 1.8 g Pathtrack Ltd. nanoFix or Biotrack/Lotek Ltd. PinPoint-40 archival GPS-loggers. GPS-loggers were programmed to record longitude, latitude, and altitude, during the nocturnal period when the birds were presumed to be active. Based on the distribution of the log of step distances for all GPS fixes, we identified locations where individual Nightjars remained stationary for > 24 h (Lathouwers et al., 2023). These stationary locations were subsequently used to divide the annual cycle of each individual into four distinct periods: the breeding period, autumn migration, the wintering period and spring migration (see Lathouwers et al. 2023 for further details). Stationary locations during each separate annual cycle stage were used as occurrence data input in our SDM's, as they coincide with points where individuals used the local environmental resources in the context of foraging and/or resting.

Additional Nightjar occurrence data were downloaded from the Global Biodiversity Information Facility (GBIF.org, 2025) using the *rgbif* package (Chamberlain and Boettiger, 2017). Records were obtained from the years 2015–2025, within a buffer of 1000 kilometres around our GPS-tracking occurrence data. These data were filtered to exclude records with spatial uncertainty above 1000 m or with other geospatial issues (e.g., zero coordinates, country mismatch, or invalid date). Accurately assigning annual cycle stages to these GBIF occurrence records for Nightjars is challenging due to variation in the timing of migration and migratory routes across geographically distinct breeding populations (Lathouwers et al., 2022b). While Nightjars breed across a broad Palearctic range, from the United Kingdom to Mongolia, they are presumed to converge in Central and Southern Africa during the non-breeding season (Lathouwers et al., 2022b). As such, GBIF records from non-breeding regions may reflect individuals from populations not represented in our tracking data, complicating interpretation. As our GPS-tracked individuals originated from only a limited number of breeding (sub)populations, the most critical gap in spatial coverage for our modelling effort was during the breeding period. To address this, we filtered GBIF records to include only those from June and July, which we defined as the core breeding months within the range covered by the 1000-kilometre buffer around GPS-tracking occurrences. To reduce sampling bias in GBIF occurrence records, we filtered records using a grid of 10° by randomly picking one record per grid cell (Stiels et al., 2021).

2.2. Environmental data

As environmental input in this model we used data from Chen et al. (2022) who present a global LULC projection dataset with a 1-km resolution for from 2015 to 2100 with 5-year intervals. This dataset provides projections for a representative range of eight socio-economic and climate change scenarios, combining the Shared Socioeconomic Pathways (SSPs) with Representative Concentration Pathways (RCPs). SSPs describe five trajectories of socio-economic development (SSP1 to SSP5), ranging from sustainability-focused to fossil-fuel-driven futures (O'Neill et al., 2017). RCPs, on the other hand, refer to greenhouse gas concentration pathways targeting four levels of radiative forcing by the end of the century (2.6, 4.5, 7.0, and 8.5 W/m^2). These frameworks can be combined into SSP–RCP scenarios, offering a wide array of plausible future development trajectories (Fig. S1).

The LULC dataset presented in Chen et al. (2022) was produced by combining the top-down land demand constraints afforded by the CMIP6 official dataset and a bottom-up spatial simulation executed via cellular automata (see Chen et al. 2022 for further details). The study generated two 1-km future global LULC datasets, one comprising seven broad land types and the other comprising 20 land types based on plant functional types. To ensure ecologically interpretable and parsimonious input for our modelling approach, we used the simplified LULC product comprising seven aggregated land types: Water, Forest, Grassland, Barren, Cropland, Urban and Permanent snow and ice.

To match LULC data to the period of occurrence data collection between 2015 and 2025, we averaged LULC across all SSP-RCP scenarios between 2015 and 2020. Recent work has highlighted the uncertainty in matching recent observational and modelled greenhouse gas concentrations (Meinshausen et al., 2020). Furthermore, although trends in emissions between 2005 and 2020 seem to exclude the most extreme SSP-RCP scenarios for the future (Pielke et al., 2022), these relatively short term observational data hinder highly accurate assessment of the plausibility of long-term SSP-RCP scenarios (IPCC, 2021). Given the above uncertainties, we opted for the averaging of environmental data input across SSP-RCP scenarios.

In addition to LULC data, we incorporated climate data obtained at a 30-second resolution from WorldClim version 2.1 (Fick and Hijmans, 2017). Complementary to our LULC data, climatic variables were selected based on their direct relevance to e.g. Nightjar physiological preferences or prey availability. We used monthly minimum temperature, maximum temperature and precipitation averaged over periods corresponding to different stages of the Nightjar's annual cycle to obtain seasonal variables of minimum temperature, maximum temperature and precipitation. Based on the temporal distribution of GPS-tracking occurrence data, we defined the breeding season as April to September, autumn migration as August to November, wintering as October to March, and spring migration as February to May.

Although bioclimatic variables, which quantify climatic parameters across the entire year or a predefined period (e.g. the warmest quarter), are commonly used in SDM, we excluded them here to prioritize interpretability and reduce multicollinearity. Indirect aspects of climate are indirectly embedded within LULC data, as vegetation structure and land cover are themselves strongly shaped by long term climatic conditions (Chen et al., 2022). By focusing on a concise set of direct climatic and LULC variables, we aimed to represent both abiotic and biotic habitat components effectively. Moreover, limiting the number of environmental predictors helps reduce overfitting and enhances model generalizability, particularly for models developed from small sample sizes. A small but expertly chosen set of predictors is often seen as most appropriate (Williams et al., 2017).

Future climatic projections were obtained for the general circulation model (GCM) MRI-ESM2–0, which has been found the most suitable in another study modelling the distribution of a Palearctic migratory insectivorous birds in the Mediterranean and African regions (Abdul-Wahab et al., 2024). We used projections for four SSP–RCP combinations (SSP1–RCP2.6, SSP2–RCP4.5, SSP3–RCP7.0, SSP5–RCP8.5), each corresponding to the future period of 2081–2100.

