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RESEARCH ARTICLE

Environmental, geographical and time-related impacts on avian malaria infections in native and introduced populations of house sparrows (*Passer domesticus*), a globally invasive species

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Abstract

Aim: The increasing spread of vector-borne diseases has resulted in severe health concerns for humans, domestic animals and wildlife, with changes in land use and the introduction of invasive species being among the main possible causes for this increase. We explored several ecological drivers potentially affecting the local prevalence and richness of avian malaria parasite lineages in native and introduced house sparrows (*Passer domesticus*) populations.

Location: Global.

Time period: 2002–2019.

Major taxa studied: Avian *Plasmodium* parasites in house sparrows.

Methods: We analysed data from 2,220 samples from 69 localities across all continents, except Antarctica. The influence of environment (urbanization index and human density), geography (altitude, latitude, hemisphere) and time (bird breeding season and years since introduction) were analysed using generalized additive mixed models (GAMMs) and random forests.

Results: Overall, 670 sparrows (30.2%) were infected with 22 *Plasmodium* lineages. In native populations, parasite prevalence was positively related to urbanization index, with the highest prevalence values in areas with intermediate urbanization levels. Likewise, in introduced populations, prevalence was positively associated with urbanization index; however, higher infection occurred in areas with either extreme high or low levels of urbanization. In introduced populations, the number of parasite lineages increased with altitude and with the years elapsed since the establishment of sparrows in a new locality. Here, after a decline in the number of parasite lineages in the first 30 years, an increase from 40 years onwards was detected.

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Main conclusions: Urbanization was related to parasite prevalence in both native and introduced bird populations. In invaded areas, altitude and time since bird introduction were related to the number of *Plasmodium* lineages found to be infecting sparrows.

KEYWORDS
haemosporidian parasites, mosquito-borne pathogens, *Plasmodium*, urbanization index, vector-borne diseases

1 | INTRODUCTION

Humans, domestic animals and wildlife are at risk of vector-borne diseases caused by pathogens transmitted by blood-feeding arthropods, such as mosquitoes, ticks and fleas (Semenza, 2016). Globally, over 80% of humans are threatened by vector-borne diseases, including malaria, West Nile virus disease, zika, chikungunya, dengue, and yellow fever (Franklinos et al., 2019; Kilpatrick & Randolph, 2012). Changes in human demography and the current unprecedented degradation of the environment affect transmission rates and incidences of many of these diseases in ways that are still largely unknown (Bedford et al., 2019; Ramalho-Ortigao & Gubler, 2020).

Many biological factors that drive the emergence and spread of vector-borne diseases are similar for pathogens that infect humans, livestock and wildlife (Daszak et al., 2000). For instance, urbanization (Ferraguti et al., 2020), as well as other abiotic and biotic factors (Chapa-Vargas et al., 2020), may influence the transmission of vector-borne pathogens, but comprehensive studies are necessary to fill the knowledge gaps on how global change processes may disrupt vector–host–parasite interactions (Clark et al., 2014; Ellis et al., 2018). This uncertainty applies to vector-borne blood parasites of wildlife, such as the avian haemosporidian parasites of the genus *Plasmodium*. A better understanding of how global change, including landscape urbanization, affects parasite transmission patterns can finally shed light on processes affecting other vector-borne pathogens of public or animal health importance.

The potential to acquire haemosporidian parasites differs among host bird species (Atkinson et al., 2001) and individuals (Valkiūnas, 2005) based on their exposure to vectors or parasites and differences in susceptibility to infection. Indeed, these wildlife blood parasites are relatively easy to study without disruption to their host populations (Valkiūnas, 2005), as their transmission dynamics are free of confounding effects (e.g., socio-economic factors) such as those that affect human malaria infections (Wilson, 2001). Hence, they serve as excellent models to investigate the influence of environmental factors (e.g., altitude, urbanization) on vector-borne disease dynamics (Rivero & Gandon, 2018).

Haemosporidian parasites have been recorded from most terrestrial areas, except for polar latitudes (Durrant et al., 2006; Martínez et al., 2018; Marzal et al., 2011; Merino et al., 2008; Oakgrove et al., 2014; Szöllosi et al., 2011; but see Fecchio et al., 2020), and their incidences vary along altitudinal and latitudinal gradients depending on the hosts, landscape, and environmental conditions (Chapa-Vargas et al., 2020). Altitude is an important driver of the prevalence of avian malaria parasites, as thermal constraints and potential vector distribution tend to reduce *Plasmodium* prevalence with increasing elevation (Ishtiaq & Barve, 2018; Lynton-Jenkins et al., 2020; van Rooyen et al., 2013). For instance, the prevalence of the genera *Plasmodium* and *Haemoproteus* has been shown to be lower at higher altitudes (González et al., 2015; Rodríguez et al., 2009), with a greater limitation of *Plasmodium* parasites (Harrigan et al., 2014; van Rooyen et al., 2013). However, a cautious interpretation of such generalizations is required because parasite assemblages at high elevations often differ from those found in lowlands (Chapa-Vargas et al., 2020, see also Atkinson et al., 2014).

Finally, the diversity of morphologically described haemosporidian species and genetic lineages, that is, different genetic strains that can have diverse effects on hosts' health (Palinauskas et al., 2018), is highest throughout the tropics (Garcia-Longoria et al., 2022; Valkiūnas, 2005). Studies analysing the synergic effects of latitude and altitude on the prevalence and richness of avian haemosporidians at global scale would be of interest, particularly including tropical geographical areas (Chapa-Vargas et al., 2020).

Accidental and intentional introduction of parasites and competent vectors, as well as land changes associated with human activities (e.g., deforestation, agricultural development, and urbanization), may also influence the dynamics of haemosporidian parasite infections by affecting the distributions of pathogens (Atkinson & Samuel, 2010) and vectors (Ferraguti et al., 2016; van Hoesel et al., 2019), as well as those of their hosts (Hernández-Lara et al., 2020). In this study, we analyse the role of urbanization in the invasion process of haemosporidian parasites, whereby cities are usually associated with a reduction in host biodiversity (Seress & Liker, 2015), with particular negative impacts on native species (McKinney, 2002; Sol et al., 2014). For centuries, humans have facilitated the invasion of introduced species, either purposefully or accidentally (Mack et al., 2000). However, whether urbanization favours the transmission of haemosporidian parasites in their avian hosts or reduces parasite prevalence and diversity remains to be determined.

