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RESEARCH ARTICLE

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Spatio-temporal integrated Bayesian species distribution models reveal lack of broad relationships between traits and range shifts

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Abstract

Aim: Climate change and habitat loss or degradation are some of the greatest threats that species face today, often resulting in range shifts. Species traits have been discussed as important predictors of range shifts, with the identification of general trends being of great interest to conservation efforts. However, studies reviewing relationships between traits and range shifts have questioned the existence of such generalized trends, due to mixed results and weak correlations, as well as analytical shortcomings. The aim of this study was to test this relationship empirically, using analytical approaches that account for common sources of bias when assessing range trends.

Location: Tanzania, East Africa.

Time period: 1980–1999 and 2000–2020.

Major taxa studied: 57 savannah specialist birds found in Tanzania, belonging to 26 families and 11 orders.

Methods: We applied recently developed integrated spatio-temporal species distribution models in R-INLA, combining citizen science and bird Atlas data to estimate ranges of species, quantify range shifts, and test the predictive power of traditional trait groups, as well as exposure-related and sensitivity traits. We based our study on 40 years of bird observations in East African savannahs, a biome that has experienced increasing climatic and non-climatic pressures over recent decades. We correlated patterns of change with species traits using linear regression models.

Results: We find indications of relationships identified by previous research, but low average explanatory power of traits from an ecological perspective, confirming the lack of meaningful general associations. However, our analysis finds compelling species-specific results.

Main conclusions: We highlight the importance of individual assessments while demonstrating the usefulness of our analytical approach for analyses of range shifts.

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KEYWORDS

climate change, data integration models, eBird, range shifts, savannahs, species distribution models, species traits

1 | INTRODUCTION

Climate change is posing an increasing threat to the survival of many species and is expected to result in the loss of species at the local or global level (Panetta et al., 2018; Urban, 2015; Wiens, 2016). Non-climatic factors, such as anthropogenic land use change, are further threatening species through degradation of habitat, changes in land cover, and fragmentation (Haddad et al., 2015; Horv  th et al., 2019; van Strien et al., 2019). Populations of species can persist despite these changes if they show plastic or evolutionary change (Hoffmann & Sgro, 2011), or simply move to other locations. While micro-evolutionary adaptation to climate change can occur over relatively short periods of time, recent examples are mainly of species with short life cycles, such as fruit flies (Balany   et al., 2006) or field mustard (Franks et al., 2007). There is increasing evidence for micro-evolutionary adaptation in taxa with longer life cycles, such as birds (Karell et al., 2011), but the effectiveness of this mitigation is unclear. One of the best-documented responses is range shifts where species distributions change to track suitable environments. There is mounting evidence for range shifts across taxa, at a global scale, accelerated by anthropogenic climate change (Chen et al., 2011; Colwell et al., 2008; Davis & Shaw, 2001; Parmesan & Yohe, 2003; P  rtner et al., 2022). Under future climate change scenarios, these range shifts are projected to continue (Thuiller, 2004; Williams & Blois, 2018). Where species are unable to emigrate the outcome can be drastic, with the first climate-driven mammalian extinction recently documented (Gynther et al., 2016). Conversely, some species that redistribute effectively may benefit from environmental changes (Tayleur et al., 2016), establishing populations in new areas. Considerable unexplained variation in species range shifts as a consequence of climate change has been recorded, with authors proposing non-climatic variables such as species interactions or traits as possible explanations (McCain & Garfinkel, 2021; Williams & Blois, 2018). Accurately quantifying range shifts and identifying the underlying drivers are crucial steps towards gaining a better understanding of the causes of such variation, ultimately enabling us to identify the most vulnerable species and inform conservation efforts (Foden et al., 2019).

The vulnerability of species to external pressures affects their ability to adapt to environmental change. Such vulnerability is characterized by the intersection of exposure and sensitivity to change, and adaptive capacity (Dawson et al., 2011; Foden et al., 2019). Exposure is typically defined as the amount of historic or future change in an environmental variable experienced across a species' observed range (Foden et al., 2019). At the species level, it can be quantified relative to a species trait (e.g. habitat suitability: Alabia et al., 2018; Gardali et al., 2012, drought threshold and climate suitability: Aubin et al., 2018). Sensitivity describes the degree to which

species might be impacted by environmental change and is considered intrinsic to the species (Foden et al., 2019). It is commonly estimated through a species' physiological traits (Foden et al., 2013; Gardali et al., 2012). Adaptive capacity is generally defined as the ability of a species to cope with the negative impacts of environmental change (Bateman et al., 2020; Thurman et al., 2020). Such adaptation includes dispersal ability, and a species exhibiting high adaptive capacity may colonize newly suitable habitat more effectively when experiencing environmental pressures than a species with low adaptive capacity. Range shifts are generally expected to occur where sensitivity and exposure overlap (Purvis et al., 2005). One species may be able to persist in areas where it is heavily exposed to a certain change because it is not particularly sensitive to it, while another species may be highly sensitive to the pressure, but lacks the ability to disperse to a different location, leading to a negative range shift, or range contraction. In cases where exposure and sensitivity are both high and dispersal ability is also high, the species may shift its range into new areas, where they are suitable. Species vulnerabilities and resulting range shifts are therefore closely tied to species traits, that is, the physiology, behaviour, and life history (Foden et al., 2013; Pearson et al., 2014; Trivi  o et al., 2013). As traits are, by definition, the only way by which species interact with the environment, it is ultimately necessary that they explain vulnerability to climate change, and many vulnerability assessments are generated partially or wholly from species trait information (Foden et al., 2019).

There has long been an interest in identifying coherent groupings of traits associated with species range shifts across a wider taxonomic range (Lavergne et al., 2004; Van Der Veken et al., 2007). Such a generalization would be a powerful tool for predicting the effects of future environmental change across many species, while also helping to identify the most vulnerable species based on their known traits (Aubin et al., 2018; Garcia et al., 2014; Pearson et al., 2014). In an effort to establish standardized and comparable trait groupings, Estrada et al. (2016) developed a traits framework, identifying broad categories of traits that might explain observed range shifts. Among these categories, they highlighted ecological generalization and movement ability as being the most important predictors (Estrada et al., 2016). Ecological generalization refers to the ability of a species to use a variety of resources in the environment (Estrada et al., 2016), which can be expressed by a broad behavioural lifestyle (e.g. locomotory niche while foraging), wide trophic niche, or ability to tolerate a wide range of climatic variables or habitat structures. Species that are strongly represented in this trait group would be expected to show lower sensitivity to environmental change, as well as a higher adaptive capacity, leading to colonization of new habitats and therefore larger range shifts (Angert et al., 2011; Buckley & Kingsolver, 2012; Estrada et al., 2016). Movement ability refers to the ability to travel beyond the natal

region (Estrada et al., 2016). In birds, higher movement ability may be associated with larger body size and longer wings, or high migratory ability, providing physiological prerequisites for covering longer distances, and thereby enabling larger range shifts (Angert et al., 2011; Buckley & Kingsolver, 2012). Conversely, high migratory ability may lead to higher fidelity to established migration sites and therefore fewer range expansions (Bensch, 1999), while a larger body size can be associated with reduced reproductive potential (Saether, 1988), potentially hindering establishment in new areas and therefore range expansions (MacLean & Beissinger, 2017). The increasing availability of trait databases spanning whole taxonomic groups, such as AVONET for birds (Tobias et al., 2022), has facilitated testing the relationships between such trait categories and range shifts empirically. Meta-analyses of studies linking traditional traits with range shifts found considerable conflicting evidence for trait effects between taxonomic groups, for most traits categories considered, and weak predictive power overall (Beissinger & Riddell, 2021; MacLean & Beissinger, 2017). Moreover, validation of climate risk assessment methods shows trait-based methods to have poor predictive ability (Wheatley et al., 2017). This led to the conclusion that traits might be surprisingly poor predictors of range shifts and not suitable contributions to climate change vulnerability assessments, unless analytical shortcomings were tested and addressed (Beissinger & Riddell, 2021).

To further investigate the predictive power of traits, Beissinger and Riddell (2021) called for better inclusion of exposure-related traits in analyses of range shifts. Traditional trait groups considered predictors of range shifts, such as ecological generalization and movement ability, tend to correspond to the adaptive capacity or sensitivity of species, and might therefore not be sufficiently explaining trends. Exposure-related traits should in theory capture the positive relationship between species exposure and range shifts (Beissinger & Riddell, 2021). Proposed exposure-related traits include morphologies that influence heat transfer, such as the plumage colouration of birds (Beissinger & Riddell, 2021). In addition, a more direct measure of sensitivity to different environmental pressures may be an informative trait group. Species sensitivity definitions have been criticized as being ambiguous (Fortini & Dye, 2017). Correlative species distribution models (SDMs) may present a solution to this problem. Since they quantify the probability of presence under different environmental conditions, they reflect a species' relationship with the environment more directly, and sensitivity may simply be quantified as the degree of influence of environmental variables on a species' occurrence.