Matching climate data to the period of occurrence data collection by averaging projections across SSP-RCP scenarios, as we did for LULC data, was not possible as future climate projections under each SSP–RCP scenario are only available in 20-year intervals from 2020 onward. We therefore used historical climate data from WorldClim version 2.1 at 30-second resolution, corresponding to the 1970–2000 baseline (Fick and Hijmans, 2017). While not explicitly matching the temporal extent of the occurrence data, this decision is consistent with other recent SDM studies (e.g., Williams et al., 2017; Abdul-Wahab et al., 2024).

2.3. *Species distribution modelling*

Using the package *dismo* (Hijmans et al., 2022) in R (R Core Team, 2022), we constructed four separate species distribution models for each distinct stage of the annual cycle, namely the breeding, autumn migration, wintering and spring migration periods, based on the corresponding occurrence data. We used the presence-background algorithm Maxent v3.4.4 (Phillips et al., 2023), one of the leading algorithms for presence-only data in contemporary species distribution models (Valavi et al., 2021). This model estimates the relative suitability of sites for a given species by comparing environmental conditions at known occupied sites to the available environmental conditions in the study region (the "background").

To ensure equal quantification of habitat use across the geographic range for each annual cycle stage, and to avoid overrepresenting locations where birds stayed for extended periods or where multiple individuals were recorded, we used the *spThin* package (Aiello-Lammens et al., 2015) to subsample our data set such that all occurrence records were separated by a minimum distance of 10 kilometres, roughly the equivalent of the distinction between local and relocation scale movements of individual Nightjars (Lathouwers et al., 2023). We defined the background extent of each model, corresponding to the region that has been accessible to the species of interest over the relevant time period (Barve et al., 2011), as a buffer of 1000 km around our occurrence datapoints. Subsequently, we randomly sampled 10,000 points within the terrestrial background area. In particular, we used the "spatSample" function from the *terra* package (Hijmans, 2025) which minimizes geographic biases such as overrepresentation of areas near the poles. For the models corresponding to the autumn- and spring migration periods we increased this number to 100,000 because of the increased geographic range of the background (Williams et al., 2017). We checked for intercorrelation between the environmental variables as defined by background extent for each separate model, using a Pearson's correlation test. Variables with a correlation value of > 0.7 or < -0.7 were no longer considered independent and were removed from further analysis (Ma et al., 2021) For all four models a significant correlation was found between seasonal minimum temperature and seasonal maximum temperature, therefore seasonal maximum temperature was excluded as a predictor in all four models. Seasonal minimum temperature and seasonal precipitation were included in all models as continuous variables, and LULC was included as a categorical variable in all four models.

Maxent model output can be highly sensitive to model settings (Merow et al., 2013). We, therefore, used the *ENMEval* package (Kass et al., 2022) to determine the optimal feature classes to include in the models, representing the possibility of relationship between the predictor variables (environmental variables) and the probability of species occurrence. Additionally, in order to balance goodness of fit with over-complexity, we determined the optimal regularization value, which adds a penalty term to the model's objective function, discouraging overly complex models that might fit the training data too closely and perform poorly on new data. We used a random k-fold cross-validation procedure with 10 replicates and selected model settings that minimized the Akaike Information Criterion corrected for small sample sizes (AICc) (Warren and Seifert, 2011). Overall model performance was tested using area under the receiver operating characteristic curve (AUC) and the True Skill Statistic (TSS) (Fielding and Bell, 1997; Allouche et al., 2006). Variable importance was estimated as the percentage loss in model performance, approximated through area under the receiving operating curve, when a given variable was randomly permuted (Phillips, 2017).

Each final model was projected onto environmental conditions for the future period 2081–2100 under four SSP–RCP scenarios. To disentangle the individual and combined effects of climate and land-use change, three types of environmental input were used. In the climate change only scenario, climate layers were updated to reflect projected values for 2081–2100, while land-use and land-cover (LULC) data were held constant at current conditions. In the LULC change only scenario, climate variables were kept at their current conditions, and LULC projections for 2081–2100 were incorporated, by averaging five-year projections across five intervals (2080, 2085, 2090, 2095, and 2100). Finally, in the combined change scenario, both climate and LULC were used to represent future conditions for 2081–2100.

All projections resulted in continuous logistic suitability values ranging from 0 (unsuitable) to 1 (highly suitable). To transform these continuous predictions into binary presence–absence maps, we applied the "maximum training sensitivity plus specificity" threshold method to each of the four models (Shabani et al., 2018), which identifies a cutoff that balances omission and commission

