Received: 21 December 2017 | Accepted: 21 December 2017

DOI: 10.1111/1365-2656.12805

RESEARCH ARTICLE

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

Ecological determinants of avian malaria infections: An integrative analysis at landscape, mosquito and vertebrate community levels

Martina Ferraguti[1] | Josué Martínez-de la Puente[1,2] | Staffan Bensch[3] | David Roiz[1] | Santigo Ruiz[2,4] | Duarte S. Viana[1] | Ramón C. Soriguer[2,5] | Jordi Figuerola[1,2]

[1]Departamento de Ecología de Humedales, Estación Biológica de Doñana (EBD-CSIC), Seville, Spain

[2]Centro de Investigación Biomédica en Red de Epidemiología y Salud Pública (CIBERESP), Madrid, Spain

[3]Department of Biology, Lund University, Lund, Sweden

[4]Diputación de Huelva, Área de Medio Ambiente, Servicio de Control de Mosquitos, Huelva, Spain

[5]Departamento de Etología y Conservación de la Biodiversidad, Estación Biológica de Doñana (EBD-CSIC), Seville, Spain

Correspondence
Martina Ferraguti
Email: mferraguti@ebd.csic.es

Present address
David Roiz, Infectious Diseases and Vectors: Ecology, Genetics, Evolution and Control, IRD (Institut de Recherche pour le Développement), Montpellier, France

Duarte S. Viana, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Funding information
Junta de Andalucía, Grant/Award Number: P11-RNM-7038, RNM118 and RNM153; Spanish Ministry of Economy and Competetion, Grant/Award Number: CGL2012-30759 and CGL2015-65055-P; European Regional Development Fund (FEDER), Grant/Award Number: FP7-261504 EDENext; BBVA Foundation

Handling Editor: Jenny Dunn

[Correction added after online publication on 14 March 2018: Affiliations for Duarte S. Viana and Ramón C. Soriguer changed]

Abstract

1. Vector and host communities, as well as habitat characteristics, may have important but different impacts on the prevalence, richness and evenness of vector-borne parasites.
2. We investigated the relative importance of (1) the mosquito community composition, (2) the vertebrate community composition and (3) landscape characteristics on the prevalence, richness and evenness of avian *Plasmodium*. We hypothesized that parasite prevalence will be more affected by vector-related parameters, while host parameters should be also important to explain *Plasmodium* richness and evenness.
3. We sampled 2,588 wild house sparrows (*Passer domesticus*) and 340,829 mosquitoes, and we performed vertebrate censuses at 45 localities in the Southwest of Spain. These localities included urban, rural and natural landscapes that were characterized by several habitat variables.
4. Twelve *Plasmodium* lineages were identified in house sparrows corresponding to three major clades. Variation partitioning showed that landscape characteristics explained the highest fraction of variation in all response variables (21.0%–44.8%). *Plasmodium* prevalence was in addition explained by vector-related variables (5.4%) and its interaction with landscape (10.2%). Parasite richness and evenness were mostly explained by vertebrate community-related variables.
5. The structuring role of landscape characteristics in vector and host communities was a key factor in determining parasite prevalence, richness and evenness, although the role of each factor differed according to the parasite parameters studied. These results show that the biotic and abiotic contexts are important to explain the transmission dynamics of mosquito-borne pathogens in the wild.

KEYWORDS
bird and mammal community, environmental predictors, mosquito community composition, NDVI, *Plasmodium*, vector-borne disease, water reservoir

1 | INTRODUCTION

The transmission dynamics of vector-borne parasites under natural conditions is determined by factors affecting the three main actors, the pathogen, its vectors and its vertebrate hosts, that are also influenced by environmental factors (Reisen, 2010). Currently, most studies have only focused on the study of pairwise interactions between two of the three main groups, while researches integrating all three groups were scarce and their relative contributions to the transmission of blood parasites remain unclear. Avian *Plasmodium* is a widespread vector-borne genus of parasites that infect birds and are transmitted by mosquitoes, mainly those of the genus *Culex* (Valkiūnas, 2005). These parasites represent an excellent bird model for human malaria and other vector-borne pathogens to investigate the ecological determinants of their transmission dynamics under natural conditions (Clark, Clegg, & Lima, 2014).