House sparrows (*Passer domesticus*, hereafter 'sparrows') are native to Eurasia and North Africa, but the species has achieved near-global range expansion during the last two centuries (Lowther & Cink, 2020). Sparrows were used as model species because they are

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found in various climates and habitats, being considered an excellent urban exploiter since their occurrence is routinely tied to human settlements (Meillère et al., 2015). Moreover, this species is commonly found to be infected by avian malaria parasites (Bensch et al., 2009; Bichet et al., 2013; Ferraguti et al., 2018; Marzal et al., 2011; Valkiūnas et al., 2006).

Marzal et al. (2011) analysed the prevalence and genetic diversity of haemosporidians in native and introduced house sparrows, showing differences in diversity and prevalence of haemosporidians between native and colonized regions. Here we expand upon this previous study at a global scale using an updated and larger database to evaluate the role of (a) environmental (urbanization index and human density); (b) geographical (altitude, latitude, hemisphere); and (c) temporal (breeding/non-breeding seasons, years elapsed since host introduction) drivers of global variation in prevalence and richness (i.e., the number of observed lineages) of avian *Plasmodium* in house sparrows. Also, we extend previous analyses to examine differences in lineage identities between introduced and native bird populations, rather than in the average number of *Plasmodium* found between the two populations.

2 | MATERIALS AND METHODS

2.1 | Study areas and bird sampling

Tshe dataset on prevalence and lineage richness of malaria parasites used in this study was partially compiled by Marzal et al. (2011) and further extended to include new data from 436 individuals from 11 additional populations (Ewen et al., 2012; Ferraguti et al., 2018; Garcia-Longoria et al., 2022; Hellgren et al., 2011; Ishtiaq et al., 2007; Marzal et al., 2011, 2018; Muriel et al., 2021). These new data added an extra 20% to the total sample size and included remote and poorly investigated tropical areas of western South America and Southeast Asia (see Supporting Information Table S1 for further information on the additional localities), thus expanding the global scope of the analyses. Overall, birds were captured by different teams in the framework of different surveys, from 2002 to 2019 at 69 sampling localities distributed over 27 countries (all continents except Antarctica, Figure 1). Bird surveys were conducted from February to November in the Northern Hemisphere and from January to December in the Southern Hemisphere thus covering both the breeding and non-breeding seasons of the species (Supporting Information Table S1). Following standard ringing protocols, birds were captured using mist nets, individually marked with a metal ring (Svensson et al., 2009), a blood sample was obtained from the brachial or jugular vein of each individual (20–40 μL), and released at the capture site.

House sparrow populations were then classified as native or introduced based on historical records in each region as determined from the literature (Supporting Information Table S1 summarizes the year of introduction at each sampling site where house sparrows were considered introduced).

2.2 | Molecular detection of *Plasmodium* parasite infections

DNA from bird blood samples was extracted using different standard procedures (Ferraguti et al., 2018; Marzal et al., 2011), and the screening of infection status was conducted at different labs by different research teams in the context of other studies. Briefly, the prevalence of infection and the identity of parasite lineages were determined through the amplification of a fragment of the cytochrome *b* gene using the nested-polymerase chain reaction (nested-PCR) protocol described by Hellgren et al. (2004). All PCR procedures included positive and negative controls. Amplification success was evaluated by running 2.5 μL of the final PCR product on a 2% agarose gel. Parasites detected by positive amplification by PCR were sequenced using the procedures described by Bensch et al. (2000). For this study, we focused on *Plasmodium* spp. parasites only and, after parasite genus identification, the identity of the lineages was determined by comparison of the sequences with those available in public databases (i.e., GenBank DNA sequence database, National Center for Biotechnology Information Blast). For the estimation of parasite lineage richness, sequences differing by at least one nucleotide substitution were considered to represent evolutionarily independent entities (lineages; Bensch et al., 2004; Ricklefs et al., 2005).

2.3 | Environmental and time-related variables

Geographical variables such as altitude, absolute value of the latitude, and hemisphere (North/South) were recorded for each sample site (Supporting Information Table S1). In addition, an urbanization index for each of the sampled localities was calculated using the URBANISATION SCORE software (available at https://keplab.mik.uni-pannon.hu/en/urbanization-index). This approach, based on the quantification of the percentage of area covered by different land uses in a defined parcel (e.g., building, roads, agriculture, vegetation, forest, water, among others), has been extensively used in studies of urban ecology (Jiménez-Peñuela et al., 2019; Meillère et al., 2015, 2017; Salmón et al., 2018). Briefly, the software takes satellite images from Google Maps covering an area of 1 km^2 around each bird-sampling point, and these images are divided into 10 × 10 cells of 100 metres. On each image, we manually designated four training points for each landscape class (vegetation, water sources, buildings, paved surface cover and others) and the software estimates the surface for each 100 × 100 m cell occupied by buildings, vegetation and pavement. The urbanization index score generated by the program corresponds to the first principal component (PC1) of a principal components analysis (PCA) calculated based on the combination of five landscape variables, specifically: the number of cells with high building density (> 50% cover, range 0–100); number of cells with high vegetation density (> 50% cover, range 0–100); number of cells with paved surface (range 0–100); mean building density score (range 0–2) and mean vegetation density score (range