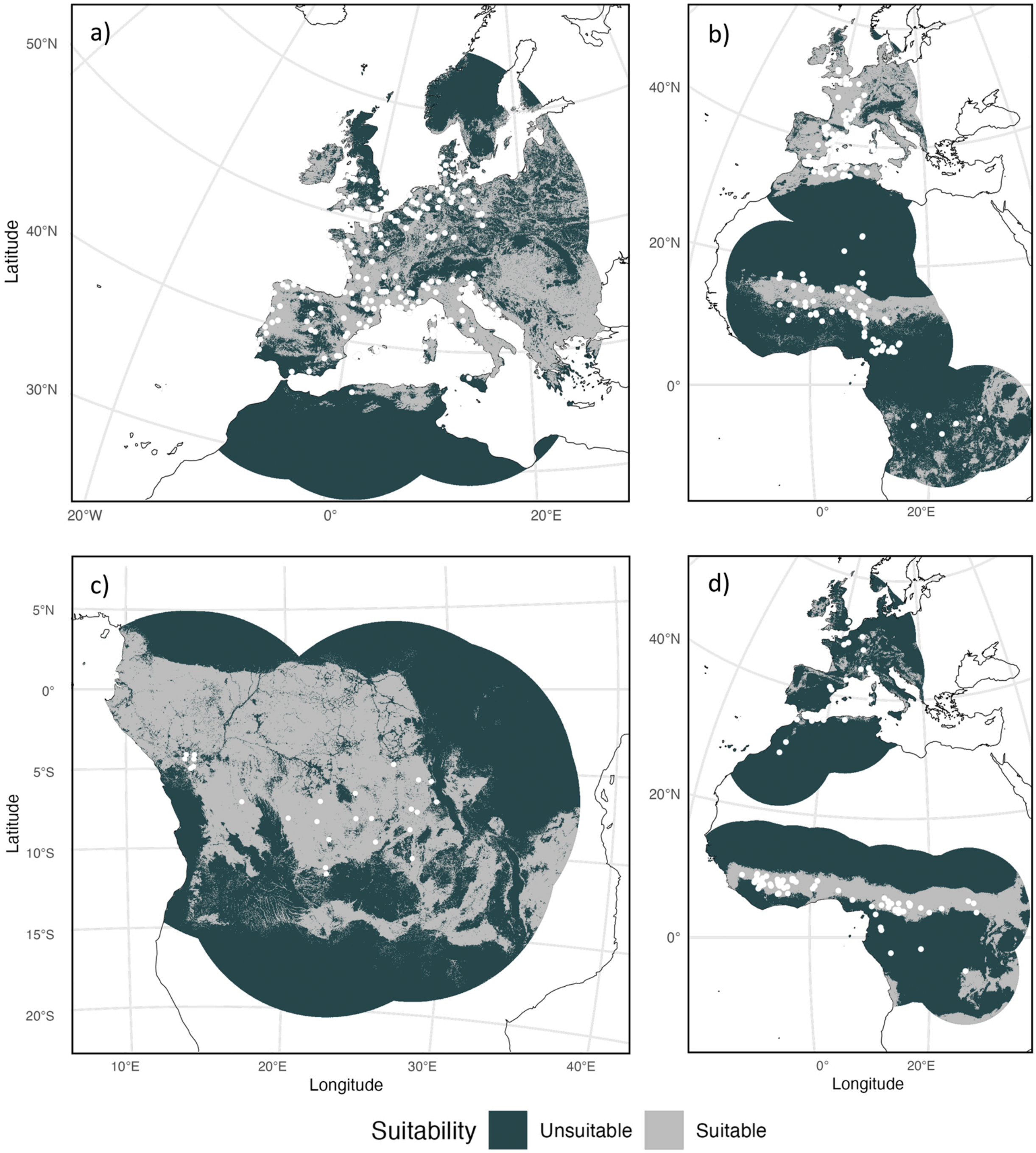

Fig. 1. Binarized maxent model output showing suitable habitat (light grey) for a) the breeding period b) autumn migration c) the wintering period and d) spring migration. White points show occurrence data included in each seasonal model.

errors. The resulting binary maps were used to calculate the total area of suitable habitat and assess spatial changes in response to each future scenario. Migration distance was estimated as the geodesic distance between the centroids of suitable breeding and wintering ranges, under both current and projected environmental conditions (Doswald et al., 2009, Zurell et al., 2018). In addition, we estimated barrier distance as the geodesic distance between suitable autumn and spring migration range centroids located north and south of 20°N, representing stopover zones on either side of the Sahara, the primary ecological barrier for avian migrants in the Palearctic—African migration system (Bairlein, 1988; Akesson et al., 2016; Lathouwers et al., 2022a).

3. Results

Out of 117 deployed GPS-loggers, we recaptured 29 loggers with usable data. The analysis of step distances between subsequent GPS fixes allowed us to define 2254 GPS fixes to be associated with local scale movements, 725 during the breeding period, 491 during autumn migration, 687 during the wintering period and 351 during spring migration. Filtered GBIF data resulted in an additional 169 occurrence records during the breeding period. After thinning the full occurrence dataset included a total of 416 records, 173 during the breeding period, 126 during autumn migration, 25 during the wintering period and 92 during spring migration (Fig. 1).

Final seasonal maxent models corresponding to the breeding season and spring migration were constructed using linear, quadratic, and hinge feature classes, with respective regularization multipliers of 2 and 3 (Table 1). Wintering and autumn migration models included the hinge feature class and regularization multipliers 2 and 3 (Table 1). Model performance was adequate across all four annual cycle stages, with AUC values exceeding 0.7 and TSS scores exceeding 0.5 (Table 1), indicating good discrimination ability. Precipitation consistently emerged as the most influential predictor of habitat suitability, with permutation importance values ranging from 58.24 % to 86.73 % across models (Table 1). Minimum temperature also contributed to model performance, with its importance varying by season, from as low as 0.53 % in the wintering period model to 24.98 % in the breeding period model (Table 1). LULC also played a notable role, with permutation importance values ranging from 5.56 % in the spring migration model to 17.72 % in the autumn migration model (Table 1). Response curves revealed distinct seasonal variation in the relationship between environmental predictors and habitat suitability across the annual cycle. For instance, cropland showed a positive association with suitability during the autumn migration period, while it was negatively associated during the breeding season (Fig. 2). Similarly, climatic responses varied between seasons. Optimal habitat suitability occurred at higher precipitation levels during wintering than in other periods, whereas lower minimum temperatures were associated with sharp declines in suitability during the breeding season (Fig. 2).

Projections of changes in suitable habitat from the current status to the period of 2081–2100 indicate distinct seasonal and scenario-dependent patterns (Fig. 3; Fig. S2-S5). For the breeding period, most scenarios suggest a net increase in suitable habitat relative to current conditions, particularly under scenario SSP5-RCP8.5 where under the combined effect of climate and LULC change suitable habitat is projected to increase with 71.6 % (Fig. 3). However, when considering land-use change alone, suitable habitat tends to somewhat decline under all SSP-RCP scenarios, by a maximum of 3.3 % in scenario SSP1-RCP2.6, suggesting that projected gains are primarily driven by climatic factors (Fig. 3).

In contrast, during autumn migration, projections under the combined effect of both climate and LULC change consistently indicate large decreases in suitable habitat across all SSP-RCP scenarios, with the strongest effect, a decrease of 48.8 %, observed under scenario SSP5-RCP8.5 (Fig. 3). Similarly to the breeding period, these losses are primarily driven by climate change, as projection showing the effect of LULC change indicate more modest losses up to 14.4 % under scenario SSP1-RCP2.6, or even a small increase by 2.1 % in suitable habitat under SSP3-RCP7.0 (Fig. 3). Interestingly, projected losses of suitable habitat under the combined effects of climate change and LULC change are not intermediate between the projections under each individual factor, but consistently somewhat greater than the effect of both climate change and LULC change separately (Fig. 3). This suggests a synergistic interaction in which climate and LULC change exacerbate each other's negative influence on habitat suitability.