The abundance, species composition and diversity of vectors may affect pathogen amplification and ultimately determine the prevalence of the pathogen in the host population (Manguin & Boëte, 2011; Martínez-de la Puente, Martínez, Rivero-de-Aguilar, Del Cerro, & Merino, 2013a; Roche, Rohani, Dobson, & Guégan, 2013; Sol, Jovani, & Torres, 2000). This could be due to multiple demographic factors, such as alterations of the ratio between insect vectors and reservoirs and the vector-host contact patterns that potentially affect pathogen amplification (Joseph, Mihaljevic, Orlofske, & Paull, 2013; Roche et al., 2013). Different studies in birds have found strong support for the positive relationship between blood parasite prevalence and the abundance of potential insect vectors (Martínez-de la Puente et al., 2013a; Okanga, Cumming, & Hockey, 2013; Sol et al., 2000). In addition, differential vector competence of mosquito species may determine the rate of parasite transmission through the specific relationships between insect species and the pathogens infecting birds (Beerntsen, James, & Christensen, 2000; Martínez-de la Puente, Martínez, Aguilar, Herrero, & Merino, 2011), as only a subset of the parasites that contact with potential insect vectors are effectively transmitted by them (Gutiérrez-López et al., 2016). However, with some exceptions (Gager, Del Rosario Loaiza, Dearborn, & Bermingham, 2008), most evidence suggests that species of avian *Plasmodium* are generalist parasites transmitted by mosquitoes of different genera (Ferraguti et al., 2013; Kimura, Darbro, & Harrington, 2010). Furthermore, the feeding preferences of insect vectors may determine the contact rates between infected and susceptible hosts, affecting the transmission dynamics of mosquito-borne pathogens (Takken & Verhulst, 2013). Although some mosquito species show an opportunistic behaviour, they usually prefer to feed on particular vertebrate taxa, as those feeding mainly on birds (i.e. ornithophilic species) or on mammals (i.e. mammophilic species) (Takken & Verhulst, 2013). Thus, the abundance and diversity of mosquitoes, especially bird biters, may determine the transmission dynamics of *Plasmodium* parasites circulating in the area and affect parasite prevalence (Roche et al., 2013). The mosquito community might, however, have a lower impact on parasite diversity and richness due to the low specificity of mosquitoes to transmit avian *Plasmodium* (Kimura et al., 2010).

The composition of vertebrate host communities may also affect the dynamics of parasites circulating in the area, due to host composition can considerably influence disease risk (Huang, Van Langevelde, Estrada-Peña, Suzán, & De Boer, 2016; Joseph et al., 2013; Kilpatrick, Daszak, Jones, Marra, & Kramer, 2006; Scordato & Kardish, 2014). In the last decades, the protecting effect of biodiversity on human health from pathogen transmission is generating an intense debate (Ostfeld & Keesing, 2012). However, most studies report an effect of host richness (the number of different species in an area) and not diversity (relative abundance of each species in an area) on pathogen prevalence, suggesting a key role of the composition structure of the host communities on the disease amplification (LoGiudice et al., 2008). Positive correlations have been reported between host abundance and richness and parasite richness (Johnson, Ostfeld, & Keesing, 2015; Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014; Lafferty, 2012), including studies on different host–parasite models (Hechinger & Lafferty, 2005; Krasnov, Shenbrot, Khokhlova, & Degen, 2004; Watters, 1992). In the case of avian *Plasmodium*, parasite prevalence increases with the density (Ortego & Cordero, 2010) and abundance of susceptible hosts (Drovetski et al., 2014; but see Zhang, Wu, Zhang, Su, & Zou, 2014). The *Plasmodium* genus contains generalist and cosmopolitan lineages, which are able to infect bird species belonging to different families (Clark et al., 2014), but there are also some lineages that infect only a restricted range of species (Moens & Perez-Tris, 2016). Thus, the bird species present in a community may drive the blood-parasite community circulating in the area (Loiseau et al., 2012), resulting in similar parasite communities in areas with similar avian communities (Fecchio et al., 2017). In fact, the diversity of *Plasmodium* lineages may reflect the composition of avian hosts cohabiting in the area and be more affected by the bird host community than the mosquito community (Ishtiaq et al., 2010). Finally, although the presence of mammal host may elevate mosquito density and rise malaria risk at regional level (Dobson et al., 2006), an increase in reservoir species richness leads to a greater dilution capacity because the mammal community can accommodate possibilities of mosquito wasted bites, yielding overall lower infection prevalence for avian pathogens (Roche et al., 2013). Thus, mammals may divert bites in the short term but increase mosquito abundance in the long term (Bouma & Rowland, 1995).

Environmental characteristics may also determine the dynamics of parasite transmission (Higgs & Beaty, 2005; Sehgal, 2015) and incidence of vector-borne pathogens (Estrada-Peña, Ostfeld, Peterson, Poulin, & de la Fuente, 2014; Fourcade, Keišs, Richardson, & Secondi, 2014; Patz, Graczyk, Geller, & Vittor, 2000; Sehgal, 2015), probably through their effects on vector and host populations (Estrada-Peña et al., 2014; Roche et al., 2013). A number of studies have highlighted the importance of factors such as vegetation cover (Lillesand, Kiefer, & Chipman, 1994; Reisen, Meyer, Tempelis, & Spoehel, 1990; Roiz, Ruiz, Soriguer, & Figuerola, 2015) and water sources (Ferraguti et al., 2016; Ishtiaq et al., 2008; Krams et al., 2010; Njabo et al., 2009) on both vector and host communities. Moreover, water availability was shown to be one of the most important predictors of avian malaria incidence in wild birds (Krama et al., 2015; Wood et al., 2007).