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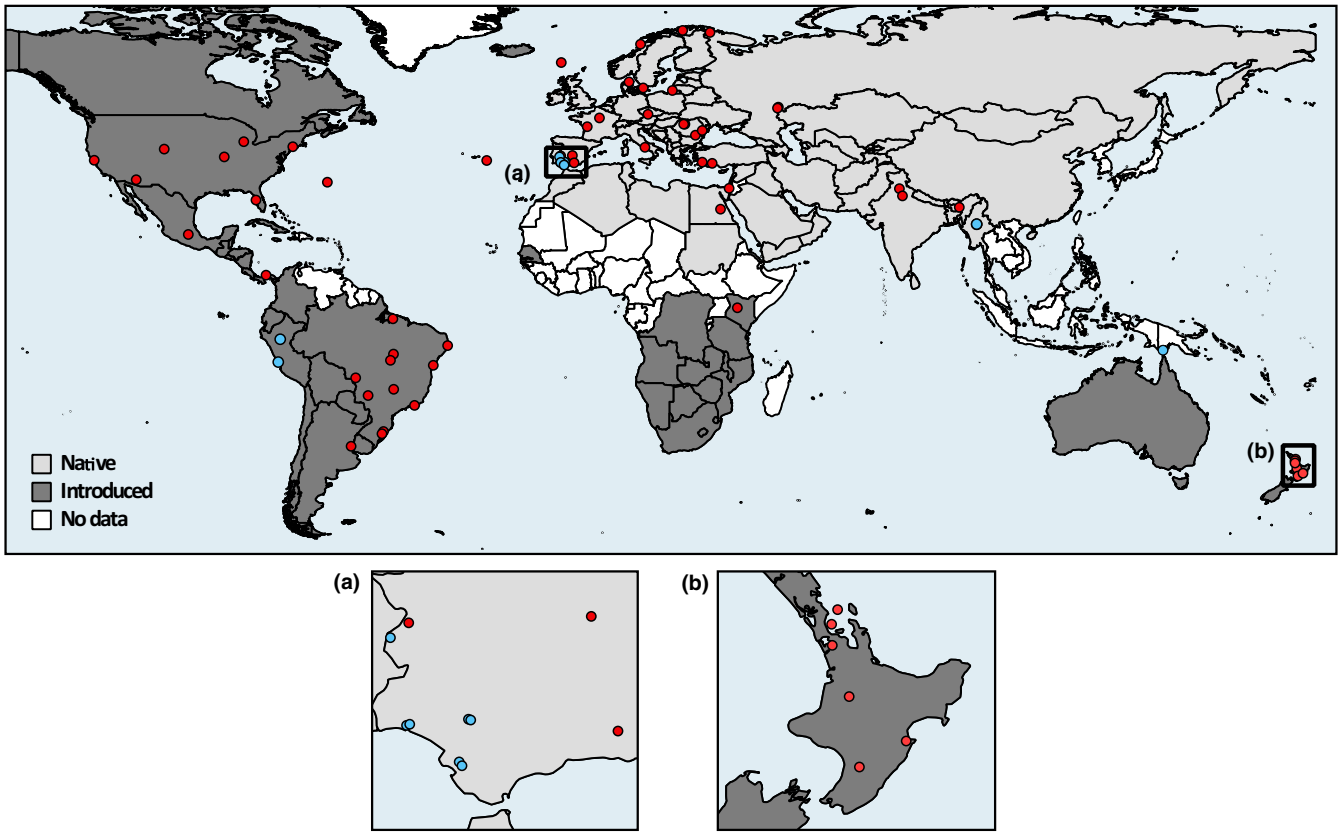


FIGURE 1 Distribution of the 69 sampling localities of house sparrows. Red dots represent localities sampled in Marzal et al. (2011); blue dots are new localities included in this study. Light and dark grey areas show countries sampled in native and introduced ranges, respectively, white areas are countries where no data have been recorded (http://datazone.birdlife.org/species/factsheet/house-sparrow-passer-domesticus/distribution). Map created by QGIS. 3.12.0 (2020). QGIS Geographic Information System, Open-Source Geospatial Foundation Project, http://qgis.org.

0–2). The urbanization index ranged from negative values for less intensely urbanized areas to positive values for more intensely urbanized areas. The scores obtained in this analysis are relative to the localities included in it (range −3 to +4 for our localities). See Czúni et al. (2012), Lipovits et al. (2015) and Seress et al. (2014) for further details of the procedure. The advantage of using this urbanization metric lies in the indexes assigned, which are based on the comparison of all localities included in the analyses, thereby homogenizing the values independently of the study of origin. In addition, human density was measured as the number of inhabitants per km^2 calculated on the municipal area of each sampling locality from available national census data in the same year as the sparrow sampling or, alternatively, from the closest year with available data (see Supporting Information Table S2 for further information). We did not find evidence for collinearity according to the variance inflation factor (VIF) between urbanization index and human density (Zuur et al., 2010) suggesting that both variables may reflect different components of urban areas. Indeed, for example, the urbanization score is related to the built-up area without considering building height, a variable that will strongly influence population density.

For the introduced bird populations, the years elapsed since a sparrow population was first recorded in a given locality were calculated by subtracting the years of the first observation of a house sparrow in the locality from the year of sampling (see Supporting Information Table S1 for further details on the first record of birds in each locality). Finally, for each locality, depending on the place of bird origin and the breeding site, we considered whether sampling occurred during the breeding season or not following Lowther and Cink (2020).

2.4 | Statistical analyses

We used generalized additive mixed models (GAMMs) and random forest (RF) regressions to evaluate the influence of environmental, geographical and temporal predictor variables on *Plasmodium* prevalence and the number of observed lineages per locality (i.e., richness). GAMMs and RFs are both computationally efficient and can automatically model high-order interactions and nonlinear responses (Breiman, 2001; Lin & Zhang, 1999). In particular, GAMMs allow statistical tests based on the *p*-value of the different variables and provide better predictions by using an additive model that varies a single covariate while keeping the other variables constant. Conversely, RF models do not assume any specific probability distribution for the variables, and can include potentially complex interactions between all covariates (Zhang et al., 2021).

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The prevalence of the parasites was estimated using. a bivariate model that utilized a two-column matrix to represent the number of infected birds in a population in relation to the number of uninfected birds. By using the *cbind* function, *Plasmodium* prevalence was modelled with binomial error and a ´logit´ link function, inherently controlling for sample size. By contrast *Plasmodium* richness, measured as the number of observed lineages per locality, was analysed with a Poisson distribution with a 'log' link function controlling for sample size as an independent variable. Collinearity between independent variables was checked using the VIF (Zuur et al., 2010), and no evidence for collinearity was found (VIF < 3 in all cases). The significance of each variable was tested using a Type II Wald chi-square test and Type-III sums of squares (when interactions were in the model). All analyses were performed in R v. 4.2.0 (R Development Core Team, 2020).

