

## RESEARCH ARTICLE OPEN ACCESS

# Non-Native Bird Populations Respond Differently to Their Environment and Exhibit Shifts in Ecological Niche Limits Across Continents

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## ABSTRACT

**Aim:** The degree to which species' niches remain stable over space and time—the niche conservatism hypothesis—is critical for predicting species' responses to environmental change. Tests of this hypothesis typically focus on changes in niche centroids and boundaries. An outstanding question is whether species' environmental associations differ within the interior of their niche space—that is, across the full range of occupied conditions—in original versus novel geographic space.

**Location:** Europe and North America.

**Time Period:** 1997–2018.

**Major Taxa Studied:** Birds.

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**Methods:** We used over 400,000 observations collected over 22 years and across 28 countries to explore whether two common songbird species—European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*) – exhibit niche conservatism between their native European and non-native North American ranges. We tested for niche conservatism via (1) an ordination approach that quantified change in niche shape and boundaries, and (2) generalised linear mixed effects models to quantify how abundance varied with the interaction between continent and climate or land cover variables.

**Results:** The ordination analysis indicated that both European starling and house sparrow exhibited niche conservatism between Europe and North America. However, abundance models revealed continental differences in how the species responded to temperature and land cover. The abundance models also revealed that areas with wetter conditions that were occupied by both species in their native European ranges were available but unoccupied in their non-native North American ranges (i.e., niche unfilling).

**Main Conclusions:** Our work demonstrates that species can exhibit apparent consistency in niche boundaries but varied abundance responses to the environment within niche boundaries. Expanding the study of niche conservatism to explore changes both at the edge of and within niche boundaries would improve the ability to assess and predict species' invasion risk or sensitivity to ongoing global change.

## 1 | Introduction

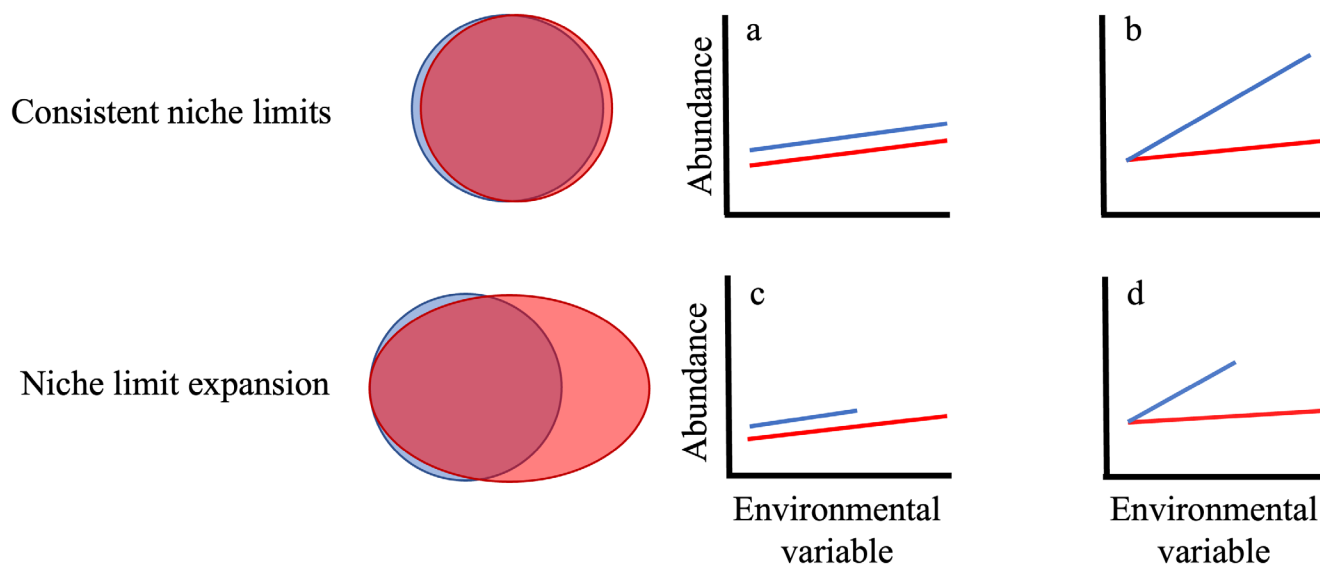
Quantifying the ecological niche (Colwell and Rangel 2009; Hutchinson 1957) is essential for predicting species' responses to global change, including identifying causes of population declines and anticipating biological invasions. Many analytical approaches that predict species' responses to climate change and the establishment potential of non-native species, such as species distribution or ecological niche models (Broennimann et al. 2007, 2012; Guisan et al. 2014; Sherpa et al. 2019), rely on the assumption that species' environmental associations are constant over space and time—that is, the niche conservatism hypothesis (Peterson et al. 1999; Wiens et al. 2010; Wiens and Graham 2005). Studies of niche conservatism primarily have focused on quantifying change in the centroid, boundaries and/or breadth of the realised niche in different geographic areas (Bates and Bertelsmeier 2021; Liu et al. 2020a). Multiple studies have demonstrated that niche limits can shift in species' non-native ranges (e.g., Atwater et al. 2018; Broennimann et al. 2007; Hill et al. 2017), but less attention has been paid to patterns of prevalence or abundance under environmental conditions that are occupied in both the native and non-native ranges. Testing for consistency in how populations respond across the breadth of the environmental conditions within their niche space could illuminate an underexplored dimension of niche conservatism (Ascanio et al. 2024; Hierro et al. 2017).