Studies have discussed issues in quantifying species ranges as a potential weakness of analyses of range shifts (Beissinger & Riddell, 2021; Şekercioğlu et al., 2008; Yalcin & Leroux, 2017). Indeed, empirical studies are difficult due to the nature of observation data used to quantify range shifts. Common issues include lack of available data, non-standard survey protocols and observer bias, autocorrelation issues due to the spatial nature of the data, and imperfect detection (Araújo et al., 2019; Beale et al., 2010; Beissinger & Riddell, 2021; Faisal et al., 2010). The increasing availability of

citizen science observations has helped fill data gaps (Feldman et al., 2021), but these data are often collected in different formats and come with a variety of sampling biases to account for (Isaac & Pocock, 2015; Zhang, 2020), making it challenging to include them in analyses. In recent years, SDMs have gained popularity, due to their ability to overcome many of the issues in estimating species ranges (Franklin, 2023; Kéry et al., 2013). The extension to spatio-temporal SDMs has shown promising results for estimating range shifts, representing the probability of transitions between time periods, taking into account spatial and temporal changes in sampling effort (Beale et al., 2013; Bled et al., 2013; Grattarola et al., 2023). The recent development of the Integrated Nested Laplace Approximation (INLA) method and its associated R-INLA package (Bakka et al., 2018; Lindgren & Rue, 2015) has made it possible to develop and run complex Bayesian SDMs with drastically reduced computation times, but similar accuracy, compared to other methods (Blangiardo et al., 2013), while accounting for common issues like spatial clumping and sparse data (Redding et al., 2017). R-INLA is continuously being developed, with the addition of the Stochastic Partial Differential Equation (SPDE) allowing efficient modelling of spatial autocorrelation (Lindgren et al., 2011), further enabling robust assessment of range shifts. The recent development of an INLA framework for data integration allows combining different data sources of species occurrence, potentially improving predictions for species with poor data availability (Grattarola et al., 2023; Isaac et al., 2020; Morera-Pujol et al., 2023; Sadykova et al., 2017).

At the core of these SDMs is the estimation of the species' niche shape. These models correlate observed occurrences of species with environmental factors, determining conditions favouring or inhibiting their presence. However, species distributions may be influenced more by dispersal constraints, like geographical barriers, than physiological limits. This leads SDMs to often reflect the realized niche rather than the fundamental niche (Franklin, 2023). For more accurate predictions under future climate scenarios, SDMs strive to approximate the fundamental niche (Booth, 2017; Peterson, 2001). To enhance this estimation, efforts include expanding SDMs beyond single regions or time frames, incorporating broader environmental conditions through methods like adding paleontological data (Jones et al., 2019) or observations of species in new habitats (Beaumont et al., 2009; Gallien et al., 2012). The availability of global climate data products and observation data reaching back decades provides an additional avenue: SDMs that include a temporal structure, that is, model species distributions within multiple time slices, can help move closer to characterizing the fundamental niche, relating species observations to changing environments over time, and hence a wider range of environmental conditions (Myers et al., 2015).

The aim of this study was to apply recently developed integrated spatio-temporal SDMs in R-INLA to estimate ranges of species, quantify range shifts, and test the predictive power of traditional trait groups, as well as sensitivity traits and an exposure-related trait. In terms of range shifts, we focused on changes in range size, a key dimension of distribution change (Yalcin & Leroux, 2017). We based our study on 40 years of bird observations in East

African savannahs. Increasing anthropogenic pressure in the form of inappropriate grazing regimes has led to accelerated conversion to bare ground in the region (Hill & Guerschman, 2020), resulting in a drastic change in habitat structure. Additionally, rainfall has become more intense on individual days (Dunning et al., 2018; Ongoma et al., 2018; Shongwe et al., 2011), while the number of dry days and frequency and duration of droughts has increased (Gebrechorkos et al., 2019a; Gebremeskel Haile et al., 2019; Nicholson, 2017; Vizey & Cook, 2012). Under current climate change scenarios, these trends are predicted to become more extreme (Finney et al., 2020; Li et al., 2021; Ogega et al., 2020). Savannah birds are known to be sensitive to these changes (e.g. Beale et al., 2013; Dean & Milton, 2001). Previous studies have identified bare ground as one of the key predictors of savannah bird ranges since reproductive behaviour as well as foraging strategies are commonly tied to the grass structure (Fisher & Davis, 2010; Schaub et al., 2010). Rainfall has been shown to directly influence savannah bird populations, due to its ties to food availability and grassland productivity (Dean, 1997; Dean & Milton, 2001; Lloyd, 1999). Due to a long-running bird observation program, the Tanzania Bird Atlas, observations are available for four decades, providing enough time to observe meaningful range shifts, as well as pronounced environmental changes. Based on Tanzania Bird Atlas data, Beale et al. (2013) provided empirical evidence that Tanzanian savannah birds have shifted their ranges over the last four decades, due to a combination of climate and habitat change, making them an ideal study group. Here, we tested the following hypotheses: (1) range shifts are positively associated with ecological generalization; (2) range shifts are positively correlated with movement ability; (3) range shifts are positively correlated with exposure-related traits; and (4) range shifts are positively correlated with sensitivity traits.

2 | METHODS

We estimated range shifts using spatio-temporal models in the R-INLA package that integrated citizen science and bird Atlas data, and accounted for sampling effort and autocorrelation. We derived species-specific occurrence–environment relationships, informed by the observed temporal change of distributions. We correlated traits, derived from trait databases and model outputs, with observed range shifts, using robust regression models. Figure 1 provides an overview of the main analytical steps included in the data analysis. A full description of the spatio-temporal integrated model is provided in the supplementary information file of this document.

2.1 | Bird data

We obtained bird observation data from the Tanzania Bird Atlas, as well as citizen science data from the Cornell Laboratory of

Ornithology citizen science database eBird (Sullivan et al., 2009). The Atlas dataset contains over 1 million bird observations, collected by volunteer and professional ornithologists since the 1960s. It consists of systematically gathered records, summarized into quarter-degree squares (approximately 50 × 50 km at the equator). Due to the systematic nature of sampling, the Atlas dataset provides broad geographic coverage of Tanzania (Beale et al., 2013). Observer effort and spatial and temporal coverage are variable but contained in the metadata. eBird is a steadily growing resource for citizen science bird observations, increasingly used in scientific studies. Data were retrieved in May 2021 for Tanzania and filtered following best practices (Strimas-Mackey et al., 2023). This included filtering the eBird records to retain only complete checklists, defined as containing all species seen on a given outing, as well as only those records that were reviewed and approved by a volunteer reviewer. We included only those records that had associated effort and only included observations that spanned less than 15 km, lasted between 5 and 360 min, and involved 30 observers or fewer, due to declining detection rates in larger groups (Strimas-Mackey et al., 2023). Because of the unstructured nature of eBird records, spatial coverage of Tanzania is considerably reduced compared to the Atlas data, and observations are biased spatially, for example, towards roads (Zhang, 2020). To account for spatial variation, we only included records that contained associated GPS locations. Both Atlas and eBird records were filtered to those records that fall inside the Tanzania country boundary, using the 'gIntersection' function in the R package 'rgeos' (Bivand et al., 2017). We chose to focus on savannah specialists, since they are, in this region, the most likely group to show detectable responses to climate change (for a discussion, see Beale et al., 2013), while also being well represented in both Atlas and eBird data. We based our choice of species on a published list of 137 Tanzanian savannah specialist birds (Beale et al., 2013). Following the initial filtering steps described above, we retained 91 species that were represented in both the Tanzania Bird Atlas and eBird datasets, as candidates for the SDMs.

2.2 | Environmental covariates

Several environmental covariates were included in the models, accessed and processed through Google Earth Engine (Gorelick et al., 2017). To reflect climatic variables, we chose factors that are known to affect grassland bird demographics. These included variables related to rainfall (annual rainfall [Sicacha-Parada et al., 2021], median annual dry spell duration as the number of continuous days with less than 1 mm of rainfall [Brawn et al., 2016]), and annual maximum temperature. We derived rainfall data from the CHIRPS version 2 dataset (Funk et al., 2015) and calculated the dryspell duration using the Google Earth Engine cloud computing platform (Gorelick et al., 2017). We accessed temperature data from the 'Climatologies at high resolution for the earth's land surface areas' (CHELSA) version 2.1 data product (Karger et al., 2017). To reflect habitat alteration, we