The role of environmental factors has been shown to play a particularly prominent role in driving the transmission dynamics of vector-borne pathogens such as malaria parasites (Balls et al., 2004; Foley, Torres, Mueller, Bryan, & Bell, 2003), including in forcing the infection dynamics of different avian *Plasmodium* lineages (Lachish, Knowles, Alves, Wood, & Sheldon, 2011). However, whether and to what extent landscape characteristics affect the prevalence of vector-borne parasites either directly (Sehgal, 2015) or indirectly through effects on hosts (Cardon, Loot, Grenouillet, & Blanchet, 2011) and/or vectors (Santiago-Alarcón, Palinauskas, & Schaefer, 2012) remains unknown. In addition, understanding the ecology of pathogens in urban environments and their consequences to hosts living in habitats of different quality is essential to manage the risk of transmission to wildlife, especially under the current human-driven environmental changes (Bradley & Altizer, 2007; Cornet, Bichet, Larcombe, Faivre, & Sorci, 2014). Differences in habitat type may influence parasite epidemiology, with an increase in the transmission of pathogens in urban areas (Bradley & Altizer, 2007). In fact, human-mediated landscape transformation may influence the dynamics of wildlife diseases by affecting the distribution of vectors (Ferraguti et al., 2016; Gilioli & Mariani, 2011), hosts (Bradley & Altizer, 2007), and consequently their contact rates and feeding ratio (Faraji et al., 2014; Valerio et al., 2010). Among others, some evidence supports the role of urban environments as amplifiers of the impact of avian malaria infections on hosts. For instance, habitat alterations and fragmentation (Shochat, Warren, Faeth, McIntyre, & Hope, 2006), as well as urbanization and alteration of trophic dynamics (Faeth, Warren, Shochat, & Marussich, 2005), affect the risk of pathogen transmission. Also, the high trace of metals concentrations is linked to the prevalence of avian malaria parasites and affects body condition of urban birds (Bichet et al., 2014), and a higher parasite virulence has been found in birds feeding on poor quantity and quality food from urban areas (Cornet et al., 2014). Finally, animal husbandry or agriculture intensification can also affect the transmission of vector-borne pathogens, including avian malaria parasites (Fourcade et al., 2014; Gonzalez-Quevedo, Davies, & Richardson, 2014; Patz et al., 2000). Thus, anthropogenic changes in landscapes and their subsequent effects on host communities can affect disease emergence in different situations (Jones et al., 2008).

Here, we used an integrative approach to disentangle the roles of the different actors: (1) mosquito abundance and community diversity, (2) vertebrate density and community diversity and (3) environmental characteristics and landscape use in mediating the prevalence, richness and evenness of *Plasmodium* parasites in wild populations of house sparrows (*Passer domesticus*). The house sparrow is an abundant and widespread species that occurs in a wide range of habitats, usually linked to human constructions, and has a highly variable prevalence of infection by *Plasmodium* in different populations (Marzal et al., 2011). Despite its adaptation to human inhabited areas, house sparrow populations are declining in many European cities (De Laet & Summers-Smith, 2007). We predicted that *Plasmodium* prevalence is determined to a greater extent by mosquito-related variables (Roche et al., 2013), while *Plasmodium* richness and diversity will be more influenced by host-related variables (Lacorte et al., 2013). Habitat characteristics were predicted to globally affect *Plasmodium* transmission in birds due to their role in structuring both mosquito (Ferraguti et al., 2016) and vertebrate communities (Fecchio et al., 2017).

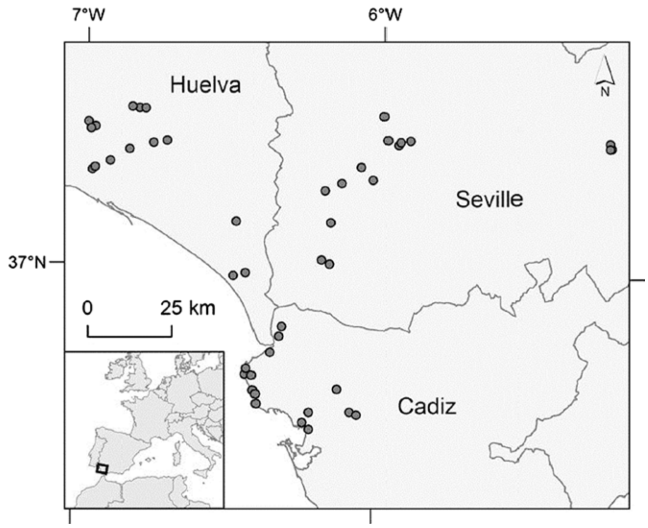

FIGURE 1 Distribution of the 45 sampling sites in the Southwest of Spain. The localities were distributed in geographically nearby triplets formed by one natural, one rural and one urban site

2 | MATERIALS AND METHODS

This study was conducted during 2013 in southwest Spain, at 45 different localities in the Cadiz, Huelva and Seville provinces (15 localities in each province; Figure 1). The study area is characterized by a Mediterranean climate, with a long dry summer season and most precipitation concentrated in autumn/winter. In each locality, we sampled three nearby areas (triplets) differing in anthropogenic use, defined as natural, rural and urban habitats. Urban habitats contained more densely populated areas than the other two habitat types; rural habitats had a higher density of livestock than the other two habitat types; and natural habitats were selected on the basis of both lower human and livestock densities than in the other two habitat types and of less human degraded landscape. The selection of these habitat categories was based on visual inspection and land-use geographical information. Vertebrate counts and mosquito and bird captures were done at each of these 45 localities. Three teams were simultaneously involved in house sparrow sampling, while mosquito trapping and vertebrate censuses were conducted during two working weeks and repeated every 45 days in all localities. All habitats within the same localities were visited during the same day to sample mosquitoes and perform the vertebrate censuses, and over consecutive days to sample birds.