Non-native species are excellent test cases for assessing the prevalence of niche conservatism because by definition they have established in a novel geographic space (Gallien and Carboni 2017; Sax et al. 2007). A widely used approach to test for niche conservatism for non-native species is an ordination-based technique known as the Centroid shift, Overlap, Unfilling, Expansion (COUE) framework (Broennimann et al. 2012; Guisan et al. 2014; Liu et al. 2020a; Petitpierre et al. 2012). The COUE framework uses occurrence data and ordination of environmental variables (often primarily climatic) to compare niche centroids, boundaries and breadth between a species' native and non-native range in two-dimensional environmental space. Niche expansion is generally considered the strongest evidence against niche conservatism (Li et al. 2014; Liu et al. 2020a; Petitpierre et al. 2012; Strubbe et al. 2013), which places an emphasis on the environmental limits of species occurrences. Research has called for more comprehensive methods to quantify and compare niche space (Ascanio et al. 2024; Lo Parrino

et al. 2023; Pack et al. 2022; Swanson et al. 2015). However, few studies have compared prevalence or abundance across the range of available environmental conditions to evaluate the consistency of species' responses in different geographies (Ascanio et al. 2024; Hierro et al. 2017).

The ecological processes that underlie shifts or expansion in a species' niche boundaries can also influence how a species responds to its environment within the interior of its niche space (Figure 1; Ascanio et al. 2024). For example, enemy or competitive release could result both in a species' environmental range expanding and/or its occupancy, abundance or demography being less strongly associated with a particular (set of) environmental variable(s) in novel compared to original geographic space (Figure 1b,d; Ascanio et al. 2024; Williams et al. 2010; Woodburn and Sheppard 1996). The use of novel resources can also change environmental associations (Figure 1b,d). Wild boars (*Sus scrofa*), for example, utilise more animal and fungal matter in their non-native range compared to their native range (Ballari and Barrios-García 2014). Multiple mechanisms could drive shifts in resource use, including phenotypic plasticity, admixture or local adaptation (Hofmeister et al. 2023; Kolbe et al. 2004; Tsutsui et al. 2000; Verhoeven et al. 2010; Willoughby et al. 2018). Niche shifts can both expand the environmental conditions that are occupied and alter the associations that organisms have with their environment (e.g., Figure 1d; Ascanio et al. 2024). Geographic differences in how biotic resources or human influences are associated with abiotic gradients also could underlie a lack of niche conservatism, particularly in relation to climate conditions (Cardador et al. 2019; Han et al. 2023; Pineda-Munoz et al. 2021; Strubbe, Jackson, et al. 2015). Ultimately, species may respond differently to similar environmental gradients in their native and non-native ranges with or without conservatism in niche boundaries (Figure 1a versus 1b; Ascanio et al. 2024).

Abundance reflects a population's demographic rates (as well as dispersal), making it a key variable of interest for conservation. For non-native species specifically, abundance underlies ecological and economic impact (Parker et al. 1999; Sofaer et al. 2018). Yet, inference regarding how shifts in the centroid or shape of a species distribution could reflect changing environmental associations with abundance is limited because abundance is not necessarily greatest at the environmental or geographic center



**FIGURE 1** | Four scenarios of how a species' abundance could vary in original and novel geographic space (blue and red circles, respectively) under consistent niche limits and niche expansion. Whether or not a species shifts its niche boundaries in novel geographic space, it could respond to its environment similarly (a and c, with similar slopes) or differently (b and d, with different slopes) in original and novel geographic space. Panel a. represents the assumption of niche conservatism inherent to species distribution and ecological models, and panel c. represents an example of a niche shift as could be identified by ordination-based analyses of niche limits. To date, more research focus has been placed on testing for (in)consistent niche boundaries than testing for consistent environmental responses.

or core of a species' range (Dallas et al. 2020; Fristoe et al. 2023; Martin et al. 2024; Osorio-Olvera et al. 2020; Santini et al. 2018). Thus, direct comparisons of patterns of abundance across environmental space between a species' native and non-native ranges can be complementary with and add rigour to current tests for niche conservatism (Ascanio et al. 2024). These comparisons also could provide insights into why models estimated based on a species' native range show lower performance in the non-native range (Elith et al. 2010; Liu et al. 2020b; Petitpierre et al. 2017; Rousseau and Betts 2022). While extrapolation into new environmental conditions is widely recognised as a major challenge for species distribution and ecological niche model prediction (Elith et al. 2010; Rousseau and Betts 2022), less emphasis has been placed on potential differences in environmental associations across shared environmental conditions in different geographic areas (Ascanio et al. 2024).

Here, we used a combination of two approaches to test for niche conservatism between the native European and non-native North American ranges for European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*). These two bird species are excellent test cases for investigating potential niche differences across continents because they are common and widespread in both their native and non-native ranges (Brlík et al. 2021; Sauer et al. 2017). To test for niche conservatism in these species, we used (1) a COUE analysis to evaluate overall niche similarity based on niche boundaries and position, and (2) generalised linear mixed effects models to assess whether species' abundance-environment relationships differed between the species' native and non-native ranges.