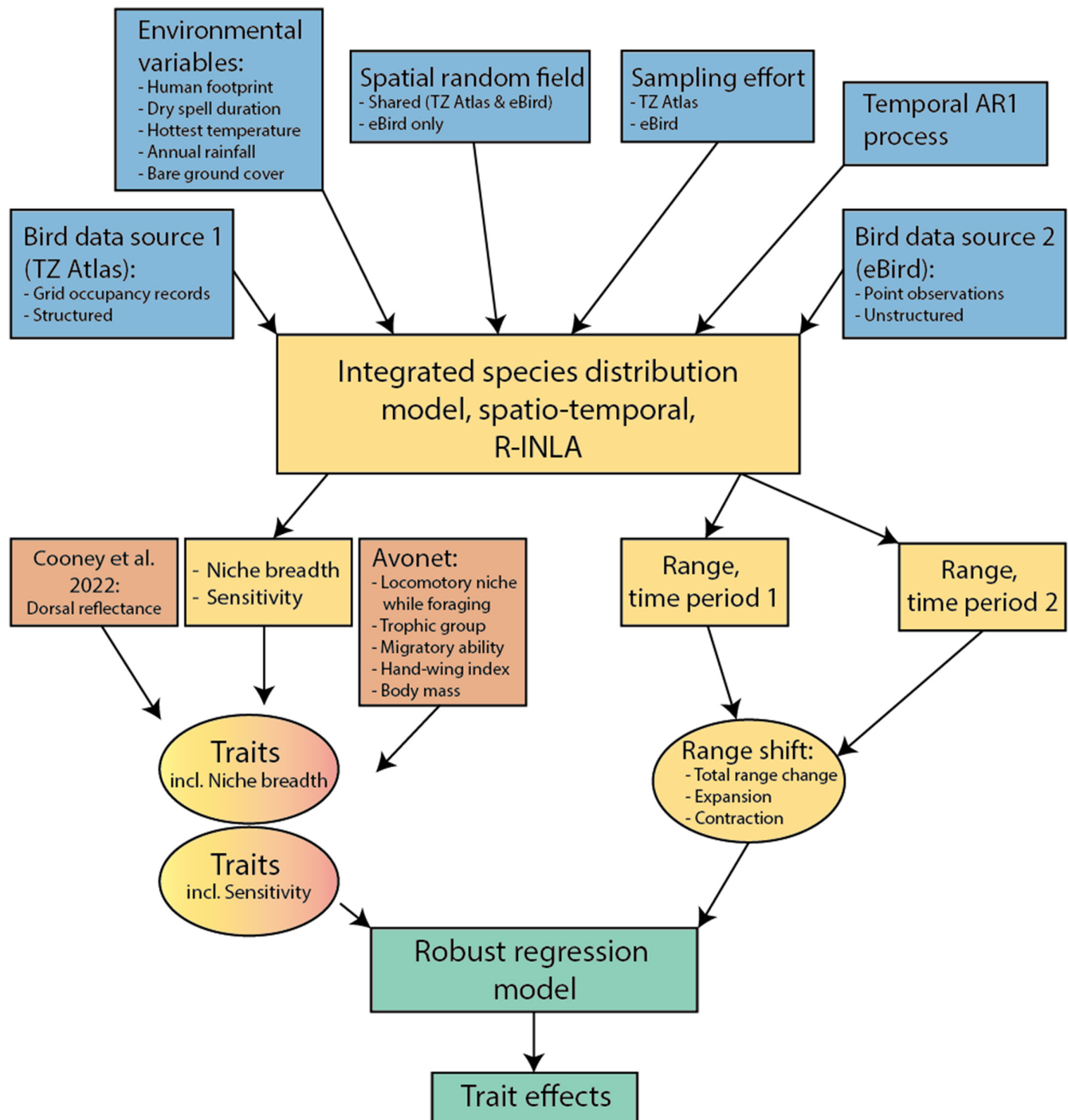


FIGURE 1 Overview of the main analytical steps conducted in the analysis. R-INLA: R package for implementing the integrated nested Laplace approximation. TZ Atlas: Tanzania Bird Atlas. Colour schemes correspond to methodological groups. Blue: Species distribution model components and inputs. Yellow: Species distribution model and outputs. Orange: Traits derived from literature. Green: Trait-range shift analysis and output.

included a measure of bare ground cover, derived from Landsat images using a machine learning algorithm (Wiethase et al., 2023). As a measure of anthropogenic pressure, we included a human footprint layer, which quantifies the amount of anthropogenic alteration of habitats (Venter et al., 2016). These environmental variables also reflected the recent environmental change experienced in the region, which include changes to dry spell duration and rainfall (Liebmann

et al., 2017; Lyon & DeWitt, 2012), increasing bare ground (Wiethase et al., 2023), increasing maximum temperatures (Daron, 2014), and growing populations leading to increasing agriculture conversion and urbanization (Bullock et al., 2021). All covariates were re-projected to the lowest resolution layer available, resulting in a pixel resolution of approximately 5 km. For a detailed overview of the covariates and data sources, see Supplementary Table S1.

2.3 | Estimating species ranges

We estimated ranges at approximately 28 km resolution using separate integrated distribution models for each species. This coarser resolution allowed us to run the distribution models at greater computational efficiency while closely matching the resolution used in similar studies (Adde et al., 2021; Morera-Pujol et al., 2023). We followed the integrated SDM approach outlined in Isaac et al. (2020), which allowed us to integrate the eBird and Atlas data in a single model, despite their differences in sampling structure (Isaac et al., 2020). In short, model-based data integration retains the structure of each dataset, while also accounting for weaknesses, such as sampling bias. This is achieved by specifying separate observation models for each dataset. As part of the data integration process, environmental covariate layers corresponding to observation data are sampled at point locations. We retained the 5 km resolution of covariates during this process rather than aggregating to a coarser resolution, to sample the corresponding covariate layers with greater precision.

The model was implemented in a Bayesian framework in the 'INLA' package version 23.04.24 (Bakka et al., 2018; Lindgren & Rue, 2015) using R version 4.2.3 (R Core Team, 2021). INLA is an alternative to Markov chain Monte Carlo methods (MCMC) for approximate Bayesian inference, with similar accuracy but higher computational speed (De Smedt et al., 2015), at the cost of limited flexibility, as it is restricted to latent Gaussian models. We modelled the true species distribution as a Log-Gaussian Cox Process (Møller et al., 1998) with an intensity function that defined the expected intensity at a given location, given the environmental covariates and a Gaussian random field. The Gaussian random field aimed to account for spatial autocorrelation and unexplained effects, and was estimated using the SPDE for computational efficiency (Lindgren et al., 2011). For each species, we included a shared random field for both data sources and a random field for eBird data alone, which accounted for unexplained variation in sampling effort unique to the eBird data (e.g. increased sampling along road networks). We modelled the intensity using a binomial model with a complementary log-log (cloglog) link function (see Adde et al., 2021). We included separate effort variables for each bird dataset. For eBird data, this was the checklist duration, automatically recorded by the eBird application in minutes. For Atlas data, this was the number of unique days any birds had been reported from a cell within the survey periods. During the model call, we specified the 'Laplace' strategy for approximations and default integration strategy.

We modelled the relationship between environmental covariates and bird occurrence in a non-linear fashion using penalized regression splines (Beale et al., 2014), in accordance with the expectation of species existing in niche spaces. We avoided smoothing approaches that fit regression curves closely to the data (e.g. random walk models in INLA), following the sentiment that such smoothing can quickly lead to biologically implausible effects in SDMs (Hofner et al., 2011). This approach reflected our prior expectation that the probability of presence relates to environmental variables in an approximately monomodal way, representing a single continuous niche space. We fitted the relationship with restricted flexibility by using a small set of regression splines, based

on thin-plate regression spline basis functions (adapted from steps provided in Crainiceanu et al., 2005). We selected control points for the regression splines based on the density distribution of covariate values covering the whole study area. In addition to the environmental fixed effects, we included the scaled coordinates as linear fixed effects in the model. This ensured that the spatial random effect fitted well in the case of species with very peripheral distributions (Beale et al., 2014).

Bird observation data and covariates were grouped into two time periods (time period 1: 1980–1999, time period 2: 2000–2020), and a temporal first-order autoregressive process (AR1) was integrated into the model structure. In AR1 models, the probability of presence in one time period is influenced by the probability of presence in the previous period. This overall model structure allowed us to estimate ranges at the two time periods while keeping the species-covariate relationships fixed, thereby reflecting the assumption that fundamental environmental limits of birds did not evolve during the time period (Radchuk et al., 2019). Simultaneously, this allowed us to better estimate the species occurrence–environment relationship, as this was influenced by the species ranges in two separate time periods, taking into account movement over time.

To derive pixel-level estimates closely related to the probability of presence produced by occupancy models, we projected posterior intensity estimates onto the study area under the assumption of constant high sampling effort (95 percentile value of overall sampling effort in the study), and we back-transformed these estimates to the probability scale. The pixel-level values therefore represented the probability of presence given that sampling effort is high. Our approach diverges from traditional occupancy models in a critical aspect. Under our framework, assuming an infinitely high sampling effort theoretically leads to a probability of presence of one (i.e. absolute certainty of presence) across all areas. In contrast, traditional occupancy models distinguish between the likelihood of presence and sampling effort, allowing for the possibility of absence regardless of sampling intensity. For the sake of readability and simplicity, we use the term 'probability of presence' to describe our estimates from here on out. We removed the estimates of the separate eBird random field from our final score. Fixing high sampling effort and removing the eBird-specific random field allowed the underlying ecological process to be visualized without variations in observation intensity due to effort. Due to the nature of the model, projected ranges are sensitive to the choice of the sampling effort constant. We conducted a sensitivity analysis, to test our assumption that this relationship with constant sampling effort should be linear and with no bearing on the ranking of species. For this, we refitted models using 55, 65, 75, and 95 percentile values for effort, checked linearity of the resulting range sizes using R-squared values, and calculated the change in the relative ranking of species by range size across the different effort quantile values.