For the wintering period, projected changes in suitable habitat are also substantial. All scenarios project increases, up to 35.3 % under scenario SSP5-RCP8.5, or maintenance of suitable habitat under climate change, while LULC change consistently leads to maintenance or slight reduction of suitable habitat, up to 9.5 % under scenario SSP3-RCP7.0 (Fig. 3). This results in relatively stable or slightly negative outcomes under the combination of both climate and LULC change (Fig. 3). Under scenario SSP3–RCP7.0, the slightly positive combined effect of climate and LULC change is intermediate between the effects of each factor alone (Fig. 3). In contrast, under

Table 1
Table showing tuning parameters (feature classes and regularization multipliers), evaluation metrics (AUC and TSS), threshold values and permutation importance of included variables for all four species distribution models corresponding the breeding period, autumn migration, wintering period and spring migration.

	Breeding	Autumn migration	Wintering	Spring migration
Feature classes	LQH	H	H	LQH
Regularisation multiplier	2	3	2	3
AUC	0.8130777	0.7244474	0.7826712	0.8434166
TSS	0.588278	0.5443927	0.5916785	0.6480893
Threshold	0.4173241	0.6544382	0.5939609	0.5963391
		Permutation importance (%)		
Minimum temperature	24.9762	15.0522	0.5328	10.2123
Precipitation	58.2412	67.2308	86.7249	84.2269
LULC	16.7825	17.7170	12.7424	5.5608

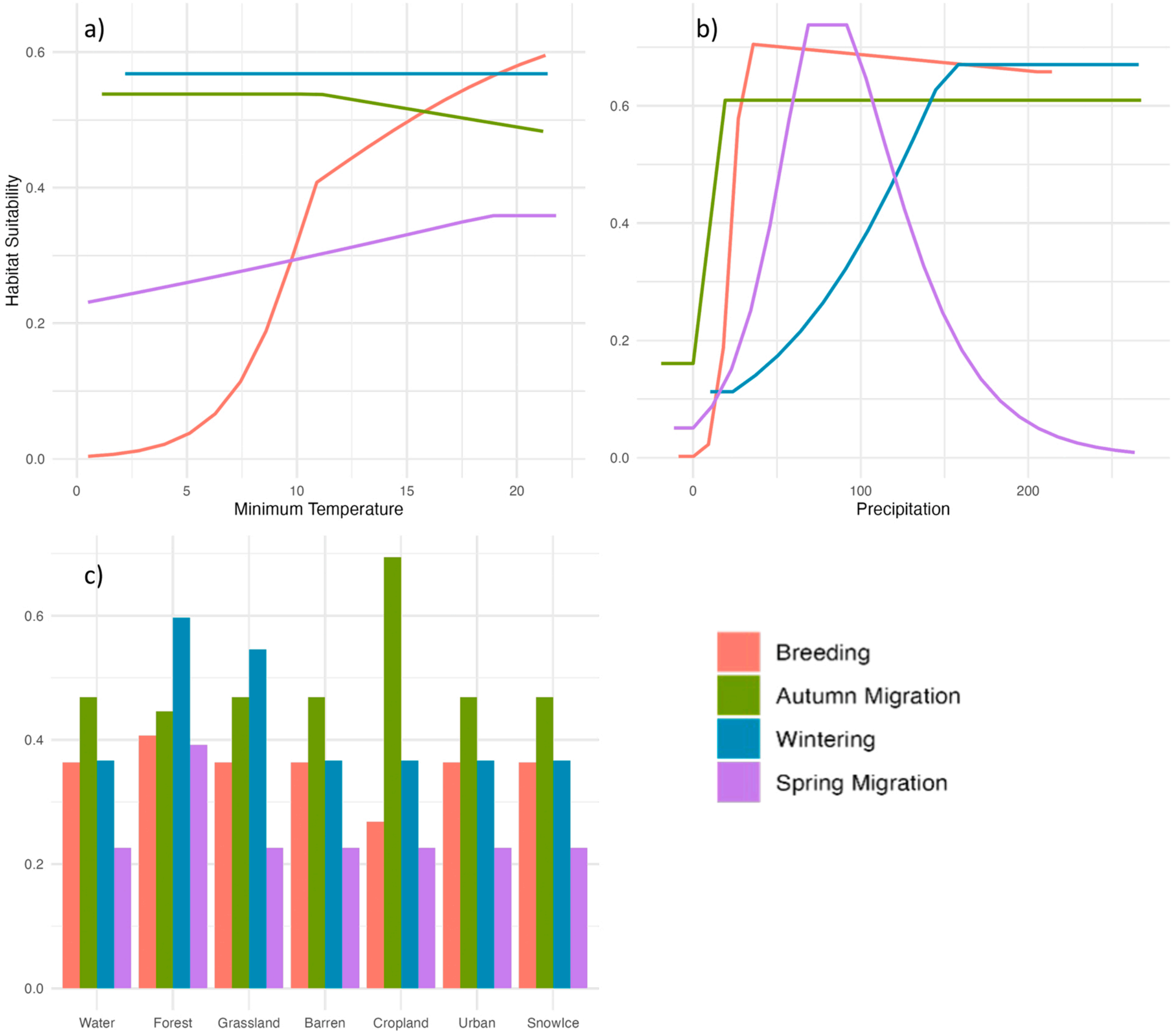

Fig. 2. Response curves for a) minimum temperature b) precipitation and c) LULC accross all four seasonal maxent across all four seasonal maxent models corresponding to the breeding period (red), autumn migration (green), wintering period (grey) and spring migration (blue).

SSP1–RCP2.6, the combined effect exceeds either individual contribution, suggesting that interactions between LULC and climate change can not only exacerbate negative impacts, as observed during autumn migration, but may also produce synergistic positive outcomes under certain conditions (Fig. 3).