Independent models were performed on the native (n = 35) and introduced (n = 34) bird datasets to investigate the effects of environmental, geographical and temporal drivers on the prevalence and number of observed lineages of *Plasmodium* spp. per locality because significant differences were found between the two populations (Marzal et al., 2018; Schrey et al., 2011). Altitude (continuous), the absolute value of latitude (continuous), urbanization index (continuous), human density (continuous) and reproductive season (categorical: breeding/non-breeding) were included as independent variables. For the introduced bird populations, years since the bird introduction (continuous), and the hemispheres (categorical: North/South) were included to account for (a) colonization time, and (b), differences between hemispheres. The variable country (categorical) was included in all models as a random factor to account for the geographical stratification of the samples. Sample size (continuous) was included in models of *Plasmodium* lineage richness to account for sampling size effects. For each GAMM, the adjusted R^2 for the model is shown, defined as the proportion of variance explained where original and residual variance are both estimated using unbiased estimators. RF regression analyses was based on 1,000 trees and stratified by the Country factor (Breiman, 2001). In the parasite prevalence regression, this variable was modelled as a percentage, always weighting the regression by the sample size. The mean of the squared residuals of the RF regression was used to validate the models, where small values mean that predicted values were close to the actual ones, thus considering the results reliable.

Finally, to determine and graphically represent the degree of associations between the *Plasmodium* lineage composition in native and introduced populations, we (a) built a heat map showing the frequency of each parasite lineage at each locality (created using the function *heatmap.2* from the package *ggplot2*), and (b) conducted a correspondence analysis (CA) of each lineage abundance at each sampling locality, which makes no assumption about distributions (Sourial et al., 2010). Only localities with more than one infected individual were considered. Axis scores from this ordination represent a gradient of similarity of parasite composition among localities.

3 | RESULTS

The dataset included samples from 2,220 house sparrows. Overall, 670 birds (30.2%) were infected by 22 *Plasmodium* parasite lineages. The number of observed lineages per sampling locality ranged from one to seven (for further information, see lineage richness in Supporting Information Table S1). The most common lineage was SGS1 (found in 31 localities), followed by GRW11 (20 localities), GRW04 (18 localities), PADOM01 (11 localities), PADOM02 (11 localities) and COLL1 (10 localities). All other lineages were observed in fewer than 10 localities. Nine lineages were only found in native populations, and nine only in the introduced populations. Four lineages were found in both introduced and native birds, with SGS1 and PADOM1 mainly recorded in native populations, GRW04 in introduced populations and GRW06 was sporadically observed in both populations (Figure 2).

The two first axes of the CAs on lineage distribution accounted for 40.37% of the variance (20.71% and 19.66%, respectively). The lineage composition of *Plasmodium* in native and invasive house sparrow populations differed significantly (χ^2 = 3,325.618, d.f. = 816; p < .001; Figures 2 and 3). In addition, within the introduced group, localities were grouped into four distinct clusters based on their geographical distribution, which were also associated with different predominant lineages (Figure 3).

3.1 | Models for native sparrow populations

GAMMs revealed a nonlinear association between latitude and both prevalence and lineage richness, with an increase up to approximately 45 degrees followed by a decline (Supporting Information Figure S1a,c). *Plasmodium* prevalence also increased significantly as the urbanization index increased (Table 1, Supporting Information Figure S1b). In addition, RF models revealed that parasite prevalence reached its maximum at intermediate levels of the urbanization index (Figure 4a), supporting the pattern observed in the GAMM analysis with the latitude for both prevalence (Figure 4b; R^2_{RF} = 13.66%, mean of the squared residuals = 0.06) and lineage richness models (Figure 4c; R^2_{RF} = 37.29%, mean of the squared residuals = 2.27).

3.2 | Models for introduced sparrow populations

GAMMs identified only a nonlinear relationship between *Plasmodium* prevalence and the years elapsed since the introduction of sparrows in a locality in introduced sparrow populations (Supporting Information Figure S2a). Overall, parasite prevalence was positively associated with the urbanization index and the years elapsed since bird introduction (Table 2, Supporting Information Figure S2a,b). Parasite lineage richness was also positively related to the years elapsed since sparrow introduction (Supporting Information Figure S2c), in addition to the altitude (Table 2, Supporting Information Figure S2d). However, patterns shown by the RF models showed

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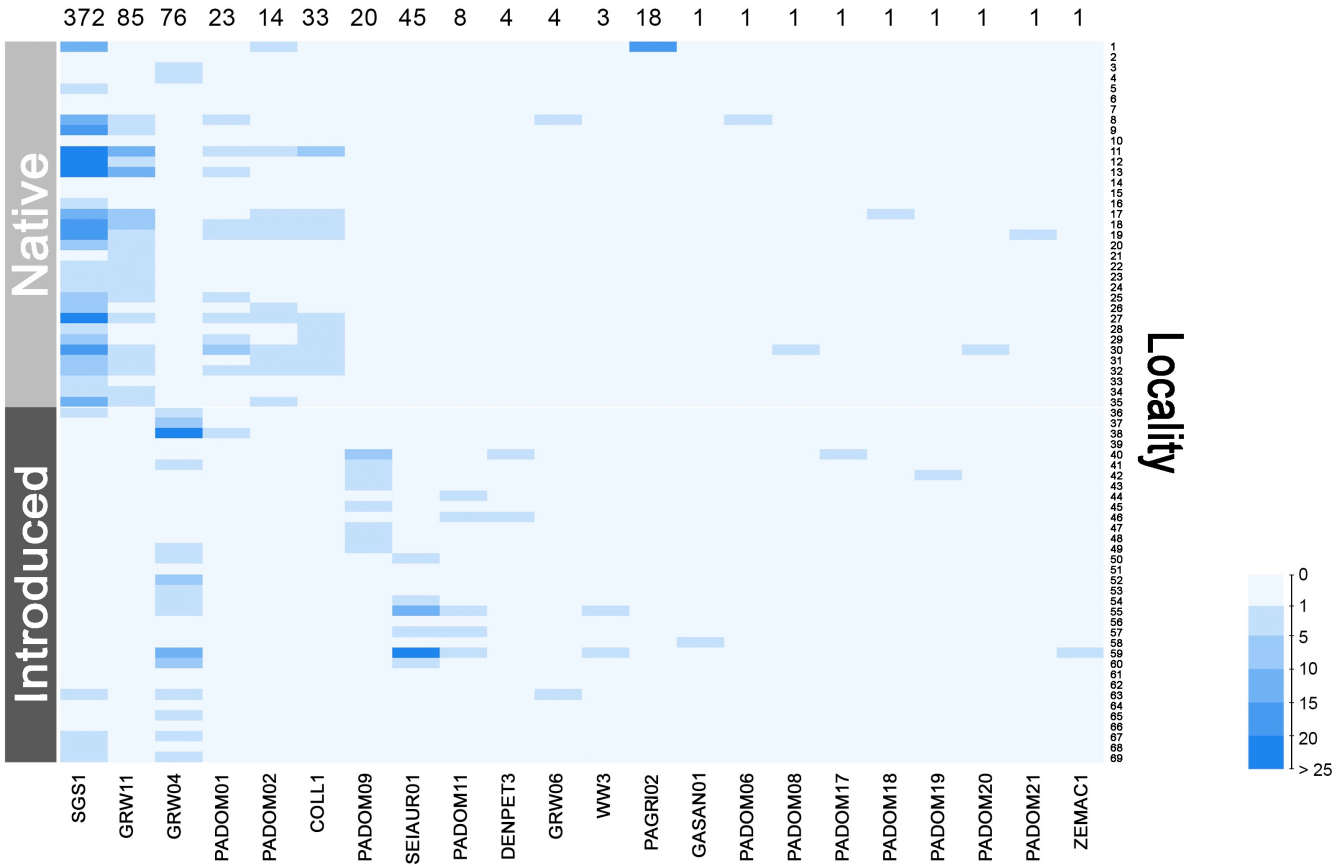