We used long-term monitoring data collected on European starling and house sparrow in Europe and North America to test for both changes in niche dimensions and for differences in how abundance correlates with climate and land cover across

continents. Previous work found climatic niche conservatism for these species in North America (Strubbe, Beauchard, et al. 2015), and we predicted the COUE framework would similarly find conservatism with respect to climate and land cover variables. Because European starling and house sparrow may exhibit local adaptation to temperature clines and/or precipitation in North America (see *Study species* section below; Hofmeister et al. 2021; Schrey et al. 2011; Stuart et al. 2023), we predicted that both species may maintain their abundance across a wider climatic range in North America compared to Europe. For European starling in particular, we expected the species may be abundant in more arid and colder areas of their non-native range than their native range, as is suggested by genotype-environment associations for the species (Hofmeister et al. 2021). Despite striking temporal declines in abundance within both ranges (Burns et al. 2021; Rosenberg et al. 2019), no studies have explicitly compared European starling or house sparrow habitat associations in their native and non-native ranges. However, because both species can utilise a variety of food resources (Cabe 2022; Lowther and Cink 2022), can exhibit substantive behavioural flexibility in novel environments (Lafleur et al. 2007; Martin and Fitzgerald 2005) and strongly associate with humans (Cabe 2022; Lowther and Cink 2022), we expected abundance responses to variables representing potential habitat (i.e., land cover variables) would be similar between their native and non-native ranges.

## 2 | Materials and Methods

### 2.1 | Study Species

European starling and house sparrow are passerines native to Eurasia/Central Asia that occur across every continent except Antarctica. While house sparrow likely evolved in the Middle

East and/or southcentral Asia, the species expanded into Europe thousands of years ago, so we refer to Europe as part of the house sparrow native range (Ericson et al. 1997; Sætre et al. 2012). Both species were introduced to North America in the mid- to late-1800s and are now common and widespread across much of the continent (Cabe 2022; Linz et al. 2007; Lowther and Cink 2022; Robbins 1973). Despite being widespread invaders and human-associated, European starling and house sparrow have experienced substantial population declines in the last 50–60 years in much of their native ranges in Europe and non-native ranges in North America (Burns et al. 2021; Heldbjerg et al. 2019; Rosenberg et al. 2019).

Our predictions that European starling and house sparrow populations may respond differently to similar environmental conditions across continents arise from evidence from morphological and genetic studies that suggest the species may exhibit local adaptation in their non-native North American ranges (Bitton and Graham 2015; Hofmeister et al. 2021, 2023; Johnston and Selander 1964, 1971, 1973; Schrey et al. 2011). For example, in North America, plumage coloration in house sparrow varies geographically in relation to temperature and humidity (Gloger's rule; Johnston and Selander 1964). In addition, recent genetic research on European starling in Europe and North America found genotype-environment associations that suggest potential local adaptation in response to aridity and low temperatures in the non-native range, despite a lack of population structure (Hofmeister et al. 2021; Stuart et al. 2023). Genotype-environment associations have not been examined for house sparrow in North America, but the species has differentiated from native European populations and exhibits genetic diversity that varies with latitude (Liebl et al. 2015; Schrey et al. 2011).

## 2.2 | Avian Survey Data

We used data from two international, volunteer-based breeding bird monitoring programs—the Pan-European Common Bird Monitoring Scheme (Brlík et al. 2021) and the North American Breeding Bird Survey (Sauer et al. 2017)—to quantify the abundance of European starling and house sparrow in their native and non-native ranges, respectively. The Pan-European Common Bird Monitoring Scheme (PECBMS) is a program that started collating data from existing European breeding bird monitoring schemes in 28 countries in the early 2000s to produce national and supranational trends (Brlík et al. 2021). Monitoring methodologies and program initiation year vary by monitoring scheme (Table S1), but methodologies are based on collecting annual counts of common breeding birds (Brlík et al. 2021). The North American Breeding Bird Survey (BBS) is a monitoring program that began in the eastern United States in the 1960s and now covers southern Canada, the United States and northern Mexico. Each North American BBS route contains 50 stops spaced approximately 0.8 km apart at which qualified volunteer surveyors conduct 3-min point counts once per breeding season (Sauer et al. 2017).

We compiled comparable datasets for European starling and house sparrow from the PECBMS and North American BBS continental bird monitoring programs. For Europe, we received

data for 28 monitoring programs (hereafter, monitoring schemes) from 26 countries (Table S1). For North America, we used data from the North American BBS in the United States and Canada, which are publicly available (Pardieck et al. 2020). For both programs, we modelled abundance using data at the level of a site (i.e., the raw data) instead of regional or national/supranational trends produced by the monitoring programs so that we could examine factors influencing local (i.e., site-level) abundance. For the North American BBS, we used data from the first stop of routes that occur on the North American mainland and met program criteria for data quality (e.g., surveys occurred at appropriate times and under appropriate weather conditions; O'Connor et al. 2000; Robbins et al. 1986). We used data from the first stop only because this resolution better aligned with the spatial resolution of the European monitoring data (1–10 km<sup>2</sup> monitoring plots for many European monitoring schemes is smaller than the 39.4-km-long North American BBS routes) and the North American BBS does not publish spatial locations of subsequent stops. For simplicity, we hereafter refer to sampling locations as sites (Figure S1). We note that sites in our European dataset can include either a single sampling location (i.e., a single point count location) or multiple sampling locations within monitoring plots or transects of variable size/length, while in our North American dataset they include only a single sampling location. We retained the sampling effort associated with each monitoring scheme to include in our models (Table S1).