2.1 | Mosquito sampling and identification

Mosquitoes were captured from April to December with BG-sentinel traps baited with BG-lure and dry ice as a source of CO_2 following the procedure detailed by Ferraguti et al. (2016). Briefly, mosquito sampling was conducted by using three traps operating for 24 hours at each sampling site. Mosquitoes were sorted by gender and date of collection, and then morphologically identified to species level (see Ferraguti et al., 2016 for further details). We quantified the number of mosquitoes captured as well as the number of ornithophilic and mammophilic mosquito species, based on available information about the feeding preferences of the different species: *Culex pipiens*, *Cx. modestus* and *Cx. perexiguus* feed mainly on birds (Balenghien et al., 2008; Muñoz et al., 2012), while *Cx. theileri*, *Anopheles atroparvus* and *Ochlerotatus caspius* feed mainly on mammals (Balenghien et al., 2008; Martínez-de la Puente, Ruiz, Soriguer, & Figuerola, 2013b; Martínez-de la Puente et al., 2012).

2.2 | Bird sampling and vertebrate censuses

House sparrows were captured at the same localities where mosquitoes were sampled after the breeding season, from July to October. Birds were captured using mist-nets, ringed with numbered metal rings (Svensson, 2006) and immediately released at the place of capture. A blood sample was obtained from the jugular vein using sterile syringes. The volume of blood extracted depended on the bird size but never exceeded 1% of the bird body mass. Blood was collected in Eppendorf tubes, maintained in cold boxes in the field and stored at 4°C for 24 hr prior to centrifugation for 10 min at 1,700 × *g* (4,000 rpm) to separate serum and cellular fractions. Samples were frozen at −20°C until subsequent molecular analysis.

Vertebrate censuses were conducted bimonthly from June to November, with a mean of 3.8 censuses per locality. Five point-counts in the surroundings of the mosquito traps were used for estimating bird abundance (Buckland, 2006). Although the vertebrate community could vary between seasons (i.e. due to the arrival of migrant individuals), we included the mean value of vertebrate censuses conducted during the whole study period in order to cover all the bird captures and because the *Plasmodium* community can be affected by the arrival of such migrant individuals through the year. A trained observer recorded the species and distance to the observer of all detected birds, both visually and acoustically, during 6 minutes in each sampling point. The density of each bird species at each locality was estimated by point transect analysis using the program DISTANCE (Thomas et al., 2006). For the mammal censuses, we counted pellets in transects of 200 m length and 1 m wide in the neighbouring area of the mosquito traps. Detected mammals included hare, rabbit, horse, cattle, red deer, fallow deer, wild boar, cat, dog and fox. Published information on the defecation rates of each species was used to estimate species densities (see Table S1 and Appendix S1).

2.3 | Molecular analyses

Genomic DNA was isolated from the cell fraction of each blood sample using the Maxwell®16 LEV system Research (Promega, Madison, WI) (Gutiérrez-López, Martínez-de la Puente, Gangoso, Soriguer, & Figuerola, 2015a). *Plasmodium* parasites were identified according to Hellgren, Bensch, and Malmqvist (2008) based on the amplification of a 478 bp fragment (excluding PCR primers) of the mitochondrial cytochrome *b* (cyt *b*) gene. Molecular analyses of negative samples were repeated to avoid false negatives (McClintock et al., 2010). Both negative controls for PCR reactions (at least one per plate) and DNA extraction (one per 15 samples) were included in the analysis. Positive amplifications were sequenced using the Macrogen sequencing service (Macrogen Inc., The Netherlands). PCR amplifications were sequenced uni-directionally from the 5′ end using the primer HaemF to reduce the costs of sequencing the high number of amplicons (see Dubiec et al., 2016 for a similar procedure). However, the identity of each lineage was confirmed by sequencing amplicons bi-directionally with the complementary primer. Multiple infections were found in five samples, as we observed two or more lineages simultaneously supported by the presence of double peaks in the chromatogram, thus we only identified parasites at the genus level in these samples. Despite the existence of methods to resolve double lineages (Pérez-Tris & Bensch, 2005), these procedures were not used due to the small number of coinfections. Sequences were edited using the software Sequencher™ v.4.9 (Gene Codes Corp., © 1991–2009, Ann Arbor, MI, USA) and identified by assigning unknown cyt *b* sequences to previously identified parasite lineages recorded in the GenBank DNA sequence and MalAvi databases (Bensch, Hellgren, & Pérez-Tris, 2009). Novel lineages were classified following the recommendations of Bensch et al. (2009) and deposited in GenBank.

2.4 | Phylogenetic analyses of *Plasmodium* lineages

We used MEGA6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013) to perform a phylogeny reconstruction including the complete dataset of 31 *Plasmodium* lineages with known morphospecies available from MalAvi (Bensch et al., 2009) and the sequences from the 12 lineages found in this study (including two lineages previously characterized morphologically as *P. relictum*: SGS1 and GRW11). Phylogenetic analyses were carried out based on the maximum likelihood algorithm. Analyses were conducted using the Tamura-Nei model and nodal support was estimated by bootstrap analysis with 10,000 replications (Felsenstein, 1981). One sequence of *Leucocytozoon majoris* (lineage LCB1, AY393804.1) was used as out-group. The lineages found infecting house sparrows in this study were grouped into three major clusters of phylogenetically related lineages, including sequences corresponding to *P. relictum*, *P. cathemerium* and *P. rouxi* morphospecies (see Section 3).