FIGURE 2 Heat map of the number of Plasmodium lineages found infecting native and introduced bird populations throughout the sampling localities. The lineages were named according to MalAvi. Number above the map indicate infected birds by each lineage. Sampling localities were ordered according to the ID number included in Table S1. Legend colour indicates the lineage frequency (number of birds infected per lineage) found on each locality. Lineages were classified according to two criteria, both for native and introduced populations: firstly, by the highest number of infected birds per locality and, secondly, by their occurrence in more localities. When the same numbers of lineages were found, they were sorted alphabetically. For further information see Table S3.

higher values of malaria prevalence associated with the highest and lowest values of the urbanization index (Figure 5a). Also, a sharp increase after 100 years of invasion was found between *Plasmodium* prevalence and the number of years since the introduction (R^2_{RF} = 8.97%, mean of the squared residuals = 0.04, Figure 5b). A similar increase was also observed between richness of lineages and the years since the first record of house sparrows in a locality, with reduction over the first 30 years followed by a positive trend from 40 years onwards (Figure 5c). Finally, the RFs showed that the number of *Plasmodium* lineages per locality increased with altitude (range 2–2,232 m a.s.l.), especially above 200 m a.s.l. (i.e., logarithmic values of 2.4; Figure 5d; R^2_{RF} = 3.47%, mean of the squared residuals = 1.29).

4 | DISCUSSION

Using an extensive worldwide sampling of native and introduced house sparrow populations we tested the association between different environmental, geographical and temporal factors and the prevalence and lineage richness of *Plasmodium* infections. To our knowledge, general patterns of infections have rarely been characterized in the same focal bird species as in the current study (but see Colautti et al., 2005). Indeed, few studies have compared the haemosporidian parasite infections in native and introduced populations within the same host species at a regional (Ishtiaq et al., 2006; Lewicki et al., 2014), inter-continental (Antonini et al., 2019; Clark et al., 2015; Lima et al., 2010; Marzal et al., 2018; Prüter et al., 2020) or global scale (Marzal et al., 2011).

Avian malaria parasites vary in their ability to infect different bird species (Zhang et al., 2014), with some lineages being extreme generalists, such as *Plasmodium relictum* GRW04, the dominant lineage found in introduced populations and the second most common haemosporidian lineage worldwide (e.g., MalAvi, Grand Lineage Summary table, accessed on 27 July 2022; Bensch et al., 2009). By contrast, *P. relictum* lineage SGS1, the most prevalent avian malaria lineage in the world (Bensch et al., 2009; Martínez-de la Puente et al., 2021), was the most abundant one in native populations. Lineage SGS1 was occasionally detected in the introduced populations, indicating that it might have been brought to the areas they occupy by infected birds. However, the results of our CAs reinforce two major associations, with a sub-aggregation within the introduced group

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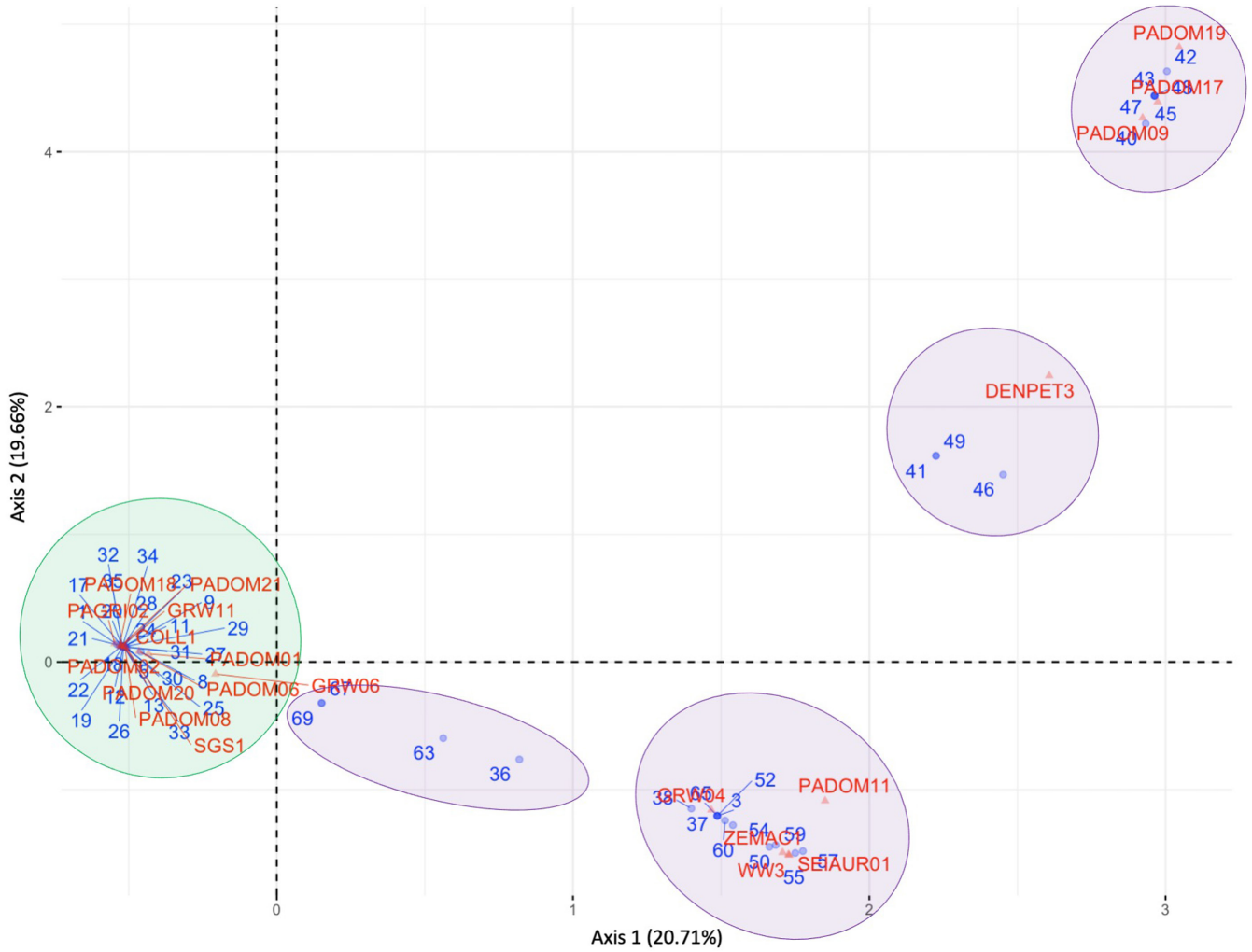