During spring migration, combined changes under most scenarios yield slight decreases (9.7 % under scenario SSP1-RCP2.6) to moderate increases (24.9 % under scenario SSP3-RCP7.0) in suitable habitat projected for 2081–2100 (Fig. 3). Yet, LULC change alone tends to reduce suitable area, again pointing to the dominant role of climate in driving potential gains (Fig. 3). Overall, these results underscore the contrasting roles of climate change and LULC change across annual cycle stages and SSP–RCP scenarios. While climate change generally contributes to expansions in suitable habitat, LULC change more often exerts a limiting effect. Notably, during autumn migration, climate change also becomes a constraining factor, leading to substantial projected declines in suitable habitat under the combined influence of both drivers. Moreover, the most pronounced change, whether positive or negative, are typically associated with the higher-end SSP–RCP scenarios (e.g., SSP3–RCP7.0 and SSP5–RCP8.5), highlighting how more severe trajectories of socio-economic development and greenhouse gas emissions are linked to greater shifts in potential habitat distribution.

Comparison of suitable habitat under current conditions versus projections for the 2081–2100 period across four SSP–RCP scenarios and annual cycle stages reveals strong seasonal and spatial contrasts. Consistent with previous findings, the breeding season is projected to experience substantial gains in suitable habitat with minimal losses of currently suitable areas (Fig. 4). In contrast, autumn migration consistently shows marked losses of currently suitable habitat, accompanied by only marginal gains (Fig. 4).

Importantly, these spatially explicit results also highlight that apparent stability in total suitable area can obscure significant internal reorganization. For instance, projections for the wintering season under SSP3–RCP7.0 (15 % net increase; Fig. 3) and for spring

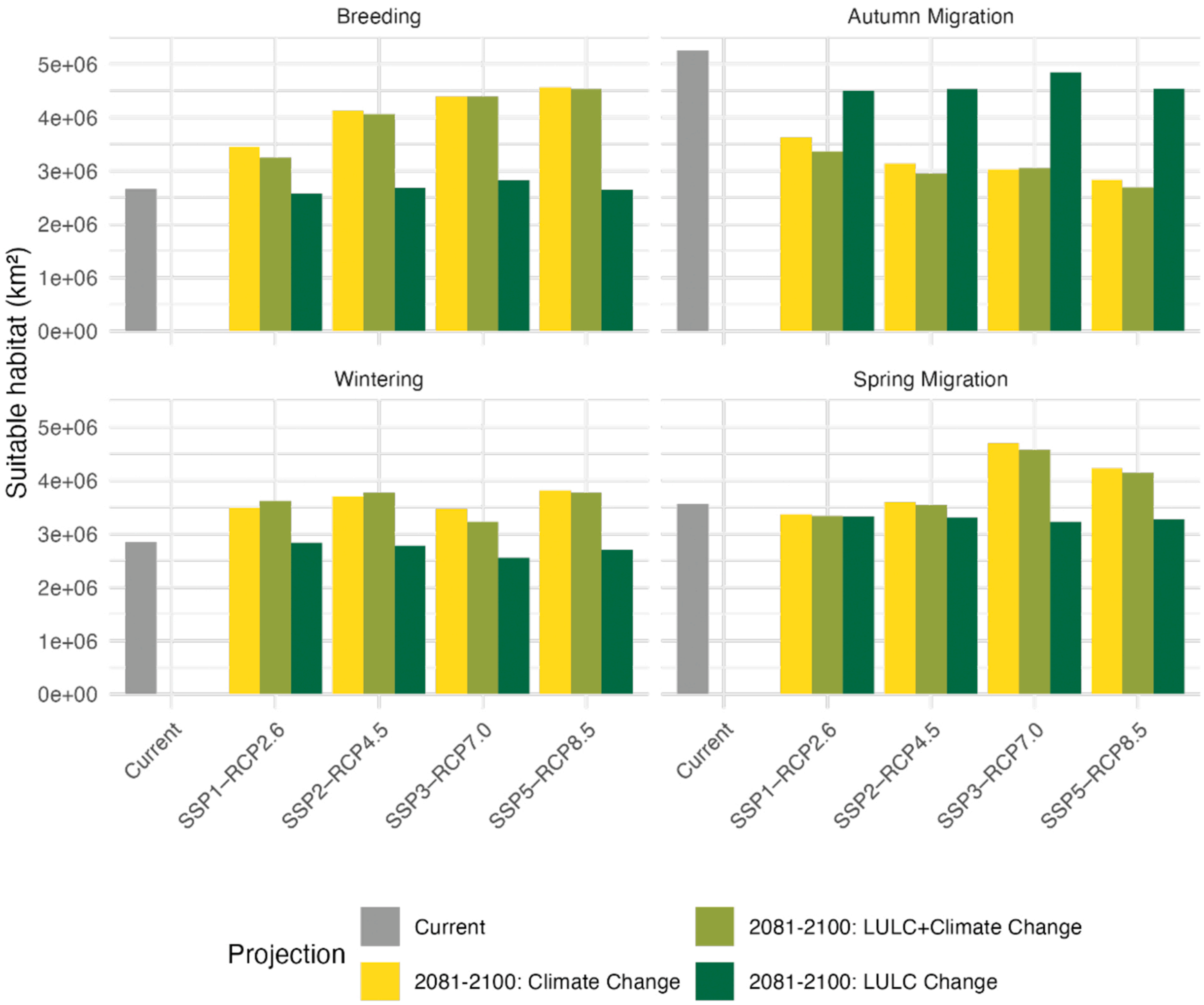

Fig. 3. Changes in amount of suitable habitat (km^2) from projections under current conditions (grey) to projections for the period 2081-2100 shown for each annual cycle stage based on the results of seperate seasonal maxent models. Projections for 2081-2100 are shown for four SSP-RCP scenarios and include projections where only climate corresponds to the projections for 2081-2100 while LULC remains constant under current conditions (yellow), both climate and LULC correspond to projections for 2081-2100 (light green) and only LULC corresponds to the projections for 2081-2100 while climate remains constant under current conditions (dark green).

migration under SSP5–RCP8.5 (13 % net increase; Fig. 3) reveal that large proportions of suitable habitat by 2081–2100 are newly gained (22 % and 28 %, respectively; Fig. 4), while simultaneously substantial areas are lost (10 % and 11 %, respectively; Fig. 4). Such habitat turnover is most pronounced under higher-emission scenarios (e.g., SSP3–RCP7.0 and SSP5–RCP8.5; Fig. 4), suggesting that intensifying anthropogenic pressures may drive not only overall changes in habitat availability, but also more extensive spatial redistribution and fragmentation of suitable habitat.