For each sampling site, we calculated the (1) *Plasmodium* prevalence, (2) richness of the three major clades found, named here on as *P. relictum* clade, *P. cathemerium* clade and *P. rouxi* clade, and

(3) evenness of clades, measured using the Shannon's equitability index (Agrawal & Gopal, 2013) (Table S2a).

Evenness was calculated as the Shannon's equitability index based on the prevalence of each *Plasmodium* clade at each locality. Shannon equitability index takes into account both species abundance and evenness.

2.5 | Landscape characteristics and remote sensing variables

Ten different landscape variables were estimated from satellite images (Table S2b). The hydrological information was obtained from cartography accessible at the "Datos Espaciales de Referencia de Andalucía (DERA)" webpage: http://www.juntadeandalucia.es/institutodeestadisticaycartografia/DERA/. We measured the distance from each mosquito trap to the nearest river, marshland patch, stretch of freshwater, coast line and main water reservoirs following the procedure detailed in Ferraguti et al. (2016). We also calculated the minimum distance to any kind of water sources. The Normalized Difference Vegetation Index (NDVI) was estimated from MODIS sensor images at a spatial resolution of 250 m and a temporal resolution (MOD13Q1 product) of 16 days. See Ferraguti et al. (2016) for further details.

2.6 | Statistical analyses

Statistical analyses were conducted with R version 2.14.2 using the vegan, lme4, car, arm, Matrix, Rcpp, MASS and MuMIn packages. We performed Linear Mixed-Effects Models (LMM) fitted by maximum likelihood with Gaussian distribution, including *Plasmodium* prevalence, richness or evenness as dependent variables. In order to enhance the statistical power of our analyses, we compared the three habitat categories (natural, rural and urban areas) within the same triplet to account for any geographical stratification of our sampling design that may influence parasite/host/vector distribution or abundance. Thus, *triplet* variable was nested within *province* variable as

TABLE 1 Estimate (est), *z*, *p* and values from the LMMs of each *Plasmodium* variable (columns) and the predictors (rows) included in the study (*N* = 45 sampling localities). Independent variables have been grouped into different categories. AOS, abundance of ornithophilic species; AMS, abundance of mammophilic species; E_H, Evenness (see the complete description of all predictors in Table S2). Significant associations ($p < .05$) are shown in bold

	Prevalence			**Richness of clades**			**Evenness**		
	est	***z***	***p***	**est**	***z***	***p***	**est**	***z***	***p***
Mosquito community									
AOS				**0.35**	**2.48**	**.01**			
AMS	**11.55**	**2.47**	**.01**	−0.23	1.43	.15			
Richness							−0.09	0.96	.32
Mosquito E_H	**−7.93**	**1.94**	**.04**				**−0.20**	**2.42**	**.02**
Vertebrate community									
Sparrows sampled	−5.51	1.21	.23	**0.26**	**1.92**	**.04**	0.09	0.93	.34
Sparrows density	−7.02	1.66	.09						
Bird density	−4.15	0.95	.34						
Bird richness				0.21	1.42	.16	−0.09	0.94	.33
Bird E_H	5.12	1.22	.23	**0.27**	**1.97**	**.05**			
Mammal density									
Mammal richness									
Mammal E_H	−5.76	1.37	.17						
Landscape									
Rural									
Urban									
Coast	8.01	1.68	.08	**0.50**	**3.47**	**<.001**	**0.48**	**6.05**	**<.001**
Rivers	6.12	1.44	.14	**0.28**	**2.24**	**.01**	0.12	1.65	.10
Water reservoirs	**10.55**	**2.01**	**.03**				**0.35**	**3.75**	**<.001**
Freshwater	−7.50	1.57	.11	0.17	1.43	.15			
Marshland	**−1.62**	**2.43**	**.02**	0.15	1.19	.22			
Total water				0.25	1.81	.07	**0.20**	**2.58**	**.01**
Spring NDVI	**9.93**	**2.21**	**.03**	0.22	1.70	.09			
Summer NDVI				0.20	1.72	.09			

random factors in any model. *Provinces* were included in the model to control for large-scale geographical variation but also to control for the logistical structure of sample collection. We checked for collinearity in independent variables by calculating their variance inflation factor (VIF) in full and final models. The covariates with the highest VIFs were excluded sequentially until all VIF values were lower than 5 (Zuur, Ieno, & Elphick, 2010). First, we compared *Plasmodium* variables across the three habitat types using one-way ANOVAs to check for any habitat type influence. Then, LMMs were estimated to model the role of the three sets of explanatory variables: variables characterizing the mosquito community, the vertebrate community and the landscape (Table S2b). To find the best (final) models for each of the explanatory sets, we fitted different submodels with all the possible combinations of explanatory variables (within each set) and selected that with the lowest Akaike's information criterion (AIC) among those with ΔAIC ≤2. All explanatory variables present in these selected models were kept in the final model. The normal distribution of all predictors and model residuals was checked by using *qq plots* in R software. The mean abundance of ornithophilic and mammophilic mosquito species and hydrologic distances were log-transformed to normalize their distributions.

Finally, we used a variation partitioning approach to determine the proportion of variation explained by the exclusive and shared contributions of the three groups of explanatory variables (mosquitoes, vertebrates and landscape) for each response variable (*Plasmodium* prevalence, richness and evenness). These groups were formed by the selected variables according to the model selection procedure described earlier (Table 1). The habitat category was included in the set of landscape variables. To calculate the variation explained by each set of explanatory variables and their combinations, we calculated the respective marginal coefficient of determination (a pseudo-R^2) for the fixed effects according to Nakagawa and Schielzeth (2013), using the R package MUMIN (Bartoń, 2015). Subsequently, exclusive and shared fractions of explained variation were determined following the procedure described in Legendre (2008).