FIGURE 3 Correspondence analysis map of *Plasmodium* lineages (red triangles) and sampling localities (blue dots). Localities from 1 to 35 represent native house sparrow populations (green circle), localities from 36 to 69 the introduced populations (purple circle/ovals).

TABLE 1 Results of the generalized additive mixed models (GAMMs) evaluating the relationships between the prevalence and the number of observed lineages per locality (i.e., richness) of avian malaria *Plasmodium* and environmental, geographical and time-related variables for native house sparrow populations ($n = 35$).

Independent variable	Prevalence				Richness of lineages			
	Estimate (± *SE*)	χ^2	*z*	*p*	Estimate (± *SE*)	χ^2	*z*	*p*
Altitude	−0.001 (0.001)	0.696	−0.835	.404	−0.004 (0.087)	0.204	−0.051	.959
Human density	−0.054 (0.0043)	1.610	−1.269	.204	0.004 (0.073)	0.001	0.060	.952
s 'Latitude'	–	14.140	–	.002	–	13.870	–	.003
Sampling size[b]	–	–	–	–	0.004 (0.003)	1.467	1.342	.180
Season (breeding)	0.000[a]	0.872	0.000[a]	.000[a]	0.000[a]	1.260	0.000[a]	.000[a]
Season (non-breeding)	−0.626 (0.670)		−0.934	.350	0.621 (0.586)		−1.060	.289
Urbanization index	0.120 (0.052)	5.308	2.304	.0212	−0.009 (0.076)	0.001	−0.121	.904
R^2	.201				.527			

Note: Adjusted R^2 variance is shown; the term 's' prefixed to a variable indicates a smoothing function of the variable included in the GAMMs; note that neither estimate nor *z*-values are given for the smoothing terms.

[a]Reference category.

[b]Sample size was not included in the prevalence model as it was already accounted for in the estimation of the dependent variable.

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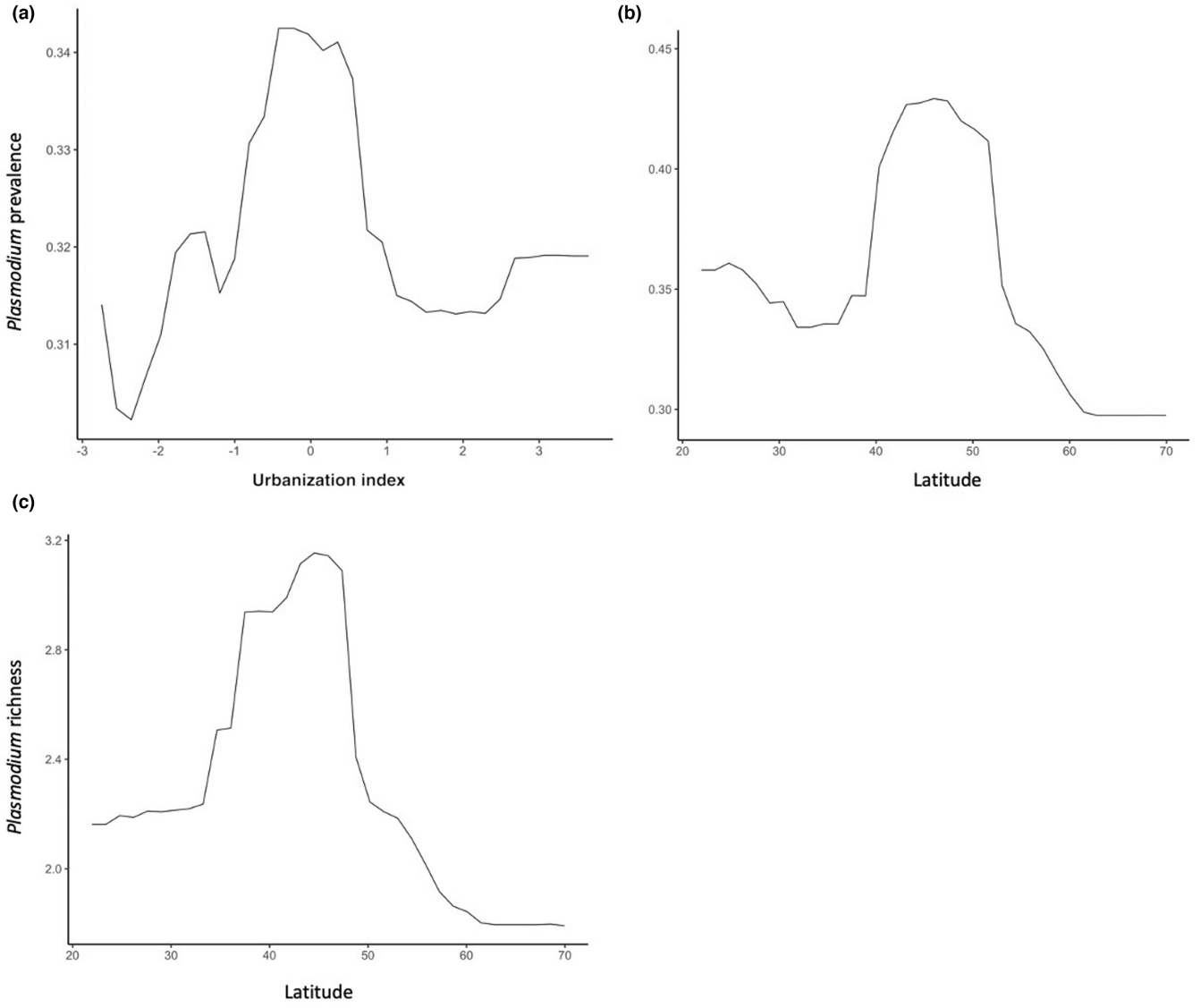