We used survey data (both detections and non-detections) from 1997 to 2018 from all sites and years for which they were available within the species' European and North American distributions (Table S1; Cabe 2022; Lowther and Cink 2022). For European monitoring schemes that used territory mapping, we were provided with the number of territories by year and site (Table S1). For European monitoring schemes that used point count or line transect survey methodologies and conducted multiple surveys in a breeding season (Table S1), house sparrow data were provided to us as a maximum count. For those same monitoring schemes, we used data for European starling at the level of the survey (i.e., instead of aggregated across surveys, as we received for house sparrow) to analyse counts of breeding adults only. European starling gathers into large, mobile flocks of adults and juveniles shortly after breeding (Feare 1984; Kessel 1957) and some European monitoring schemes do not account for flocks in their reported count unit (e.g., by converting total counts that include flocks into a number of pairs). Thus, for those countries that provided survey-level counts and did not formally incorporate flocks into their count unit, we filtered those European starling data to observations that occurred before June to avoid including juveniles in the count data (Table S1). We then averaged European starling counts across surveys and rounded values up to the nearest integer to obtain a count per survey location and breeding season (i.e., year). We did not apply this same filter to our North American dataset as the North American BBS occurs primarily in June (Sauer et al. 2017), but only 0.3% of our European starling dataset from North America (179 records) had a count greater than 5, indicating few flocks were included. Ultimately, our datasets included 229,530 observations from 26,605 sites for European starling and 242,627 observations from 28,652 sites for house sparrow (Figure S1).

## 2.3 | Environmental Data

We generated land cover covariates from the European Space Agency Land Cover CCI Climate Research product (Grekousis et al. 2015; Santoro et al. 2017). This global land cover product contains annual land cover data for over 20 land cover classes from 1992 to 2018 at a 300-m<sup>2</sup> spatial resolution. Six classes in this data product represent potential habitat for European starling and house sparrow: four classes of agriculture ('cropland, rain-fed'; 'cropland, irrigated or post-flooding'; 'mosaic cropland/natural vegetation'; 'mosaic natural vegetation/cropland'), one class for urban areas and one class for grassland (Santoro et al. 2017). To align with the most common sampling design of the monitoring schemes in Europe (Table S1), we quantified the annual proportion of habitat land cover types within a 1-km-radius buffer surrounding the centroid of survey locations in Europe and the first stop of BBS routes in North America (Pellissier et al. 2020). We summed the proportions of the two cropland classes and, separately, the two mosaic cropland and natural vegetation classes to obtain a proportion for cropland and for mosaic cropland and natural vegetation per site and year (1997–2018). Thus, we focused on analysing abundance responses to four focal land cover types—(1) grassland, (2) cropland, (3) mosaic cropland and natural vegetation and (4) urban areas.

Due to evidence of potential local adaptation in response to temperature and precipitation in European starling (Hofmeister et al. 2021) and of latitudinal morphological and genetic gradients in house sparrows (Johnston and Selander 1964, 1971, 1973; Schrey et al. 2011), we tested for different responses to breeding season temperature and precipitation in our models. We used the CHELSA climate monthly time series dataset (30-arc-sec spatial resolution; Karger et al. 2017, 2018) to calculate temperature and precipitation variables for each year from 1997 to 2018. We calculated average daily temperature (hereafter, temperature) as the average of monthly mean daily temperature and cumulative average precipitation (hereafter, precipitation) as the sum of average monthly precipitation during the breeding season within a 1-km-radius buffer surrounding each site. We considered the breeding season to be March–June for European starling and February–July for house sparrow (Cabe 2022; Lowther and Cink 2022); summarised weather data from each year was matched to the year of the avian survey data.

We used multiple software programs to process our climate and land cover variables for inclusion in our statistical models. We used ArcGIS Pro to clip our climate and land cover rasters to each focal continent (Environmental Systems Research Institute 2021). We used Google Earth Engine to reproject the rasters into a global Equal-Area Scalable Earth Grid (EASE-Grid 2.0 Global, CRS code 6933) and to calculate the proportion of our focal land cover and climate variables within a 1-km-radius buffer surrounding each site (shown visually in Figures S2–S7; Gorelick et al. 2017). Thus, despite varied spatial grains in the original data, our climate and land cover were summarised within a consistent spatial extent. We note that the size of our buffers captured an area larger than that surveyed for some monitoring schemes (see 'Area sampled' column in Table S1). However, previous studies using the PECBMS

and/or North American BBS data have found correlations between avian occupancy or abundance and climate and/or land cover in Europe and North America at a 1-km spatial resolution (e.g., LeBrun et al. 2016; Pellissier et al. 2020).

## 2.4 | Niche Analyses

To explore the sensitivity of European starling and house sparrow abundance to the environment, we fit generalised linear mixed effects models in the frequentist framework to species count data and the climate and land cover data from Europe and North America. Bird counts were assumed to arise from a negative binomial distribution and we used a log link function to model the correlation between our response variable (counts of European starling or house sparrow) and focal covariates. Because repeat site visits within a short time period were unavailable for most monitoring schemes, we could not account for detection probability in our models. As a result, our models provide inference on patterns of relative abundance—that is, the number of birds detected—rather than population densities. We use 'relative abundance' to refer to inference based on the raw counts; we did not relativize abundance within communities or across the ranges.