3 | RESULTS

A total of 340,829 female mosquitoes were collected, of which the most trapped species were *Cx. theileri* (282,891 ind.), *Oc. caspius* (21,155) and *Cx. pipiens* (19,268). In addition, *Cx. perexiguus* (5,939), *An. atroparvus* (5,387) and *Culex modestus* (1,237) reached high abundances in the study area.

The overall prevalence of infection by *Plasmodium* was 29.6% (765 of 2,588 house sparrows) comprising 12 different lineages, five of them identified for the first time in this study. The two most common parasite lineages were SGS1 (GenBank accession number KR049254; prevalence 67.5%) and COLL1 (=Donana07) (AY831747, prevalence 13.5%). The phylogenetic analysis of the *Plasmodium* sequences found in this study revealed that these were grouped in three main clades with previously morphologically characterized *Plasmodium* lineages (Figure 2). The lineages DELURB4 (EU154346), GRW11 (=Rinshi-7) (KR049255), SGS1, PADOM25 (KX438373), PADOM26 (KX438374) and PADOM28 (KX438376) were grouped in the *P. relictum* clade with a 99% bootstrap support, while COLL1, PADOM02 (=Rinshi-8) (AB477127), PADOM1 (DQ058611), PADOM27 (KX438375) and PADOM29 (KX438378) were included in the *P. cathemerium* clade with a 63% bootstrap support and the lineage PAGRI02 (JX196865) clustered with one lineage corresponding to *P. rouxi* with a 99% bootstrap support. Parasites of the *P. relictum* clade (23.22%) showed the highest prevalence of infection followed by those of the *P. cathemerium* clade (5.99%) and *P. rouxi* clade (0.15%).

We did not find any significant difference on *Plasmodium* prevalence or richness between habitat categories (ANOVA: all $p > 0.05$). A marginal significant difference was found between habitat categories for *Plasmodium* evenness (χ = 5.2, df = 2, p = .06), with rural habitat showing higher values than natural areas (Tukey's post hoc test: z = 2.31, p = .05).

As predicted, the effect of mosquito, vertebrate and landscape predictors varied among the different *Plasmodium* indexes. *Plasmodium* prevalence was positively associated with the abundance of mammophilic mosquitoes, the distance to water reservoirs and spring NDVI, but decreased with the evenness of mosquitoes and distance to marshlands (Table 1). No relationships were identified between *Plasmodium* prevalence and the vertebrate community variables.

Plasmodium richness significantly increased with the abundance of ornithophilic mosquitoes, evenness of bird community, total number of sparrows sampled and distance to the coast and rivers. The relationships between *Plasmodium* richness and distance to any source of water and both NDVI indexes were marginally significant (Table 1).

Plasmodium evenness was negatively related to the mosquito evenness and positively related to the distance to the coast, water reservoirs and to any sources of water. No significant relationship was found between *Plasmodium* evenness and the vertebrate community variables (Table 1).

The global models, which included the three sets of explanatory variables, explained a total variation in *Plasmodium* prevalence, richness and evenness ranging from 46.2% to 60.0% (Figure 3). Overall, landscape characteristics exclusively explained the highest fraction of variation (21.0%–44.8%). For the case of *Plasmodium* prevalence, the mosquito and vertebrate communities explained similar fractions of exclusive variation (5.4% and 5.5%, respectively), and the shared fraction between landscape and the mosquito community explained a large proportion of the variation (10.2%) (Figure 3a). Both the mosquito and vertebrate communities explained variation in parasite richness, although the vertebrate community explained a larger fraction (3.5% compared with 1.1%) (Figure 3b). *Plasmodium* evenness was also largely explained by the exclusive contribution of the mosquito community (6.8%), whereas the vertebrate community explained a limited amount of variation (2.5%) (Figure 3c,d). Explained variation shared between landscape and the mosquito