2.4 | Mesh specification, prior choice, and model evaluation

In INLA, the SPDE method for approximating the spatial random field achieves computational efficiency by utilizing a

computational mesh, that is, a surface of triangles covering the study area (Lindgren et al., 2011; Lindgren & Rue, 2015). The specification of the spatial resolution of the mesh, that is, the triangle size, has to be considered carefully, as growing research highlights the potential effect of this parameter on model results (Dambly et al., 2023; Righetto et al., 2020). In the absence of well-established guidelines on choosing the optimal mesh size, we initially followed rules of thumb, that is, basing first values for the mesh size on the estimated spatial range of model predictions (Bakka, 2017). Following this, we opted to model bird distributions using a range of different mesh size specifications close to these initial values, for each of the study species, with triangle sizes of 0.55°, 0.75°, 1°, 1.45°, and 1.65° (approximately 61, 84, 111, 161, and 183 km). Two hyperparameters, namely range and marginal variance (sigma), exert control over the spatial fields. The range determines the smoothness of the spatial field, that is, the distance between the high and low points, while the variance dictates the amplitude of these peaks and troughs. In the Bayesian framework, prior values must be assigned to these hyperparameters. We adopted the Penalized Complexity (PC) priors framework, which is a technique that provides easy-to-interpret and modifiable priors (Simpson et al., 2017). PC priors are weakly informative, which allows the data to mainly dictate the posterior for each hyperparameter. For each combination of a species and mesh resolution, we chose a separate set of priors for either the shared or eBird random field. We chose the range and sigma priors relative to the spatial extent of the presence records of each individual species, as 0.5, 0.7, or 0.9 times the spatial extent, to test the effect of prior choice on model results. We set the probability that the range is below the chosen value, and the sigma is above the chosen value, to 50%. This combination of PC priors and mesh resolutions resulted in a sensitivity analysis containing 15 different model configurations per species, for a total of 1365 models. To evaluate the performance of each model, we calculated the logged negative sum of the conditional predictive ordinate scores (log-CPO), a recommended procedure for choosing the optimal mesh resolution (Righetto et al., 2020), where a lower score corresponds to the better fitting model. Additionally, we checked model outputs for visible convergence issues (e.g. regions with probability scores of 1 only and no spatial smoothness, or effect plots with abrupt drops to zero or 1 on the y-axis), and derived the spatial range of the random field estimated by the model (where a range much larger than the total study area indicates poor estimation of the spatial effect). For each species, candidate models were those that passed visual convergence checks and showed successful estimation of the spatial effect, and the final model was chosen based on the lowest log-CPO score. For a final measure of model fit, we extracted model predictions at the bird observation points (eBird and Atlas) using the 'extract' function in the package 'terra' (Hijmans et al., 2023). We then compared model predictions with observed presence and absence data separately for each time period, and calculated the area under the receiver

operating characteristic (ROC) curve (AUC), as well as sensitivity (proportion of correctly predicted presences) and specificity (proportion of correctly predicted absences) using the package 'pROC' (Robin et al., 2011) in R. While AUC can be problematic when generating pseudo-absences with presence-only data (Lobo et al., 2008; Shabani et al., 2016), issues are reduced for detection/non-detection data as used in this study.

In addition to the PC priors, we specified Gaussian fixed effect priors, equally for all species. These parameters describe the slope of the relationship between the covariate and occurrence on the link function of the response, and are applied to the fixed effects of the model. We chose Gaussian priors on the fixed effects with 0 mean and precision of 1, suitable as a vague prior given the complementary log-log link function used here.

2.5 | Species traits

We included traits broadly falling under the categories set out in Estrada et al. (2016), as well as an exposure-related trait and sensitivity (Estrada et al., 2016). Table 1 gives an overview of the traits and associated data sources. The sensitivity traits were quantified from the SDM estimates based on variance partitioning, broadly following Beale et al. (2014). This was the percentage of variation in presence probability explained by any of the environmental covariates alone. Sensitivity was therefore quantified in line with the IPCC definition, as the degree to which a species is affected by or susceptible to environmental change (IPCC, 2007). Due to the fact that both sensitivity and range shift scores were derived from the same distribution models, an important consideration is the potential for the two variables to be inherently correlated with each other, that is, with larger range shifts coinciding with higher sensitivities. If this were the case, we would expect to find consistent and statistically clear positive correlations between range shifts and sensitivity, an outcome that our analysis tested implicitly. Model-derived environmental niche breadth was quantified based on the estimated niche shape, as the range of values associated with a probability of presence above 50%. This quantification relied on the assumption of a single environmental niche. Where effect plots showed a probability of presence above 50% at low as well as high environmental values, this therefore indicated issues in estimating the niche shape. Since in those cases, the SDM still identified high presence associations with low and high environmental values regardless of the niche shape, we set the niche breadth to the maximum. Acknowledging that this is an imperfect solution, we quantified the extent of the issue and its effect on the final regression analysis. We expected the relationship between body mass and range shifts to be non-linear, meaning that a hypothetical difference of 5 grams of body mass should play a larger role for small species than for large species (up to 8 kg body mass in this study). Hence, we transformed mass measurements using a natural log. All continuous traits were centred and scaled to a mean of zero and standard deviation of one.

TABLE 1 Overview of the traits included in the analysis of range shifts.

Mechanism	Trait	Description	Source
Ecological generalization	Locomotory niche while foraging	Aerial, Terrestrial, Insessorial, Generalist	AVONET
	Trophic group	Omnivore, Herbivore, Carnivore	AVONET
	Niche specialization	Niche breadth ^a	Model-derived
Movement ability/Site fidelity	Migratory ability	Low, Medium, High	AVONET
	Hand-wing index	(100 * Kipp's distance)/Wing length	AVONET
	Body mass	Species average (gram)	AVONET
Exposure-related	Mean dorsal reflectance	300–700nm	Cooney et al. (2022)
Sensitivity	Sensitivity to environment ^a	Variation of presence probability explained	Model-derived

Note: Sensitivity and niche breadth were derived from the integrated species distribution model and corresponded to the environmental covariates included in the model formula (highest temperature, annual rainfall, longest dry spell duration, bare ground cover, human footprint). Niche breadth was calculated as the range of covariate values where $P(\text{presence}) > 0.5$, while sensitivity was calculated as the percentage of model variation explained by the covariate. Mean dorsal reflectance was adapted from data published by Cooney et al. (2022). All other traits were derived from the AVONET database (Tobias et al., 2022). 'Kipp's distance' describes the distance between the tip of the first secondary feather and the tip of the longest primary feather.

^aHottest temperature, annual rainfall, longest dry spell, bare ground cover, human footprint.

2.6 | Quantifying range shifts

We analysed the effect of traits on three measures of range shifts for each species: Total range change, and two transition scores (expansion, contraction). Due to the nature of the model (projections under an assumption of high constant sampling effort), these transition scores represented the change in estimated intensity. We calculated the measures of range shifts based on the pixel-level probability of presence in time period 1 ($P(\text{presence})_{1980-1999}$) or time period 2 ($P(\text{presence})_{2000-2020}$), using the sum of probabilities (presence or transitions) over all pixels i to derive a single measure that related to geographical area (total range size or range expanded/contracted). We calculated the total range change as the range size in time period 2 divided by the range size in time period 1, log-transformed to scale proportional increases the same as proportional decreases (1):

$$\text{Total range change} = \log \left(\frac{\sum_i P(\text{presence})_{2000-2020,i}}{\sum_i P(\text{presence})_{1980-1999,i}} \right) \quad (1)$$

We calculated the pixel-level probability of range contraction as the probability of absence in time period 2 multiplied by the probability of presence in time period 1, and calculated the sum over all pixels i to derive the expected total range lost (2):

$$\text{Range lost} = \sum_i ((1 - P(\text{presence})_{2000-2020,i}) \times P(\text{presence})_{1980-1999,i}) \quad (2)$$

We calculated the pixel-level probability of range expansion as the probability of absence in time period 1 multiplied by the probability of presence in time period 2, and calculated the sum over all pixels i to derive the expected total range gained (3):

$$\text{Range gained} = \sum_i ((1 - P(\text{presence})_{1980-1999,i}) \times P(\text{presence})_{2000-2020,i}) \quad (3)$$

Importantly, we normalized the transition metrics by a stochastic uncertainty score. It necessarily follows from the transition

calculations above that in places where little to no change occurred, pixel-level contraction and expansion probabilities were highest if the probability of presence was 0.5 in both time periods (e.g. $(1 - 0.5) \times 0.5$ is larger than $(1 - 0.1) \times 0.1$ or $(1 - 0.9) \times 0.9$). Initial testing revealed that such areas of high sustained stochasticity can inflate transition scores if not accounted for, producing misleading transition metrics. We therefore defined a stochastic uncertainty score, as the binomial variance in time period 1 (1980–1999) (4). Where the probability of presence was closest to 0.5 in both time periods (i.e. contraction or expansion scores were inflated due to high stochasticity), this uncertainty score was equal to the transition metrics, allowing effective normalization by division. The sum of the uncertainty score over all pixels i represents the area of high stochastic uncertainty (4):

$$\text{Stochastic uncertainty score} = \sum_i ((1 - P(\text{presence})_{1980-1999,i}) \times P(\text{presence})_{1980-1999,i}) \quad (4)$$

The normalized transition scores represented the ecologically meaningful area gained or lost, beyond stochastic noise. Like the total range change metric, these scores were log-transformed. Henceforth, they are referred to as 'Meaningful contraction' (5) and 'Meaningful expansion' (6). On the linear scale, a score of 1 indicated that changes were exactly as expected by chance (area gained or lost equal to the area of high uncertainty), and a value of 2 indicated that there were twice as many expansions or contractions as expected by chance. A score of 0.5 indicated that 50% fewer transitions occurred than expected by chance.

$$\text{Meaningful contraction} = \log \left(\frac{\text{Range lost}}{\text{Stochastic uncertainty score}} \right) \quad (5)$$

$$\text{Meaningful expansion} = \log \left(\frac{\text{Range colonised}}{\text{Stochastic uncertainty score}} \right) \quad (6)$$