FIGURE 4 Partial dependence plot for native populations ($n = 35$) between *Plasmodium* prevalence and (a) the urbanization index, (b) latitude; and between the number of observed *Plasmodium* lineages (i.e., richness) and (c) latitude.

of four clusters, probably related to the geographical distribution of the predominant lineages. Indeed, lineages such as PADOM19, PADOM17, PADOM09 and DENPET3 circulated mainly in introduced populations in South America (e.g., Brazil), while GRW04, PADOM11, ZEMAC1, SEIAUR01 and WW3 were found in North American birds (e.g., USA, Florida) thus suggesting that these associations correspond to new host–pathogen interactions generated after the introduction process and not occurring in the native area.

4.1 | Environmental variables affecting *Plasmodium* prevalence and richness in native versus introduced sparrow populations

GAMM analyses revealed significant associations between parasite prevalence and the level of urbanization in both native and introduced populations, even though this variable was not considered to have a smoothed response relationship. Urbanization significantly affected the parasite prevalence in native populations of house sparrows, with values peaking at intermediate levels of the index in the RF analyses. This could be because these environments correspond to transitional habitats, such as less urbanized human population centres. By contrast, RFs revealed two prevalence peaks, one at low and one at high urbanization levels, in introduced populations. Patterns described underline the importance of combining both statistical approaches to explore the complex trends of *Plasmodium* infections in wild bird populations, as the RF approach was able to detect fine-scale associations that the GAMMs could not.

A theoretical transmission model of host–parasite dynamics during a host range expansion shows that populations of introduced individuals should have either lower prevalence or lower diversity of parasites compared to native source populations (Phillips et al., 2010). According to the model, stochastic events (e.g., serial founder events) in low-density populations result in local extinctions of

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TABLE 2 Results of the generalized additive mixed models (GAMMs) evaluating the relationships between the prevalence and the number of observed lineages per locality (i.e., richness) of avian malaria *Plasmodium* and environmental, geographical and time-related variables for introduced house sparrow populations ($n = 34$).

	Prevalence				Richness of lineages			
Independent variable	Estimate (± *SE*)	χ^2	*z*	*p*	Estimate (± *SE*)	χ^2	*z*	*p*
Altitude	0.001 (0.001)	3.001	1.732	.083	0.150 (0.076)	3.959	1.990	.047
Human density	−0.087 (0.070)	1.539	−1.240	.215	−0.095 (0.065)	2.184	−1.478	.139
Latitude:Northern hemisphere	−0.039 (0.024)	2.580	−1.594	.111	−0.036 (0.022)	3.479	−1.640	.101
Latitude:Southern hemisphere	−0.026 (0.032)		−0.797	.425	−0.051 (0.027)		−1.863	.062
Sampling size[b]	–	–	–	–	0.009 (0.009)	1.132	1.064	.287
Season (breeding)	0.000[a]	1.809	0.000[a]	.000[a]	0.000[a]	0.253	0.000[a]	.000[a]
Season (non-breeding)	0.718 (0.533)		1.345	.179	0.200 (0.398)		0.503	.615
s 'Years since introduction'[c]	–	16.92	–	< .001	0.014 (0.007)	4.312	2.077	.038
Urbanization index	0.256 (0.097)	7.036	2.653	.008	0.086 (0.075)	1.326	1.152	.249
R^2	.342				.321			

Note: Adjusted R^2 variance is shown; the term 's' prefixed to a variable indicates a smoothing function of the variable included in the GAMMs; note that neither estimate nor *z*-values are given for the smoothing terms.

[a]Reference category.

[b]Sample size was not included in the prevalence model as it was already accounted for in the estimation of the dependent variable.

[c] Years since introduction in the richness of lineages model refers to a non-smoothed term.

hosts, or failure of parasite transmission, leading to a dominance of uninfected, introduced hosts. Here, corroborating the theoretical model of Phillips et al. (2010), house sparrows living in transitional areas within invaded areas, may show lower prevalence. Also, another comparison of American urban and non-urban (disturbed agricultural) habitats revealed that house sparrows inhabiting highly urbanized areas showed lower prevalence of parasites (Santiago-Alarcón et al., 2020). The patterns we found may partly explain the contrasting results found in the literature, where different studies may focus on different portions of the urbanization gradient or different contexts, although the mechanisms behind these patterns still remain unknown.

4.2 | Geographical variables affecting *Plasmodium* prevalence and richness in native versus introduced sparrow populations

Avian malaria prevalence varies along a latitudinal gradient in native populations. Our models suggest that *Plasmodium* may expand its transmission range to more northern latitudes, indicating that native birds may be exposed to new parasite communities in the future (Loiseau et al., 2012). *Plasmodium* richness of lineages also increased along the altitudinal gradient in invaded areas, possibly due to changes in the host and vector community composition and environmental conditions (Chapa-Vargas et al., 2020). Indeed, parasites infecting wild birds are also affected by global change (e.g., under a climate change scenario) occurring at increasingly higher elevations (LaPointe et al., 2010), likely altering parasite ecology in areas where hosts or parasites were previously absent (e.g., at higher elevations, Loiseau et al., 2012).

Nowadays, studies focusing on the relevance of lineage identity are globally on the rise (de Angeli Dutra et al., 2021; De La Torre et al., 2022; Ellis et al., 2020; Fecchio et al., 2021). Here, we join this trend emphasizing the importance of examining the genetic identity of parasites and the richness of lineages in the light of understanding how different sources of environmental heterogeneity may influence parasite–vector–vertebrate host interactions.