These changes in extent and spatial configuration of suitable habitat because of projected environmental change are expected to result in increased migration distances. Under current conditions, the estimated migration distance between the centroids of suitable breeding and wintering habitats is approximately 5986 km, while the distances between suitable stopover areas north and south of the Sahara are approximately 4607 km during autumn migration and 4822 km during spring migration. Projections for the 2081–2100 period indicate increases in migration distance across SSP–RCP scenarios. The largest increase of 343 km, or 5.7 % of the migration distance under current environmental conditions, is observed under SSP3–RCP7.0 when both climate and land-use change are accounted for, whereas scenarios including only land-use change project a slight decrease of up to 1.0 % (Fig. 5). Projected changes in barrier distance during autumn migration are more pronounced, with increases of up to 1851 km, or 40.2 % of the current barrier distance, under SSP3–RCP7.0, and consistently elevated values under climate change scenarios across all SSP–RCP scenarios (Fig. 5). In contrast, the effect of land-use change alone is smaller and less consistent across SSP-RCP scenarios, with changes ranging from a 4.2 % decrease to a 3.1 % increase in barrier distance (Fig. 5). Spring barrier distances appear more stable, with projected changes ranging from a 1.2 % decrease to a 2.8 % increase (Fig. 5). These findings highlight a substantial potential increase in the spatial separation of stopover and seasonal habitats, particularly during autumn migration when, under scenarios of high-emission and

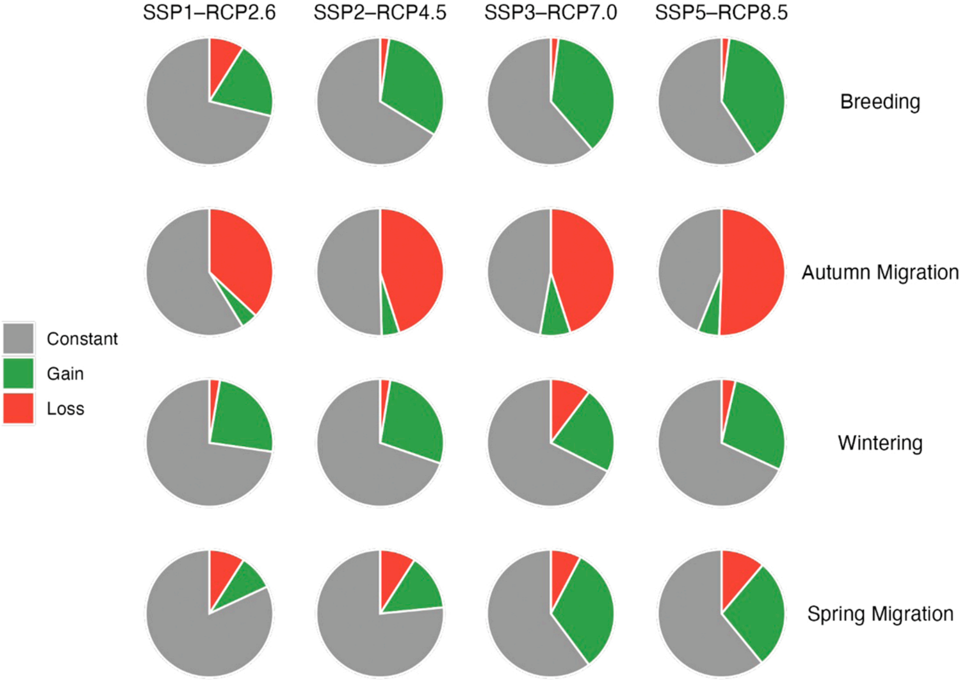

Fig. 4. Pie charts showing the fractions of suitable habitat classified as constant (grey), gained (green) and lost (red) between projections under current conditions and projections for 2081-2100 where climate and LULC change according to four SSP-RCP scenarios. Results are shown for each annual cycle stage, based on seasonal maxent models, including the breeding period, autumn migration, wintering period and spring migration.

intensive land-use trajectories, projected suitable habitat in the Sahel region is reduced (Fig. S2).

4. Discussion

We use high-accuracy GPS tracking data and open-source occurrence records in combination with climatic variables and LULC to inform spatiotemporally explicit species distribution models for an avian migrant, in order to project changes in suitable habitat under diverse socio-economic scenarios. Seasonal precipitation emerged as the most influential variable across all models, particularly during the wintering period and autumn migration. Minimum temperature also played an important role, especially during the breeding period. LULC, more specifically forest, grassland, cropland and urban land, additionally contributed substantially. These results highlight the importance of both climatic and land-cover drivers in shaping seasonal habitat suitability. Seasonal variation in responses to environmental variables revealed divergent relationships according to known variation in niche requirement of Nightjars during distinct annual cycle stages (Lathouwers et al., 2023).

The impact of LULC change on Nightjars' potential distribution was assessed under four representative shared socio-economic and concentration pathways until 2081–2100. The results showed that LULC change is predicted to significantly affect the distribution of suitable habitat. Depending on the annual cycle stage, a slight to moderate decrease in the predicted suitable area was observed under all SSP-RCP scenarios. In the Central African wintering areas of Nightjars within our study populations a large-scale conversion of open woodlands, habitat associated with known wintering sites (Evens et al., 2017b; Lathouwers et al., 2023), is projected across various SSP-RCP scenarios, with effects being most pronounced under SSP3-RCP7.0 (Chen et al., 2022), corresponding with the observed reduction in suitable habitat in our results (Fig. 3). Further declines of suitable habitat during the breeding period are likely driven by projected increases in cropland across Europe, particularly under scenarios emphasizing sustainable development and reduced CO_2 emissions, i.e. SSP1-RCP2.6 (Fig. 3). Although these scenarios aim to mitigate climate change, they are also associated with increased investment in the cultivation of bioenergetic crops, which previous studies have shown to associated with a projected negative impact global species richness (Hof et al., 2018). Our findings support these results, suggesting that agricultural expansion under such scenarios could substantially reduce suitable habitat for Nightjars.