2.7 | Trait–range shift relationship

For a statistical test of the trait–range shift relationship, we built additive linear Bayesian regression models with default priors in the R-INLA package (R version 4.3.1, R-INLA version 23.09.09). We chose robust regression models over more traditional methods since they effectively reduce the weight of outliers through a *t*-distributed error structure (Wang et al., 2018). In essence, this was chosen to help capture broad underlying trends, decreasing the potential influence of outlier species. We fitted separate regression models with each of the three measures of range shifts as a response, and the species traits as explanatory variables. In the regression dataset, each row represented range shift metrics and associated traits for an individual species in the study. Since higher sensitivity generally coincides with smaller niches (Rinnan & Lawler, 2019), likely leading to a correlation between the two, we fitted separate models containing either sensitivity and all other traits as independent variables, or niche breadth and all other traits. This specification of model formulas led to a total of six separate linear models. We conducted cross-validation model checking to evaluate the goodness of fit of the models. For each model, this was based on the probability integral transform (PIT) values, a recommended method of Bayesian model criticism (Feringstad et al., 2017). For a well-fitting model, we expected uniformity in the distribution of PIT values, translating into a good match between observations and model predictions (Gneiting et al., 2007; Wang et al., 2018). We fitted posterior model estimates to the observation data using posterior marginals of linear combinations. This allowed us to conduct a final visual inspection for outliers that might be driving results despite the robust regression approach. Where such outliers were identified, we compared model results with and without the outlier included. We evaluated the statistical importance of traits based on the distance of posterior estimates from zero, taking into account 95% credible intervals. Where credible intervals did not overlap zero and were narrow, trait effects were considered especially well supported by the model. Due to the potential influence of phylogenetic relatedness on results (Angert et al., 2011), we first retrieved taxonomic information for our study species from the National Center for Biotechnology Information (NCBI) database using the 'taxize' package in R (Chamberlain & Szöcs, 2013). We then refitted the linear models specifying a random intercept term of family nested in order as an 'iid' model with default priors (Faraway, 2016) and checked the influence on model results.

3 | RESULTS

Of the initial list of 91 savannah birds that we built SDMs for, 79 species were well supported based on the aforementioned model evaluation steps. Twelve species were excluded from further analysis since either none of the models converged or models failed to produce any estimates that passed evaluation steps. Expert review of the model output confirmed plausible predicted ranges for all 79 species, reflecting expert knowledge of distributions and geographical boundaries. The average model AUC was 82.3%, suggesting the model output reflected the observation data well. Average dorsal reflectance values were not

available for a set of 22 species, and we excluded these species from the regression analysis. The trait category of 'Trophic level: Scavenger' contained only one species (White-backed vulture, *Gyps africanus*) and was therefore removed from the analysis. The final dataset contained a total of 57 species belonging to 26 families and 11 orders (Supplementary Table S2). Supplementary Table S2 provides an overview of the number of detections for each species and observation dataset, and supplementary table 3 provides an overview of the sample sizes for each trait category. As expected, we found that range size estimates were sensitive to the choice of the effort constant. Testing revealed that range size estimates increased with effort in a highly linear way, with little change to the relative species ranks for most species (Supplementary Figure S1). We found only very minor effects of including a random effect of phylogeny in the linear models (Supplementary Figure S2), and the results presented here are based on the simpler models without random intercepts. We found cases of improperly estimated niche shapes in 11 of the 57 species. However, this was predominantly found for human footprint niche breadth (8 cases), followed by niche breadth of dry spell duration (3 cases) and rainfall (1 case). Re-running the models with the 11 species excluded revealed that the relevant model estimates were not affected (Supplementary Figure S3).

Kori bustard (*Ardeotis kori*) showed one of the largest range contractions, disappearing from its Western range (Figure 2a, 30% greater contraction than expected by chance). Among the species with the highest meaningful expansion scores was the Von der Decken's hornbill (*Tockus deckeni*), showing a westward range extension into miombo woodland areas (Figure 2a, range gained 220% greater than expected by chance).

Total range changes varied between species and were predominantly positive (Figure 2b), meaning that most species increased their range relative to the initial range size. In the case of the bare-eyed thrush (*Turdus tephronotus*), this expansion was as high as 3.9 times larger than what would be expected by chance. Overall, meaningful contractions rarely exceeded what was expected by chance and were often lower than expected chance transitions. For a number of species, including Kori bustard, both contractions and expansions were considerably higher than total range changes (Figure 2b). In those cases, large range losses in one region coincided with large gains in another (Kori bustard expanding its Southern range, Figure 2a), highlighting the importance of considering more than total range change alone.

3.1 | Ecological generalization

We found a statistically significant increase in total range change in generalist foraging species (Figure 4a), driven by fewer contractions and more expansions (Figure 3). However, the statistical significance was barely conserved between models including niche breadth or sensitivity covariates (the group 'generalist' contained only three species), indicating a poor statistical signal and limited interpretability (Figure 3). There was no clear association between any range shift metric and trophic levels, as well as most measures of niche breadth (Figure 3). Hottest