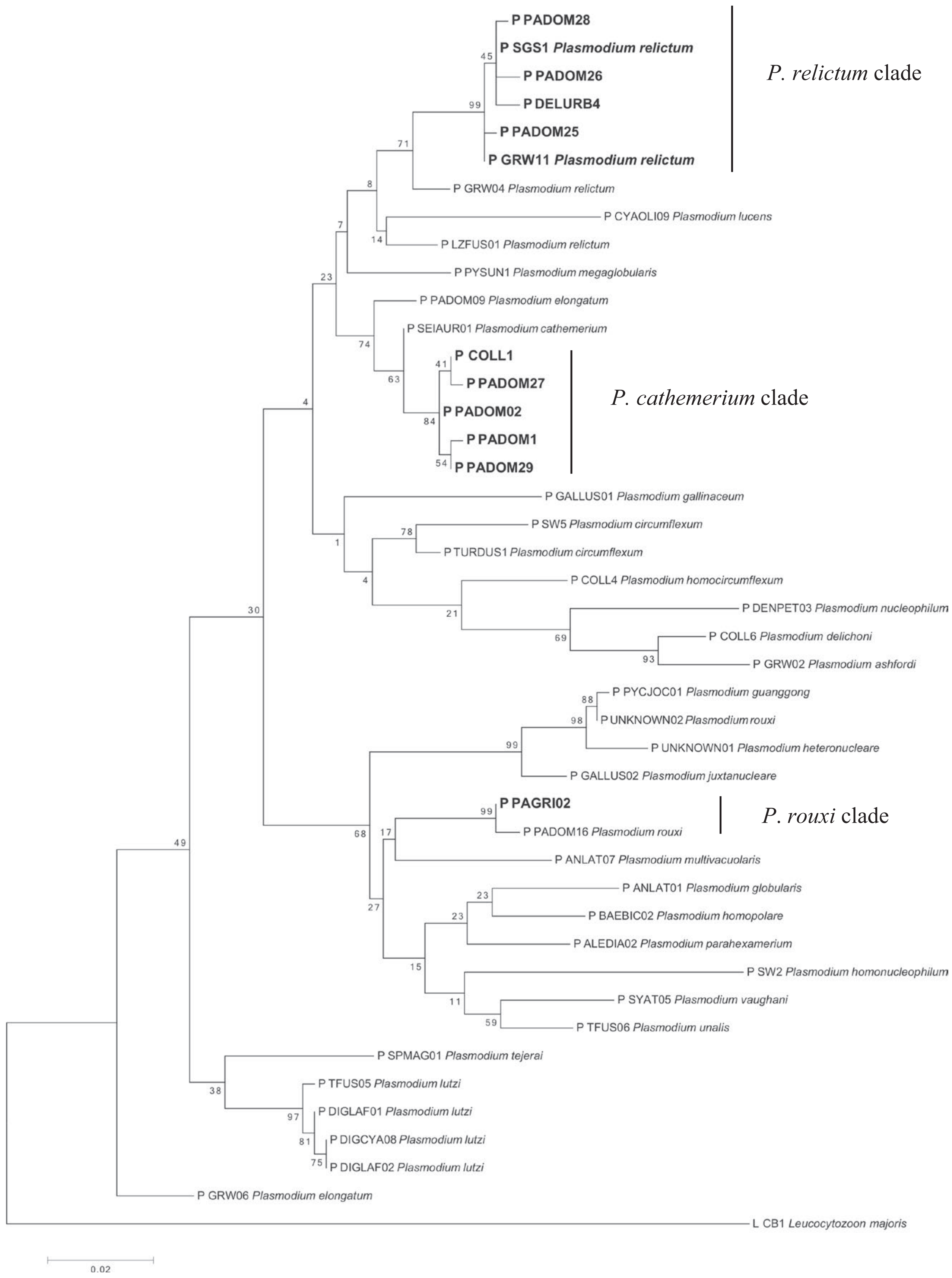

FIGURE 2 Phylogenetic tree of the lineages isolated from house sparrows in this study (in bold) and the *Plasmodium* lineages corresponding to morphospecies available in MalAvi database (Bensch et al., 2009). The three main clades were named according to the morphospecies included in each cluster

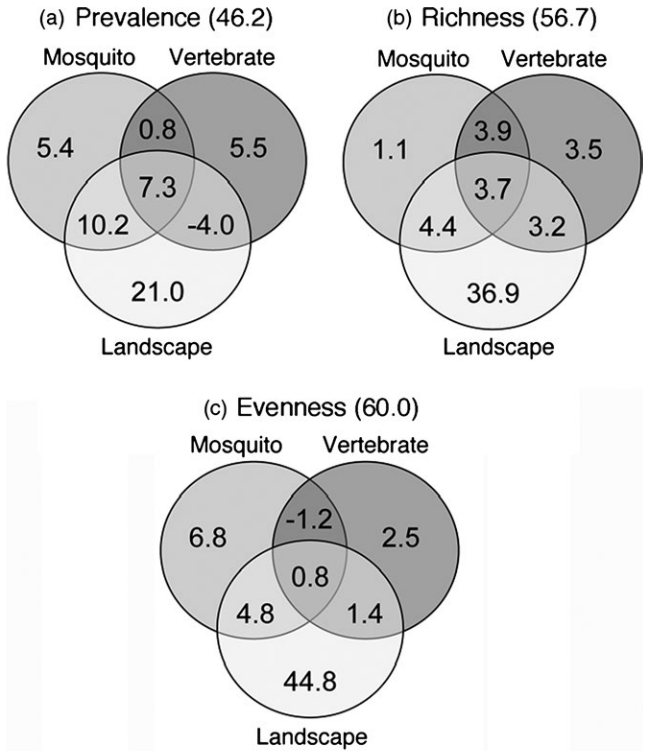

FIGURE 3 Venn diagrams of the variation partitioning results for the *Plasmodium* prevalence (a), richness (b) and evenness (c). All fractions are given in percentage (%). The global coefficient of variation (R^2) is provided in each panel title within brackets

community was higher than that between landscape and the vertebrate community for parasite prevalence, richness and evenness.

4 | DISCUSSION

Parasite infections are known to vary in space and time, and several abiotic or biotic parameters are likely responsible for this variation (Higgs & Beaty, 2005). Our large-scale survey was based on an unprecedented analysis of the role of vectors, hosts and environment in determining parasite prevalence, richness and evenness. This integrative approach allowed us to quantify their relative importance in explaining parasite biodiversity. Overall, our results support that landscape characteristics and their role in structuring the vector and host communities is the most likely factor driving *Plasmodium* biodiversity. The mosquito community also explained a large proportion of variation in *Plasmodium* prevalence, while the vertebrate community was more important in explaining parasite richness.