To test for niche conservatism using the COUE framework (Broennimann et al. 2012; Guisan et al. 2014; Liu et al. 2020b), we characterised native and non-native niche space based on the same temperature, precipitation, and land cover variables used in our abundance analysis (abundance analysis variables described below). Using the quantified niches, we calculated the magnitude of the COUE niche dynamics metrics—niche stability, unfilling and expansion (all proportions ranging from 0 to 1). We quantified the change in niche position, also referred to as niche similarity, using the Sørensen's similarity index and quantified niche breadth using the niche breadth ratio *sensu* Liu et al. (2020a). Sørensen's similarity index and the niche breadth ratio both range from 0 to 1; for Sørensen's index, this range reflects zero to complete niche overlap, and for the niche breadth ratio, values near 0 indicate that the breadths of the native and introduced niche are the same. Finally, we performed a niche similarity test to statistically compare observed versus expected Schoener's *D* (Rödder and Engler 2011; Schoener 1968; Warren et al. 2008), which is a measure of overlap of the native and non-native niche space. The niche similarity test evaluates whether the observed niche overlap is greater than expected given the available environment in each range. We include additional details about our COUE analysis in the Data S1.

To explore whether responses of relative abundance to environmental conditions differed in the native versus non-native range, we fit 2-way interactions of continent with a linear and quadratic term for our focal climate and land cover variables in our generalised linear mixed effects models. We also included a 2-way interaction of continent with a linear and quadratic term for year (treated as a continuous variable) to allow population trends to vary nonlinearly by continent. A fixed effect for temporal survey effort and a logged offset term representing area sampled *sensu* Pellissier et al. (2020) were used to account for differences in sampling methodologies between

monitoring schemes within and across continents (Table S1). We included random effects for monitoring scheme (i.e., the 29 monitoring programs for which we had data) and site (sites were surveyed in multiple years). If the interaction of continent with either the linear or quadratic form of a focal covariate was statistically significant, we considered that indicative of statistically significant variation in abundance responses by continent, and we interpreted only those relationships in the results. Correlations between covariates and variance inflation factors were checked and continuous covariates were standardised prior to model fitting (Fox and Weisberg 2019). We fit a model separately to data for European starling and house sparrow. To evaluate the goodness of fit of our models, we calculated Nakagawa's marginal and conditional  $R^2$  values for mixed models (Nakagawa et al. 2017). We also evaluated model diagnostics and tested for evidence of spatial and temporal autocorrelation in model residuals.

We conducted all data processing and statistical analyses for our niche analyses in R (R Core Team 2024). We used the *tidyverse* package to wrangle and visualise data and analysis results (Wickham et al. 2019). For our abundance analyses, we used the *car* package to calculate variance inflation factors (Fox and Weisberg 2019), the *glmmTMB* package to fit our generalised linear mixed effects models (Brooks et al. 2017), the *DHARMa* package to evaluate model diagnostics and test for evidence of spatial autocorrelation (Hartig 2021), the *timetk* package to test for evidence of temporal autocorrelation (Dancho and Vaughan 2022), and the *performance* package to calculate Nakagawa's  $R^2$  (Lüdtke et al. 2021). For our COUE analyses, we used the *ecospat* package to quantify environmental niche space, calculate the COUE niche dynamics metrics, and perform the niche similarity test (Broennimann et al. 2025; Di Cola et al. 2017). We used the *here* and *renv* packages for file and environment management, respectively (Müller 2020; Ushey and Wickham 2025).

### 3 | Results

Niche dynamics metrics from the COUE framework suggested both European starling and house sparrow exhibit niche conservatism in their native European and non-native North America ranges (Table S2 and Figure S8). Both species occupied the same environmental space between the continents (stability = 1) and did not exhibit niche expansion (expansion = 0; i.e., the species did not occupy niche space in the non-native range that was available but unoccupied in the native range; Table S2 and Figure S8). Niche breadth and position were similar between the native and non-native ranges (Sørensen's similarity index ~1 and breadth ratio ~0 for both species) and the similarity tests for niche overlap were statistically significant for both species ( $p < 0.02$  for both species; Table S2).

In contrast to evidence suggesting niche conservatism from the COUE analysis, we found differences in how abundance responded to the environment between the native and non-native ranges for both European starling and house sparrow (Figures 2 and 3 and Tables S3 and S4). European starling relative abundance exhibited a steeper Gaussian relationship