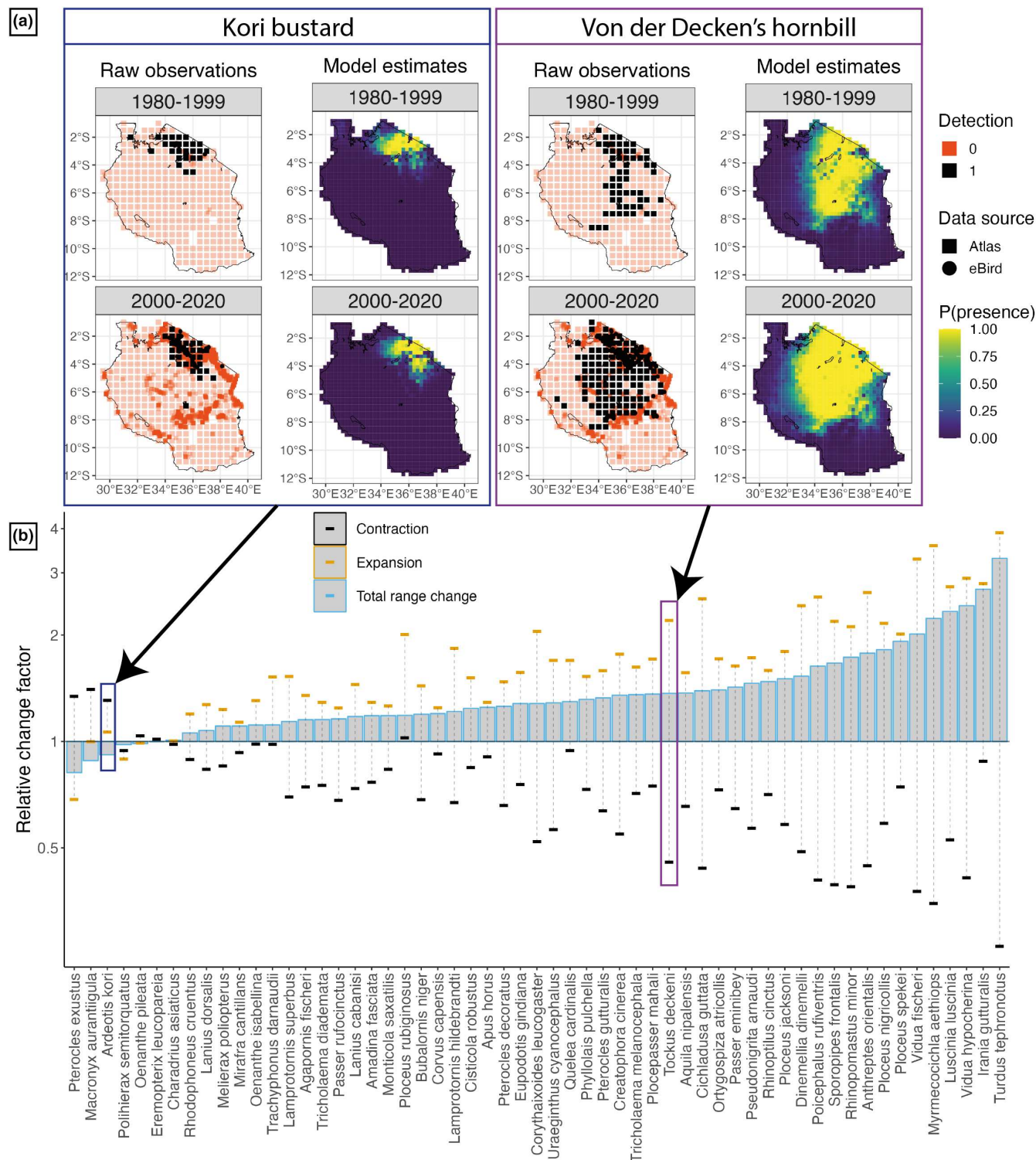


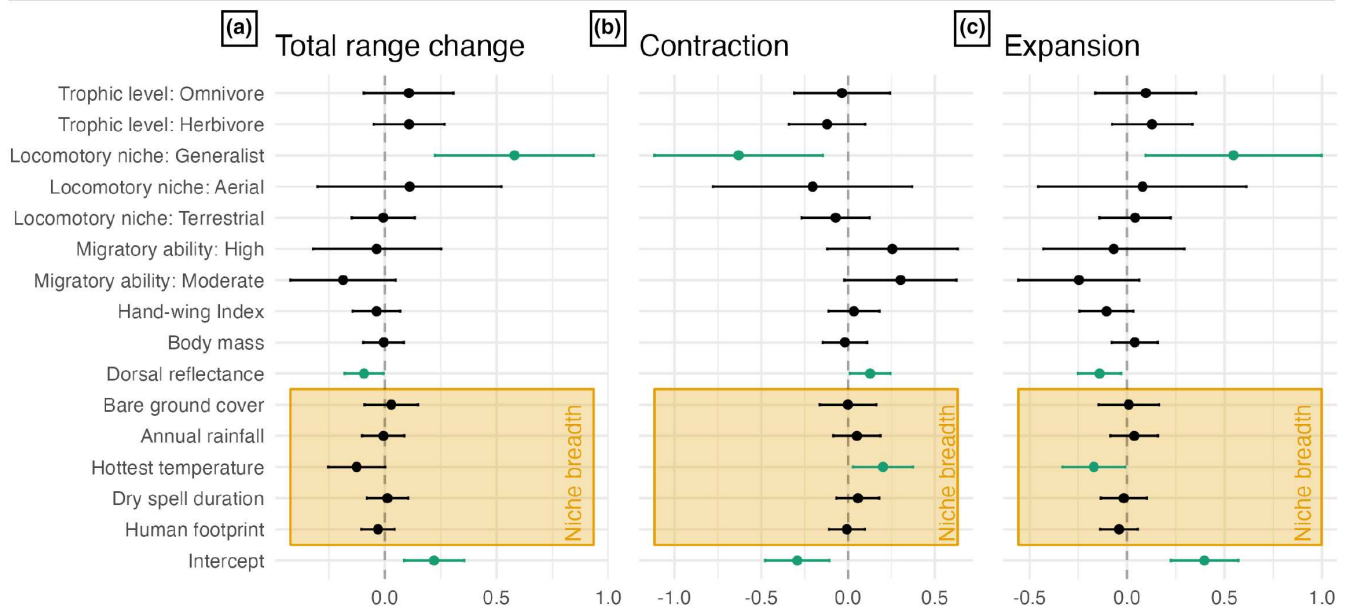
FIGURE 2 Overview of range shifts observed in the study. (a) Raw presence and absence data and posterior median probability of presence estimates, for example, species in the study. Red points/squares on the raw observations plots show raw species detections, while black points/squares show nondetections. Points represent eBird data records, and squares represent Bird Atlas records. The colour gradient in the model estimates plots shows the probability of presence as estimated by the model, with more yellow colours signifying a higher probability of presence. Dark blue and dark purple colour outlines highlight the amount of range shifts corresponding to the example species. Dark blue: Kori bustard (*Ardeotis kori*); dark purple: Von der Decken's hornbill (*Tockus deckeni*). (b) Relative change factor for range shifts of individual species between the time periods of 1980–1999 and 2000–2020, separated into total range change, meaningful contraction scores, and meaningful expansion scores. Values on the y-axis are presented on the linear scale. A relative change factor of 1 corresponds to no meaningful change for contractions or expansions (area lost or gained equal to area of chance transitions), and no change for total range change (range in 1980–1999 equal to range in 2000–2020). A relative change factor of 2 corresponds to a doubling of area, and a factor of 0.5 to a halving of area.

temperature niche breadth showed a statistically significant positive correlation with contractions and a negative correlation with expansions (Figure 3b,c). However, this effect was small, with an 11.9% increase in contractions for a 10 Celsius increase in niche breadth (Figure 4b).

3.2 | Movement ability

We found no clear associations between migratory ability, body mass or hand-wing index, and any range shift metric (Figure 3).

Results for models containing niche breadth, as range of covariate values where $P(\text{presence}) > 0.5$



Results for models containing sensitivity, as percentage of model variation explained by the covariate

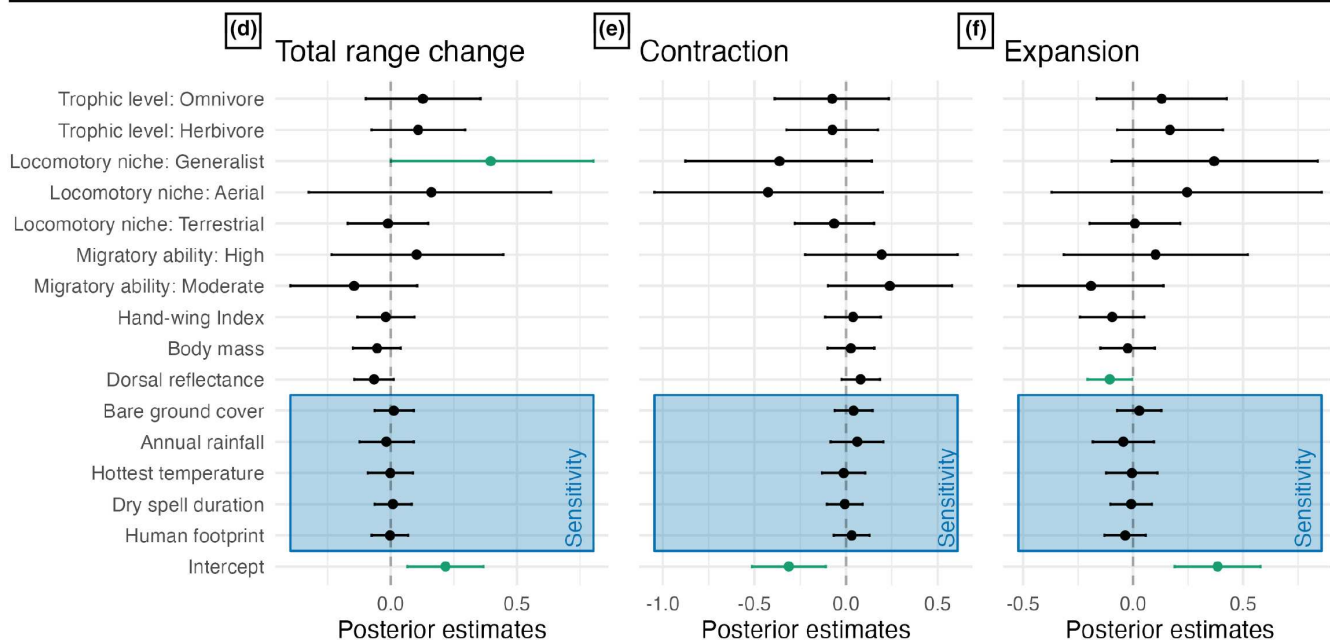


FIGURE 3 Parameter estimates and their 95% credible intervals for INLA model results predicting three measures of range shifts: Total range change, meaningful contraction scores, and meaningful expansion scores. Figure (a–c) are derived from models including human footprint, longest dry spell duration, hottest temperature, annual rainfall, and bare ground cover as niche breadth scores (highlighted in orange). Figure (d–f) are derived from models including that same set of variables as sensitivity scores (highlighted in blue). Parameters with credible intervals that do not overlap zero, or credible intervals of other factor levels for categorical variables, may be considered strong effects in the Bayesian models, and are highlighted in green. For categorical parameters, this signifies that a trait level within a category is statistically different from the reference level. The reference levels are ‘Migratory ability: Low’, ‘Locomotory niche: Insectivore’, and ‘Trophic level: Carnivore’.