Interestingly, however, our results also show a positive association between habitat suitability and cropland during the autumn migration period. Nightjars are known to forage in extensively managed agricultural landscapes during the breeding season (Evens et al., 2017a), and use of such habitats has been observed during the wintering period as well (personal observation). This suggests that extensive agriculture may play a significant role as stopover habitat during migration, warranting further investigation into its ecological importance for Nightjars during this critical annual cycle stage, as such habitats are experiencing significant losses globally due to both intensification and agricultural abandonment (Volpato et al., 2024). Important to note is that the thematic resolution of the land cover data used in our study does not allow us to distinguish intensively managed, low-quality agricultural habitats from more

Fig. 5. Changes in migration distance and barrier distance (autumn and spring) (km) from projections under current conditions to projections for the period 2081-2100 based on the results of seperate seasonal maxent models. Results for 2081-2100 are shown for four SSP-RCP scenarios and include projections where only climate corresponds to the projections for 2081-2100 while LULC remains constant under current conditions (yellow), both climate and LULC correspond to projections for 2081-2100 (light green) and only LULC corresponds to the projections for 2081-2100 while climate remains constant under current conditions (dark green).

ecologically valuable extensively managed areas rich in insect prey. Therefore, future studies should aim to incorporate more specific predictor variables and finer-scale habitat data to better understand the mechanisms driving habitat use during migration.

In contrast to LULC, climate change projections for 2081–2100 are predicted to increase the amount of suitable habitat during the breeding period, wintering period and spring migration period. The most pronounced increases in suitable habitat during the breeding period are associated with high-emission SSP–RCP scenarios, likely reflecting the influence of rising temperatures in temperate regions (IPCC, 2023). While having a negative impact on species diversity (Voskamp et al., 2022), such warming trends may enhance climatic suitability for certain species depending on their specific ecological traits (Stiels et al., 2021; Kufa et al., 2022; Zvidzai et al., 2024). As our results show a positive association between minimum temperature and habitat suitability during the breeding period (Fig. 2), projected temperature increases may improve climatic conditions in parts of the Nightjar’s temperate breeding range (Fig. S2). However, this interpretation warrants caution as our models are centred on the Western European population, and the overall net effect of climate change on the species’ breeding range cannot be assessed without considering potential losses elsewhere. Interestingly, the Iberian Peninsula appears to retain suitability even under severe climate change scenarios, despite ongoing population declines in southern Iberia (Keller et al., 2020), suggesting complex region-specific dynamics that merit further investigation.

Similar to the results for the breeding period, increased precipitation projected for the Nightjars' wintering grounds in central Africa may lead to a modest expansion of climatically suitable habitat, as indicated by our results (Fig. 2; Fig. 3). In contrast, during the autumn migration period, projected changes in temperature and precipitation in key stopover regions such as the Sahel are expected to significantly reduce the extent of suitable habitat (Fig. S3). These patterns are consistent with projections for other insectivorous migratory birds, including European Bee-eater *Merops apiaster* (Linnaeus, 1758), for which climate change is anticipated to exacerbate drought, lower vegetation productivity, and limit food availability in parts of the Sahel, thereby reducing climatic suitability. Meanwhile, central Africa is projected to become more favourable for overwintering bee-eaters (Abdul-Wahab et al., 2024).

The Sahel serves as vital stopover regions for Nightjars (Lathouwers et al., 2022a, 2023). Thus, despite localized improvements in wintering conditions, broader climatic changes along the migratory flyway may impose new seasonal constraints. These projected habitat losses are particularly alarming in light of the existing pressures from agricultural expansion and land degradation in the region (Maisharou et al., 2015; Knauer et al., 2017). This decrease in crucial stopover habitats for migrating Nightjars may be the weakest link that is most likely to drive major population effects in the migration phase. Although adaptive behaviours during active migration (Lathouwers et al., 2022a) or during stopovers (Lathouwers et al., 2023) may allow Nightjars to negate these effects to some extent, large scale losses of habitat in north Africa and the southern fringe of the Sahara will substantially increasing the length of inhospitable barriers to be crossed (Zurell et al., 2018) and reduced suitable habitat throughout the flyway, limiting refuelling opportunities (Davies et al., 2023).

A key insight from our spatially explicit analyses is that stability in total suitable habitat area can mask substantial turnover. Modest net changes in habitat area co-occur with large proportions of both gain and loss (Fig. 4; Fig. S2-S5). This redistribution could impact migratory efficiency and survival if birds are unable to locate or adapt to newly suitable areas. Whether migratory birds will be able to cope with such effects of global change is a topic of active debate. Current migrants have evolved an innately programmed migration route over thousands of years in order to take advantage of fluctuating available resources at specific points *en route* (Thorup et al., 2017; Pedersen et al., 2020). While some obligate avian migrants, including Nightjars, are known to prefer locally fragmented landscapes in stopover zones as a time minimizing strategy serving to quickly encounter their preferred foraging habitat (Cohen et al., 2014; Lathouwers et al., 2023), a drastic shift in the distribution of resources across the flyway over just a few decades raises the question whether migratory birds can rapidly respond to major changes in their migratory programs. Some studies have indeed shown how small numbers of species such as Eurasian blackcap *Sylvia atricapilla* (Linnaeus, 1758) and Richard's pipit *Anthus richardi* (Vieillot, 1818) are able to change migration behaviour in only a handful of generations and adopt novel migration routes as a potential response to human induced global change (Berthold et al., 1992; Dufour et al., 2021; Van Doren et al., 2021), although such changes are likely extremely species and context specific. For example, factors such as cultural transmission can play an important role in determining the routes of long-distance migratory birds and may increase their ability to adapt to land use change (Byholm et al., 2022; Madsen et al., 2023).