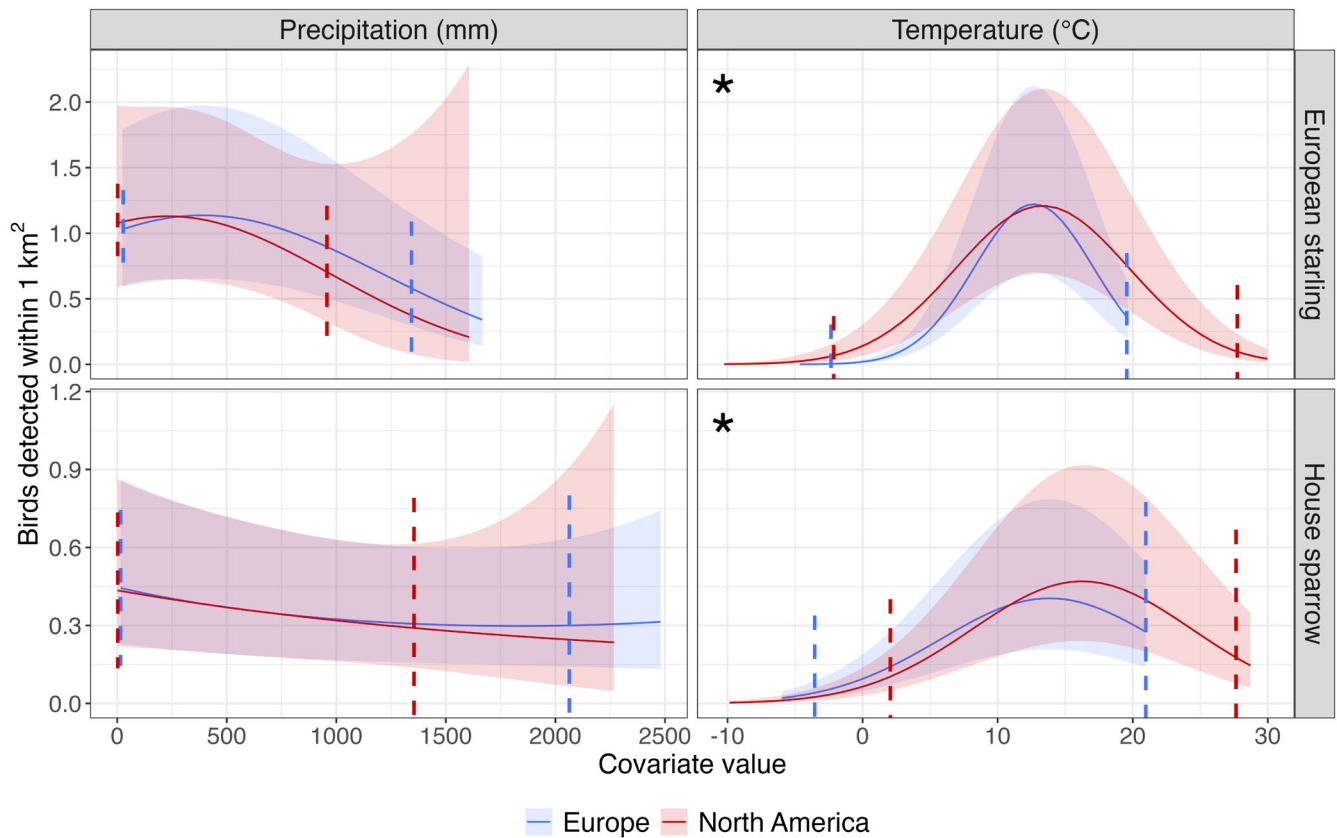
to temperature in Europe, while house sparrow relative abundance exhibited a steeper Gaussian relationship to temperature in North America. Both species also showed evidence of shifts in their climatic range limits, as they were detected across either a wider or different range of precipitation and/or temperature conditions in their non-native North American versus native European ranges (indicated by dashed lines, Figure 2). Areas with wetter conditions that were occupied by both species in their native European ranges were available but unoccupied in their non-native North American ranges. Similarly, house sparrow was detected in areas with cooler conditions in Europe that were available but unoccupied in North America (Figure 2).

We found differences between Europe and North America in the associations between abundance and some land cover types for both European starling and house sparrow (Figure 3 and Tables S3 and S4). European starling relative abundance was more positively associated with mosaic cropland and natural vegetation in Europe while house sparrow relative abundance was more positively associated with this land cover type in North America (Figure 3). House sparrow relative abundance also was more positively associated with the proportion of grassland in Europe than in North America. Responses to cropland and urban areas were similar across continents for both species (Figure 3). Overall, the relative abundance of both European starling and house sparrow was more strongly associated with land cover than climate variables, as models predicted higher relative abundance in relation to land cover than climate gradients (Figures 2 and 3).

We did not find strong evidence of spatial nor temporal autocorrelation in our model residuals for either species (Tables S5 and S6). For European starling, the fixed effects in our model explained 25% (marginal  $R^2 = 0.25$ ) and the random effects explained an additional 68% of the variation in relative abundance (conditional  $R^2 = 0.93$ ). For house sparrow, the fixed effects in our model explained 21% (marginal  $R^2 = 0.21$ ) and the random effects explained an additional 76% of the variation in relative abundance (conditional  $R^2 = 0.97$ ). For both species, the site-level random effect explained more variation in relative abundance than the monitoring scheme random effect (Tables S3 and S4).

### 4 | Discussion

Modelling abundance can reveal differences in the responses of native versus non-native populations within a similar occupied environmental range. Niche dynamics metrics from the COUE framework indicated niche conservatism for both European starling and house sparrow, aligning with previous research on niche dynamics for the species (Strubbe, Beauchard, et al. 2015). However, abundance models revealed continental differences in how the species responded to some of the climate and land cover variables examined in this study (temperature, mosaic cropland and natural vegetation and/or grassland). Together, our findings demonstrate that apparent consistency in niche boundaries does not indicate similar abundance or demographic responses across environmental space. This pattern highlights understudied complexity in