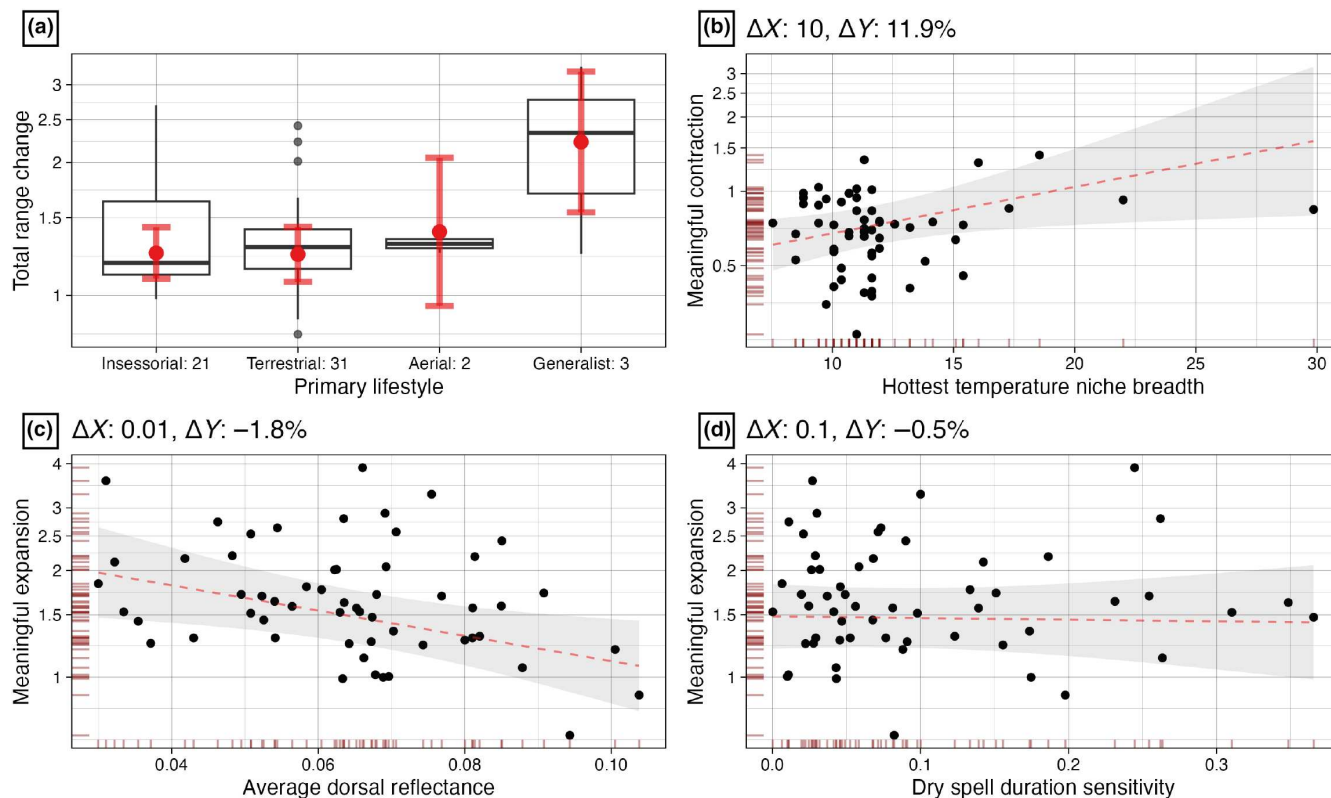


FIGURE 4 Selected effect plots showing the correlations between covariates and different measures of range shifts. All effect plots can be accessed in the supplementary material (Supplementary Figures S4–S9). Boxplots represent categorical covariates, while scatter plots represent continuous variables. Numbers on x-axis labels represent sample sizes for levels of categorical variables. Values on the y-axis are presented on the linear scale. A score of 1 indicates that changes are exactly as expected by chance (area gained or lost equal to the area of high uncertainty transitions), and a value of 2 indicates that there are twice as many meaningful expansions or contractions as expected by chance. A score of 0.5 indicates that 50% fewer transitions occurred than expected by chance. Black points are drawn on the raw data provided to the models, red dashed lines, as well as red points with red error bars are posterior model estimates derived from linear combinations. The rug plots visualize the density of the data points. ΔX is the change along units on the x-axis that corresponds with a ΔY change of units on the y-axis. (a) Correlation between primary lifestyle and total range change. (b) Correlation between hottest temperature niche breadth and meaningful contraction scores. (c) Correlation between average dorsal reflectance and meaningful extinction scores.

3.3 | Exposure-related trait

Dorsal reflectance tended to be negatively associated with total range change, driven by fewer meaningful expansions, and more meaningful contractions (Figure 3). However, effect sizes were small, with a 1.8% decrease in expansions for a 0.01 increase in plumage reflectance (Figure 4c). The correlation with total range change and contractions was statistically significant only for models including niche breadth covariates, indicating limited interpretability.

3.4 | Sensitivity

We found no statistically significant relationships between any species sensitivities and range shift metrics (Figure 3d–f).

3.5 | Individual species associations

Individual species showed strong associations, as remarkable range change values coupled with remarkable trait values. Some individual

species showed a strong association between range shifts and sensitivity, with bare-eyed thrush (*T. tephronotus*) exhibiting a dry spell duration sensitivity of 0.25 (25% of model variation explained by dry spell duration) that coincided with a large expansion score of 3.9 times larger than expected by chance. Sensitivity to bare ground cover explained roughly 11% of variation in the distribution model of the horus swift (*Apus horus*). This was associated with an expansion roughly 21% larger than what would be expected by chance alone. Narrow niche breadth coincided with large declines in individual species. Chestnut-bellied sandgrouse (*Pterocles exustus*) showed one of the largest declines in the study, losing about 25% more of its range than expected by chance, while also exhibiting one of the narrowest niche breadths for human footprint. We observed similar declines in Kori bustard (*A. kori*), also associated with a relatively narrow human footprint niche.

4 | DISCUSSION

We succeeded in creating plausible species-specific range shift estimates of high agreement with observation data, taking into account sampling bias and unobserved effects, and reflecting known trends

(e.g. range contraction of the kori bustard in East Africa, Senyatso et al., 2013). Our sensitivity analysis of effort used in model predictions supported the validity of our approximation of the probability of presence as derived in occupancy models. Furthermore, the lack of strong positive correlations between sensitivity traits and range shifts asserted that results were not driven by circularity between model-derived traits and range estimates. Our model of trait-range shift relationships indicated some trends similar to previous studies (e.g. Beissinger & Riddell, 2021; Yang et al., 2020). However, despite considering a wide range of species traits, effects were small overall, even where statistically significant. This questions the ecological significance of these effects, adding to growing research identifying a lack of broad, generalizing trends between most traits and range shifts across multiple taxa (Angert et al., 2011; Beissinger & Riddell, 2021; Buckley & Kingsolver, 2012; Howard et al., 2023; MacLean & Beissinger, 2017; Reif & Flousek, 2012).

We found that savannah birds primarily showed positive total range changes, meaning that most species had larger ranges in the later time period, compared to the initial range. This change was generally a function of higher expansion rates. Tanzania has had a higher-than-average deforestation rate compared to the rest of Sub-Saharan Africa, with an estimated 0.9% annual decline in forest cover since 1995 (Nzunda & Midtgaard, 2019). If some of these forests were converted into habitat suitable for colonization by savannah bird species, this might help explain the high rates of expansions. However, patterns of change are complex, often resulting in increased cultivated land, and the rate of grassland loss being nine times higher than that of deforestation (Nzunda & Midtgaard, 2019). Additionally, Tanzania has experienced increasing bush encroachment, further modifying habitat structure (Selemani, 2018). Overall, the core species ranges appeared to be surprisingly stable, with most birds showing fewer contractions than what would be expected by chance. This might be especially surprising given the aforementioned rapid changes in Tanzanian grasslands over the past decades. More research is needed to link these patterns of land cover change to individual trends and habitat preferences of species, which are frequently unknown.

Contrary to our first hypothesis, we did not find broad, statistically clear positive associations between range shifts and most traits reflecting ecological generalization in this study (i.e. trophic level, most niche breadth metrics), and effect sizes tended to be small. The finding of significantly higher total range changes in generalist foraging species (although this result did not hold where accounting for phylogenetic relationships between species; Supplementary Figure S2) is in line with previous research (MacLean & Beissinger, 2017). As generalist species can exploit a wider range of food sources, they are thought to be more successful at colonizing new habitats, and although ambiguous, evidence of this relationship exists in the literature (MacLean & Beissinger, 2017). The lack of an effect of niche breadth regarding rainfall suggests that studies of range shifts might not necessarily be more informed by the addition of hygric niches, as suggested in the literature (Beissinger & Riddell, 2021). However, due to the taxonomic and geographical

restrictions of this study, there is a need for additional work to confirm this. The finding of more contractions and fewer expansions with wider hot temperature niches is surprising: as species with a wider niche breadth have the potential to tolerate more extreme hot temperatures, and the frequency of extreme heat days has increased in East Africa (Das et al., 2023), one might expect an opposite trend. However, maximum temperatures may simply not have increased enough yet in the area (although they are projected to increase in the future, Das et al., 2023) to impact species ranges in a way that leads to detectable associations with niche breadth, and given the small effect size, interpretability is limited. Alternatively, since species range responses can lag behind climatic change, not enough time might have passed for species to shift their ranges in response to temperature (Howard et al., 2023). The range shifts observed in this study might have been caused by factors affecting species survival faster than climate, such as land cover change (Faurby & Araujo, 2018; Sirami et al., 2008).

The results of this study tended to disprove our second hypothesis regarding movement ability. Although previous studies found stronger migratory behaviour to be commonly associated with fewer range shifts in birds, attributed to their higher level of site fidelity to their home range (MacLean & Beissinger, 2017), no such pattern emerged in our results. Although a small effect, HWI tended to be negatively associated with range expansions. Previous work has identified HWI as being strongly positively correlated with dispersal ability across many bird taxa (Arango et al., 2022), meaning we would have expected to see more expansions as HWI increases. However, this effect may be confounded by the reproductive strategies of smaller birds with lower HWI. As they tend to exhibit higher reproductive rates and shorter generation times (Saether, 1988), smaller birds might colonize new areas more successfully, resulting in more range expansions (MacLean & Beissinger, 2017). In fact, if we consider HWI as approximately proportional to body size, the negative correlation with range shifts found here is in agreement with multiple studies using birds (Beissinger & Riddell, 2021; Brommer, 2008; Yang et al., 2020).

Contrary to our third hypothesis, our results indicated that species with higher dorsal reflectance (i.e. lighter-coloured birds) tended to show lower total range changes, driven by fewer expansions, and more range contractions. Theory suggests that lighter-coloured birds should be better able to cope with higher heat loads, due to increased reflectivity (Medina et al., 2018). In a recent study on the Iberian Peninsula, including 96 bird species, researchers found that lighter birds were less geographically restricted from occupying hotter areas, having a wider thermal niche (Galván et al., 2018). Virtually all of East Africa has seen an increase in maximum temperatures of nearly 2°C (Gebrechorkos et al., 2019b), so it is surprising to see an indication of lower total range changes in lighter-coloured birds. However, as with the other trait effects, the degree of the correlation was small, limiting interpretability. If we assume a mechanistic relationship between dorsal reflectance and range change, our results suggest that the recent increase in temperatures is not yet high enough in Tanzanian savannahs to lead to a strong positive signal,

limiting new expansions of thermally restricted species. However, it has been hypothesized that thermoregulatory behaviour is more important than plumage reflectance alone (Stuart-Fox et al., 2017), further calling into question the assumed positive relationship between reflectance and range shifts.