4.3 | Time-related variables affecting *Plasmodium* prevalence and richness in native versus introduced sparrow populations

The number of lineages infecting birds in invaded areas may be also affected by the time since the introduction of birds and consequently the time elapsed for the establishment of new interactions between birds and parasites. Indeed, we observed both an initial decrease of *Plasmodium* prevalence and richness of lineages (during the initial 30 years after introduction) in the introduced populations, followed by an increase in both parasite metrics, especially after 100 years from colonization (Figure 5b,c). New host–vector–parasite relationships are likely to arise through the establishment of local parasites (Cable et al., 2017; Cressler et al., 2016). Also, haemosporidian parasite prevalence increased with years since bird introduction across Kenyan populations, although over a much shorter time frame (Coon & Martin, 2014). Importantly, these outcomes suggest that native populations are at equilibrium with the

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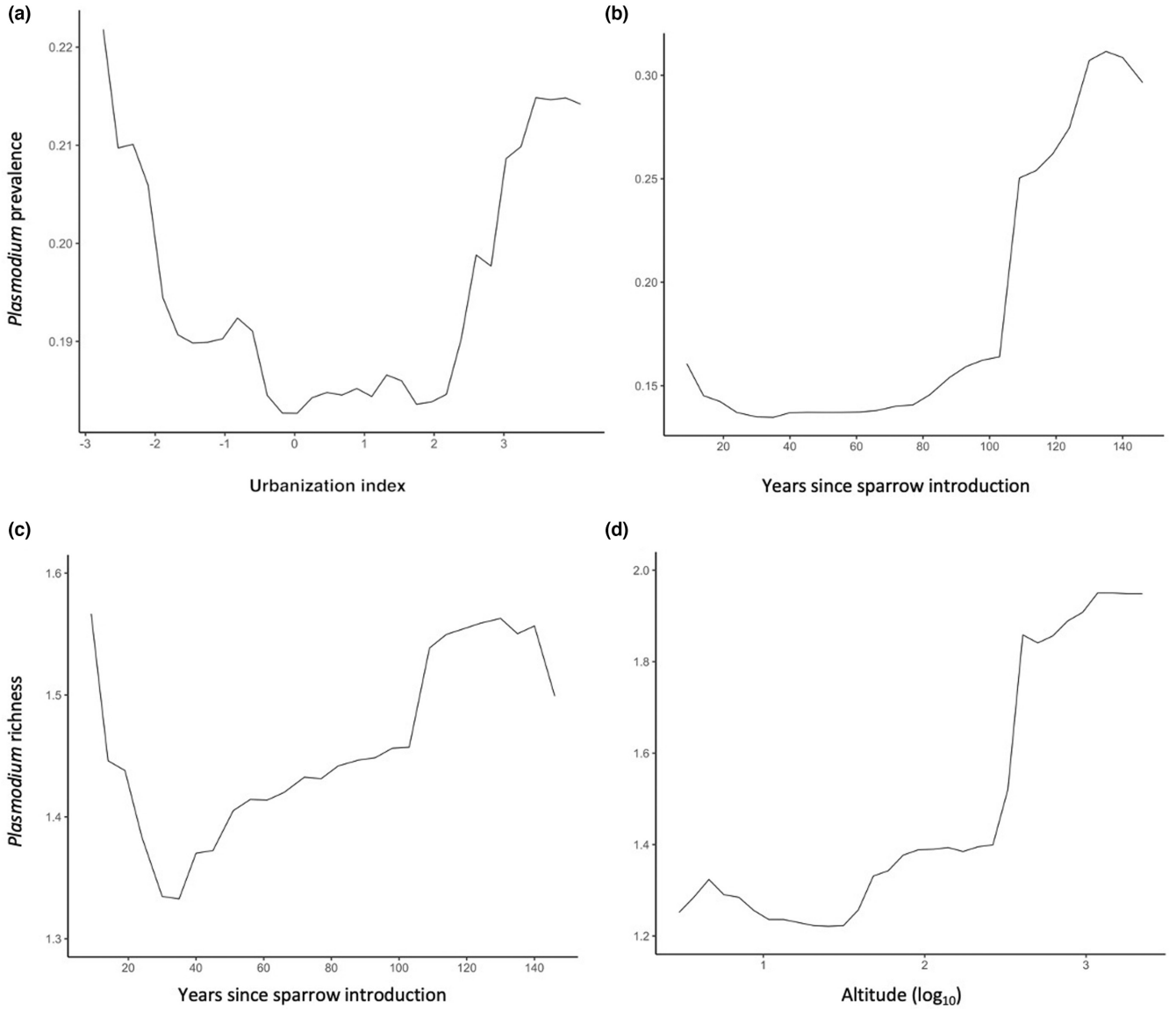


FIGURE 5 Partial dependence plot for introduced populations ($n = 34$) between *Plasmodium* prevalence and (a) the urbanization index, (b) years elapsed since the introduction of sparrow populations; and between the number of observed *Plasmodium* lineages (i.e., richness) and (c) years elapsed since the introduction of sparrow populations, and (d) altitude ($\log_{10}$ transformed) of each sampling site. For information about the first observation of house sparrows in each locality, see Supporting Information Table S1.

local parasite fauna, while introduced populations are yet to reach an equilibrium state, especially as soon as a population is established. Given that *Plasmodium* parasites may have major impacts on the survival and productivity of their hosts, the lack of such balances in introduced host populations has favoured the establishment and initial spread of house sparrows.

5 | CONCLUSIONS

Malaria infection prevalence in both native and introduced house sparrow populations was affected by urbanization. Geographical and time-related variables, including altitude and the time since house sparrows were introduced in the invaded areas were related to the number of parasite lineages found to be infecting house sparrows. Because richness of lineages increased with years elapsed since first observation of an introduced population, this study system could be useful for analysing the process of pathogen spillover and adaptation to a new host and how hosts might respond to novel environments, including exposure to new parasites. While in native populations environmental and geographical variables explained population variance in prevalence and/or richness, in introduced populations factors related to the time and place of introduction were relevant. This indicates that the introduction process has long-lasting effects on the host–parasite interactions with possible consequences for the impact of infections on host populations, a topic that undoubtedly deserves to be explored in the future.

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AUTHOR CONTRIBUTIONS

MF and AM conceived the idea of the study and organized the database; all authors collected and provided samples used to create the database for this study; MF performed the statistical analyses; JJP calculated the urbanization index and drew the map. MF wrote the first draft of the manuscript with supervision from AM. All authors read, contributed to, and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data supporting the conclusions of this study are available in the supplementary material to this article. Any further details are available from the corresponding author on reasonable request.

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BIOSKETCH

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SUPPORTING INFORMATION

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