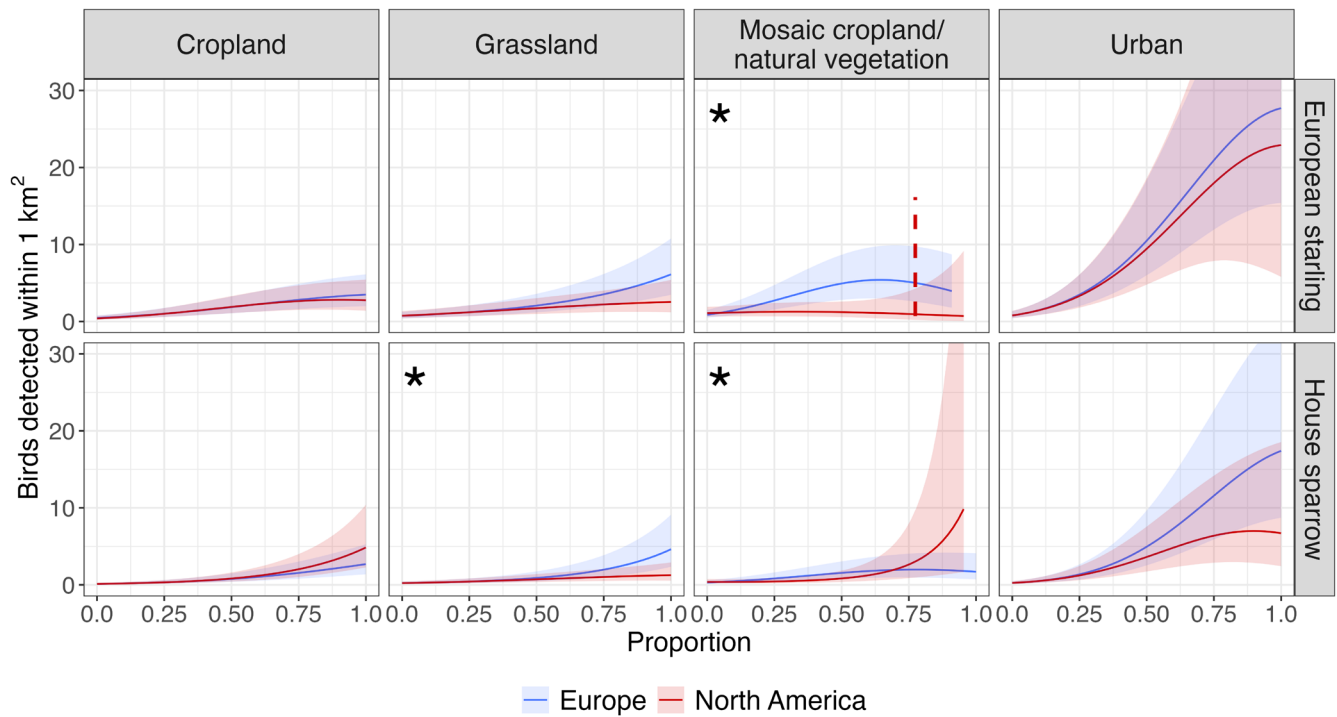


**FIGURE 2** | Predicted number of birds detected within one square kilometre (means and 95% confidence intervals) as a function of breeding season temperature and precipitation within a 1-km-radius buffer around survey locations in Europe and North America for European starling and house sparrow (blue and red and top and bottom rows, respectively). Predictions were generated from generalised linear mixed effects models fit to count data for the species from the two continents from 1997 to 2018. Asterisks denote covariates for which the interaction of continent (Europe or North America) and the focal covariate (either the linear or quadratic form) was statistically significant ( $\alpha=0.05$ ). Dashed vertical lines denote the limits of species' detections, while predictions were made to the limits of available environmental space for each species and continent represented in our datasets. Precipitation limits differ between species because they were summarised over different months.

niche dynamics and suggests that ordination-based tests for niche conservatism can be complemented by quantifying variation in abundance along key environmental gradients (Ascanio et al. 2024; Pack et al. 2022).

We found that continental differences in abundance responses varied by focal environmental covariate and reflected the full spectrum of potential abundance-environment responses conceptualised in Figure 1a–d. For climate, we predicted European starling and house sparrow populations would respond differently to breeding season temperature and precipitation across continents. This prediction was supported by our findings for responses to average breeding season temperature. However, despite evidence that European starling may have adapted to colder and drier environments in North America following colonisation (Hofmeister et al. 2021), we found the species occupied similarly cold and arid areas on both continents. European starling and house sparrow populations also responded similarly to cumulative breeding season precipitation across continents, in contrast to our prediction. Yet, wet conditions occupied in Europe were available but not occupied in North America—that is, potential niche unfilling. Given the long residence time in North America and high dispersal capabilities of these species, this pattern is unlikely to simply reflect a dispersal lag due to

invasion dynamics. Range unfilling under the wettest conditions also was not simply due to a lack of human-created environments, as 25% and 11% of these sites had some urban land cover in their surroundings for the European starling and house sparrow datasets, respectively. Both European starling and house sparrow are considered strongly human-associated and house sparrows are considered commensal with humans (Cabe 2022; Lowther and Cink 2022; Ravinet et al. 2018; Sætre et al. 2012), and research on urban environments more broadly has found that these environments can support species' persistence in otherwise unsuitable climates via providing concentrated supplemental food resources (e.g., bird feeders) and/or generating microclimates, such as providing warmer or more stable temperatures (Deshpande et al. 2025; Kempainen et al. 2024). Yet, the strength of our focal species' associations with humans varies across the species' native and non-native ranges. A recent analysis of non-native bird species' associations with humans found that in Europe, house sparrow was more closely associated with humans than European starling, and both species were equally strongly human-associated in North America (Marjakangas et al. 2024). In our study, European starling and house sparrow populations responded to some human-modified land cover types more strongly in Europe and responded to others more strongly in North America.