However, our results show that opposing shifts in seasonal ranges and changes in stopover site distribution will likely increase overall migration distances and especially distances of ecological barrier crossings. Therefore, if migrants are able to adjust their routes in response to the spatial redistribution of suitable habitats, such adaptations may lead to greater energy expenditure (Lindstrom and Alerstam, 1992; Doswald et al., 2009; Zurell et al., 2018), and as a result, increase stopover durations for refuelling purposes (Schmaljohann et al., 2017; Lindström et al., 2019). These increased time costs may not be easy to accommodate in the annual cycle of many migrants given the trade-offs between time spent on migration and e.g. breeding (Newton, 2008; Zurell et al., 2018; Lathouwers et al., 2022b). In order for a migratory species to cope with shifts in distribution it is therefore crucial to conserve and protect not only the present-day habitats but also the areas that may become suitable habitats in the future. Of particular importance is conserving areas that will act as future corridors and refugia, to allow organisms to disperse and survive under altered environmental conditions (Stralberg et al., 2020).

Our spatiotemporally explicit SDM approach demonstrates the value of disaggregating the life cycle of migratory species to identify stage-specific environmental sensitivities. This supports growing calls to integrate spatiotemporal variation into SDMs to better reflect the ecological complexity of migratory systems (Williams et al., 2017; Goodman et al., 2022). However, significant limitations remain. Habitat requirements and selection processes often vary at fine spatial and temporal scales, making it difficult to fully capture these dynamics within an SDM framework. While models that distinguish between breeding, migration, and non-breeding periods improve ecological realism, they likely still fall short of encompassing the full complexity of habitat selection, food availability, phenology, intra-specific variation and their population-level consequences in long-distance migrants (Dobson et al., 2023; Winter et al., 2024). For example, our use of seasonal predictors is consistent with Hutchinson's niche concept, which holds that organisms respond only to conditions they directly experience (Hutchinson, 1991). Therefore, species distribution models should rely on environmental variables relevant to the period when a species is actually present (Soberón and Nakamura, 2009; Godsoe, 2010). Moreover, our reliance on direct climatic and land-use variables aligns with the emphasis on the importance of proximal factors in ecological niche modelling (Austin, 2002). However, other research demonstrates the potential value of including distal environmental variables. For example, Engler et al. (2014) found that the breeding distribution of Citril Finch *Carduelis citronella* (Pallas, 1764) was more accurately predicted when winter climatic extremes, acting as distal predictors, were included in the SDM. This suggests that factors outside the immediate breeding season may constrain distributions in ways not captured by proximal variables alone. However, adding such predictors also risks model overfitting and challenges strict interpretations of realized niches. Our findings raise the need for future work to carefully weigh the ecological interpretability of seasonal niche models against the risks of incorporating temporally or spatially distal variables in migratory systems. Finally, practical limitations also affect the generalizability of our results. For example, our projections outside of the breeding season are based solely on data from male Nightjars, potentially overlooking female-specific habitat preferences and migratory strategies. Preliminary findings suggest females may differ in migration timing (own unpublished data), and evidence from other species indicates sex-based differences in stopover use and movement behaviour (Bennett et al., 2019).

Another critical limitation is the interpretative scope of SDMs. These models estimate habitat suitability based on climatic and environmental variables correlated with observed species occurrences but do not necessarily reflect optimal conditions for survival or reproduction. Consequently, SDM outputs should not be interpreted as definitive measures of ecological viability. To improve conservation planning, these models must be paired with demographic data, including population growth rates, to inform spatial prioritization efforts (Araújo et al., 2019; Titeux et al., 2019). Moreover, while our study examined the individual effects of LULC and climate change, it did not assess their dynamic interactions. Our findings nonetheless suggest that combined effects may exceed those of either factor alone (Fig. 3). Negative synergies, where LULC impedes species' ability to track shifting climatic niches, are well-documented and can lead to population declines and reduced species richness (Newbold et al., 2019; Haddou et al., 2022). Yet, interactions are context-dependent. For example, species adapted to drier conditions may benefit from certain LULC changes, such as agricultural conversion (Frishkoff et al., 2016), underscoring the need to account for species-specific traits and ecological requirements.

Future research should build on our findings to assess the combined direct and indirect impacts of climatic variables and land-use/land-cover changes, while incorporating variability across spatial and temporal scales and intra- and inter-individual differences (Winter et al., 2024). Emerging tools in remote sensing, biologging and analytical frameworks offer new opportunities to assess how global change reshapes dynamic migratory systems (Dobson et al., 2023). Such insights will enhance our ability to protect both current and projected future suitable habitats, particularly those that enable seasonal transitions, which will be essential for the conservation of long-distance migratory species.

CRediT authorship contribution statement

Michiel Lathouwers: Conceptualization, Methodology, Formal Analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Visualization. **Natalie Beenaerts:** Conceptualization, Funding Acquisition, Writing – Review & Editing, Supervision, **Ruben Evens:** Conceptualization, Resources, Writing – Review & Editing, Supervision, Funding Acquisition, **Tom Artois:** Conceptualization, Funding Acquisition, Writing – Review & Editing, Supervision, **Greg Conway:** Resources, Writing – Review & Editing, **Ian Henderson:** Resources, **Mike Shewring:** Resources, **Tony Cross:** Resources, **Eddy Ulenaers:** Resources, **Nicolas Dendoncker:** Conceptualization, Funding Acquisition, Writing – Review & Editing, Supervision.

Ethics statement

The Belgian research protocol received ethical approval from the Ethics Committee on Animal Experiments of the University of Hasselt (license number: 202041), and were authorized by the Agency for Nature and Forest (license numbers: ANB/BL-FF/V18–00086 and ANB/ BL-FF/19–00087-VB). In the UK, the research protocol was approved by the Special Methods Technical Panel and licensed by the British Trust for Ornithology. All protocols were carried out in accordance with the relevant guidelines and regulations.

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Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03777.

Data availability

Data available from the OSF Digital Repository: https://osf.io/7kg3t/

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