Our results indicated that relationships between range shifts and sensitivity traits were surprisingly weak, contrary to our fourth hypothesis. The human footprint is increasing globally at an accelerated pace, particularly in areas of high biodiversity, and East Africa is no exception (Venter et al., 2016). Reflective of human-made structures like urban areas, roads, agricultural land, and other forms of developed land, this metric represents the most significant habitat alteration, virtually erasing natural features where human activities are most intense. Thus, the human footprint layer includes factors known to lead to habitat fragmentation on a landscape scale, such as road networks and increasing agriculture. While a recent study found that this kind of fragmentation has been shown to adversely affect the local survival of savannah bird species (Herkert, 1994), we found surprisingly weak relationships between range shifts and sensitivity to human footprint. A reason for this could be that such areas may not have expanded sufficiently to cause widespread contractions in sensitive bird species. A recent study found that the amount of anthropogenic infrastructure more generally negatively impacted bird functional diversity in an African savannah in and around the Kruger National Park, South Africa (Lerm et al., 2023). Continued monitoring of those species most sensitive to human footprint is therefore recommended, as simply not enough time may have passed since the landscape changed to cause a reduction in range. It is perhaps surprising that, on average, no strong associations with sensitivity to bare ground emerged. However, previous research found that, while land degradation such as an increase in bare ground was an important predictor of savannah bird ranges in Tanzania, this relationship likely occurred at fine spatial scales (Beale et al., 2013). By integrating eBird point data of higher spatial resolution, our study went towards analysing these finer scale patterns, although we allowed eBird resolutions of up to 15 km, a necessary condition to include a reasonable number of records. Overall, we summarized range changes over a fairly large spatial and temporal scale, and while this allowed us to investigate broad relationships, it is unlikely to reflect fine-scale relationships between land degradation and species ranges.

Although we were unable to identify meaningful general relationships across species between traits and range changes, it is important to note that some individual species showed strong associations between range shifts and traits, potentially indicative of ecological trends. Horus swift, for example, showed large range expansions coupled with high sensitivity to bare ground. As this is a species that relies on sandy riverbanks for nesting (Piot & Bacuez, 2021), it might have benefited from the trend of increasing bare ground in the region (Piot & Bacuez, 2021), providing the conditions for additional breeding grounds. In the Von der Decken's hornbill, the large range increase was associated with relatively low sensitivity to temperature and length of dry days, potentially indicating mitigating traits

underlying the expansion. The large decline coupled with a narrow human footprint niche in the chestnut-bellied sandgrouse, on the other hand, might highlight the species' challenge to persist under recent anthropogenic changes in Tanzania. As the species is both reliant on grassland and is being hunted, the decline might be indicative of the increased fragmentation and hunting pressure associated with increasing human pressure (Thiollay, 2006). Similarly, the large decline in kori bustard coincided with a relatively narrow human footprint niche, with the species known to be threatened by hunting and habitat change (Mmassy, 2017). Despite the absence of broad trends, these individual associations provide meaningful insights into species–environment relationships and could inform vulnerability assessments and conservation efforts. Under the projection of increasing environmental change in East Africa (Dunning et al., 2018; Moore et al., 2012), these individual assessments will become more important in the region.

Our study demonstrates the potential of a spatio-temporally structured, integrated model in R-INLA to estimate range changes of species. The spatial random effects definition allowed us to capture dataset-specific observation bias, reducing the impact of common issues associated with citizen science records (Isaac & Pocock, 2015). Additionally, it accounted for unexplained effects that weren't included in the model, hence reducing spatial autocorrelation issues commonly associated with species distribution models (Beale et al., 2010, 2014; Beale & Lennon, 2012; Faisal et al., 2010). While this is a powerful method for accounting for bias, model results are, to an extent, sensitive to sample size (Simmonds et al., 2020). Our citizen science data source, eBird, has experienced a rapid increase in popularity, leading to an increase in data availability (Sullivan et al., 2014). While users are able to submit observations retrospectively, such observations are outweighed by the constant inflow of new checklist submissions, leading to uneven sample sizes and effort between the two time periods in our study. This might potentially lead to false colonization estimates if absences in the earlier time period are due to the species having been missed. However, the coverage of the Atlas grid surveys is extensive, leaving very few gaps across the study area, and the additional temporal autoregressive process included in the model structure helps alleviate any unevenness: where species were reported through eBird or Atlas records in the later time period, 2000–2020, the model assigned a probability of presence in the same places in 1980–1999, as a function of environmental conditions. A different case of inflated colonization estimates may be presented through increased taxonomic awareness of species, and more reliable species identification through the availability of improved field guides. It is unlikely, however, that this source of bias would affect overall multi-taxa results. Finally, it should be noted that the lack of strong statistical associations might, to some degree, be a result of low statistical power in the analysis. While the relationship with continuous traits was supported by the full set of species, some levels of the categorical traits were represented by a small number of species, leading to low statistical precision. This warrants more investigation of these categorical

traits, supported by higher statistical power. The hypotheses in our study, however, were driven by sets of traits containing both categorical and continuous variables (e.g. movement ability as migratory ability, but also HWI and body mass), reducing the effect of statistical power on the validity of inferences made in this study.

The set of traits included in this study was extensive, building on a trait framework designed to encompass the most important predictors of range shifts, and adding additional traits related to sensitivity and exposure, both important traits determining a species range (Foden et al., 2019). Species sensitivity has traditionally been challenging to assess, with definitions being criticized for being arbitrary and ambiguous (Fortini & Dye, 2017). Our sensitivity measures directly quantified the degree to which a species' probability of presence is determined by different conditions in the environment. It is a potentially less ambiguous measure of sensitivity, arising from the realized species distribution. Such range-specific metrics have previously been proposed in the context of vulnerability assessments of species, for example, in the form of 'Range exposure' (Rose et al., 2023). Our quantification of sensitivity may be a valuable contribution to future studies. However, the aforementioned potential for circularity issues has to be considered, and since this sensitivity metric is only based on the realized niche, it likely paints an incomplete picture. Past studies included additional traits not considered in our analysis, for example, related to reproductive behaviour or additional physiological features (Estrada et al., 2016). However, many of these will strongly covary with the traits included in our study. Body mass, for example, correlates with clutch size and annual fecundity (Bohning-Gaese et al., 2000). Similarly, our model-derived sensitivity might reflect adaptive behaviour such as hiding in shade during the hottest hours of the day: a higher degree of successful adaptive behaviour would likely be correlated with lower sensitivity. Hence, our set of traits likely reflected other species' characteristics not explicitly included. Due to the lack of meaningful average associations between range shifts and any trait considered in our study, additional traits not explicitly included likely would not diverge markedly from this pattern. However, more research is needed to confirm this, and to test how transferable these results are to other taxonomic groups, such as plants where the synthesized associations between traits and range shifts appear less contradictory (Beissinger & Riddell, 2021; Stahl et al., 2014).

Individual studies exist that found some traits to be predictive of range shifts across multiple bird species, such as an example for birds in China (Yang et al., 2020) and Europe (Estrada et al., 2018). Importantly though, the methodologies applied in these examples to assess range shifts diverged markedly from our study. In the case of Yang et al. (2020), range shifts were quantified on a simple binomial scale (1 or 0), significantly reducing nuance in the analysis. In the case of Estrada et al. (2018), range shifts were based on climate suitability models rather than observation data, which suffer from many of the methodological challenges we aimed to overcome in this study, such as unaccounted spatial autocorrelation or non-climatic effects (Beale et al., 2014; Gaspard et al., 2019). Notably, a recent publication on range shifts in European birds found directly contradictory

results, with most traits having poor predictive power (Howard et al., 2023). This is indicative of the wider trend of inconsistent and weak results concerning the trait-range shift relationship identified in comprehensive reviews and meta-analyses, leading some authors to discourage the use of traits in conservation planning unless analytical shortcomings were addressed (Beissinger & Riddell, 2021; Buckley & Kingsolver, 2012; MacLean & Beissinger, 2017). Multiple possible reasons for this weak predictive ability of traits have been proposed (see Beissinger and Riddell (2021) for an overview). We believe that this study provides empirical evidence that analytical issues are an insufficient explanation of this trend.

5 | CONCLUSION

The lack of trends across species between traits and range shifts identified in this study calls into question the usefulness of traits when analysing range shifts over higher taxonomic levels. The novel analytical techniques we used accounted for shortcomings identified in previous assessments of range shifts and further corroborated this result. While acknowledging the taxonomic and geographical restrictions of our study, we suggest that research into the effect of environmental change on range shifts of taxonomic groups may not necessarily benefit from the inclusion of traits. However, where individual species are considered, traits can provide important insights into the drivers of observed distribution changes.

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CONFLICT OF INTEREST STATEMENT

None of the authors have any conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

R code and data for the analysis can be accessed using the following link: <https://doi.org/10.5061/dryad.m63xsj47c>.

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BIOSKETCH

Joris H. Wiethase is a quantitative ecologist, with a special interest in species distribution modelling and remote sensing. Focus lies on analysing the drivers and patterns of environmental change and their consequent effects on species distributions and vulnerabilities.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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