**FIGURE 3** | Predicted number of birds detected within one square kilometre (means and 95% confidence intervals) as a function of land cover composition within a 1-km-radius buffer around survey locations in Europe and North America for European starling and house sparrow (blue and red and top and bottom rows, respectively). Predictions were generated from generalised linear mixed effects models fit to count data for the species from the two continents from 1997 to 2018. Asterisks denote covariates for which the interaction of continent (Europe or North America) and the focal covariate (either the linear or quadratic form) was statistically significant ( $\alpha=0.05$ ). Both species occurred across the full range of proportion values in our datasets for cropland, grassland and urban land cover types on both continents, with the exception of mosaic cropland/natural vegetation; in North America, European starling was not detected in sites with greater than ~77% mosaic vegetation (dashed line).

Combining approaches to quantify environmental niche space can be useful when there is interest in both an overall summary of change in niche dimensions as well as a more nuanced view of niche dynamics based on responses to specific environmental variables (Ascanio et al. 2024; Pack et al. 2022). To translate information about niche change into practical insights—for example, to inform management actions that support populations of native species or reduce impacts from populations of non-native species—it is essential to quantify species' responses to individual environmental gradients (Ascanio et al. 2024). In addition, and consistent with our findings, previous research has found that compared to methods that quantified niche space as multidimensional (rather than two-dimensional from ordination) or as species' responses to environmental gradients, the COUE approach suggested niche conservatism while the other methods found evidence of niche expansion or divergence (Ascanio et al. 2024; Pack et al. 2022). Analytical approaches that quantify both change in overall niche dimensions and species' responses to specific environmental gradients could advance our understanding of niche conservatism while also generating insights that could inform conservation planning and non-native species management.

Variation in how species respond to their environment across geographic space raises questions about the transferability of models focused on species' niches and distributions (Atwater et al. 2021; Elith et al. 2010; Liu et al. 2020b, 2022; Rousseau and Betts 2022). Violations of the niche conservatism hypothesis as identified by the COUE framework (i.e., niche shifts) can

affect model transferability (Atwater et al. 2021; Liu et al. 2022). Studies have highlighted pervasive challenges with transferability and extrapolation of species distribution models generally (Howard et al. 2023; Huang et al. 2023; Liu et al. 2020b), with a focus on poor performance due to extrapolation in environmental space (Elith et al. 2010). Intraspecific variation in environmental responses may also contribute to poor transferability (Collart et al. 2020; Rousseau and Betts 2022), especially when species enter novel geographic space within their environmental range boundaries. For example, Sofaer et al. (2018) found that errors from species distribution models were more common in areas with more similar conditions to where a species occurred than in more distant environmental space, which was dominated by true negatives. Many aspects of the environment differ across geographies even when climate conditions and broad land cover categories are similar, which complicates the ability to anticipate when models will or will not transfer reliably.

The feasibility and utility of conducting analyses of species abundance–environment relationships will depend on data availability and the intended purpose of the analysis. We quantified native and non-native niche space for European starling and house sparrow populations in Europe and North America because long-term abundance datasets were available for these continents and the species are well-established in their non-native ranges in North America (Cabe 2022; Lowther and Cink 2022). Still, our abundance data did not include the entirety of the species' native and non-native ranges, highlighting pervasive availability limitations

for abundance data and constraining interpretation of our findings to our focal spatial extent. The challenge of data availability is even more pronounced for other demographic and fitness metrics, which could provide a link to mechanisms of niche conservatism or divergence and thus a stronger basis for inference than macroecological studies can offer alone. Measures of abundance (and prevalence) can also be less reliable at invasion fronts, and within the invaded range more broadly, due to lag times in population growth and dispersal (Bradley et al. 2018).

The assumption of niche conservatism is foundational to analytical methods for quantifying species' responses to global change, and our findings reinforce that how species respond to environment gradients may not be consistent across geographic space (Ascanio et al. 2024; Connor et al. 2019; Crosby et al. 2019; Rousseau and Betts 2022). Because our focal species are human-associated (Cabe 2022; Lowther and Cink 2022) and European colonisation of North America altered Indigenous urban and agricultural environments to be like those in Europe, other species may show even more striking differences in their responses to the environment in their native and non-native ranges. Further investigation into (1) the pervasiveness of differences in species' abundance responses to the environment between their native and non-native ranges and (2) whether the degree of similarity in environmental range boundaries correlates with similarity in abundance responses to shared environmental space would improve the reliability of species distribution and ecological niche models. With a more nuanced and comprehensive examination of the niche concept (Ascanio et al. 2024; Pack et al. 2022; Swanson et al. 2015), we can improve our ability to predict how biological communities will be sensitive or resilient to ongoing global change.

## Author Contributions

K.P.D., H.G.S., H.H. and L.P. designed the study; A.G., A.A., L.B., T.C., D.P.E., B.F., J.A.K., P. Kmecl, P. Kurlavičius, A. Lehtikoinen, Å. Lindström, I.J.Ø., J.R., N.S., T.S., C.A.M.T. and T.V. collected and/or compiled data; K.P.D. and H.R.S. performed modelling work; K.P.D., H.R.S., H.G.S., H.H. and L.P. interpreted initial results. K.P.D. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data and code that support the findings of this study are available in Zenodo ([10.5281/zenodo.14920997](https://doi.org/10.5281/zenodo.14920997)).

## Peer Review

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ddi70100-sup-0001-Supinfo.docx.

## Biography

**Kristin P. Davis** is a population ecologist and conservation scientist. Her research primarily has focused on investigating patterns of species–environment relationships for bird species from local to international scales. She also has conducted research related to private lands conservation, conservation social science, and equity in mental health support and resources for graduate students in the life sciences.