Landscape features explained most of the variation in all *Plasmodium* variables, both exclusively and through their role in structuring the mosquito and vertebrate communities. The exclusive contribution of landscape might also affect mosquitoes and vertebrates in ways that are not captured by the variables measured in this study. For example, habitat variables can affect their community composition and relative abundances and in turn explain parasite dynamics. Thus, environmental factors such as the distance to water sources and NDVI, reflecting characteristics such as vegetation cover and phenology, have been shown to be good predictors in the transmission dynamics of pathogens (Foley et al., 2003; Omumbo, Hay, Snow, Tatem, & Rogers, 2005; Sehgal, 2015). Strong relationships between landscape use and the prevalence of blood parasites infecting birds have previously been shown (Fourcade et al., 2014; Patz et al., 2000), which may be due to the effect of landscape features on the vector community (Norris, 2004). For instance, the scarcity of suitable vectors has been identified as the most likely reason of the low prevalence or absence of *Plasmodium* in birds from marine and saline environments (Figuerola, 1999; Gutiérrez-López et al., 2015b; Martínez-de la Puente et al., 2017; Mendes, Piersma, Lecoq, Spaans, & Ricklefs, 2005) and deserts (Merino, Barbosa, Moreno, & Potti, 1997). Indeed, environmental characteristics strongly determined the mosquito abundance and community composition in the study area (Ferraguti et al., 2016). In particular, we found positive relationships between *Plasmodium* prevalence, richness and evenness with the distance to different manmade water reservoirs, and a negative association between the distance to the marshland and *Plasmodium* prevalence. As saltmarshes provide suitable environments for halophytic mosquito species (Leisnham & Sandoval-Mohapatra, 2011), marshland could strongly affect the abundance of some mosquitoes in the studied areas (Ferraguti et al., 2016). Moreover, in addition to mosquito breeding, it is also possible that the landscape affects the mosquito host-seeking behaviour potentially affecting the dynamics of parasite transmission. Here, these results agree with previous studies reporting an increased probability of *Plasmodium* infection in the proximity of freshwater, ponds and slow rivers in mosquitoes (Ishtiaq et al., 2008; Njabo et al., 2009) and birds (Krams et al., 2010; Wood et al., 2007). In addition, the environmental conditions reflected by higher NDVI values may be related to the availability of breeding and resting habitats for both mosquitoes and birds (Lillesand et al., 1994; Reisen et al., 1990). In fact, the NDVI has been related to the spatial distribution of mosquitoes (Diuk-Wasser, Brown, Andreadis, & Fish, 2006; Roiz et al., 2015). Therefore, the positive association between vegetation cover and mosquito presence, abundance and diversity may explain the associations between spring NDVI and *Plasmodium* prevalence reported here. Also, previous studies reported a peak in prevalence during spring in the bird breeding season, when vector populations and the proportion of immunologically naive juveniles in the host population are high and higher levels of sexual steroid hormones depress the immune system, allowing parasites to survive (Saino, Møller, & Bolzern, 1995; Wedekind & Følstad, 1994). This fact is supported by the high shared contribution (10.2%) of the mosquito community and landscape characteristics to explain *Plasmodium* prevalence, which supports the role of the environment in structuring the vector community and contributes to explain parasite prevalence in house sparrows. However, this association should be also due to the human transformation of the habitat owing to the creation of artificial habitats such as water deposits, swimming pools or urban sewage that act as alternative breeding sites for mosquitoes (Bradley & Altizer, 2007; Overgaard, Ekbom, Suwonkerd, & Takagi, 2003).

The mosquito community alone also explained most of the variance in *Plasmodium* prevalence, supporting that vector abundance and diversity are determinants of the prevalence of vector-borne parasites in birds (Martínez-de la Puente et al., 2013a; Sol et al., 2000). The abundance of mosquitoes could affect avian parasite prevalence (Manguin & Boëte, 2011), especially the ornithophilic species that are responsible for successful transmission (Simpson et al., 2012; Takken & Verhulst, 2013). By identifying ornithophilic mosquitoes involved in the transmission of *Plasmodium* parasites (Ventim et al., 2012), we predicted an increase in *Plasmodium* prevalence in areas with a higher abundance of ornithophilic species (Kimura et al., 2010; Santiago-Alarcón et al., 2012), while a significant effect was not necessarily expected for the case of mammophilic mosquitoes. We found a positive association between the abundance of ornithophilic mosquitoes and *Plasmodium* richness but, contrary to our prediction, the prevalence of *Plasmodium* was positively correlated with the abundance of mammophilic mosquito species. Although the feeding preference of these mosquitoes is clearly biased towards mammals, this is not a strict behaviour, with a proportion of individuals feeding also on birds and interacting with avian blood parasites (Ferraguti et al., 2013). Moreover, under altered environmental conditions, vectors specialized in a group of vertebrate hosts can be forced to feed on other groups of organisms because of changes in host community structure (Lyimo & Ferguson, 2009). For example, the mammophilic *Oc. caspius* include birds in their diet, with species including chickens and house sparrows representing 18.1% and 9.1% of the blood meals of mosquitoes trapped in two areas of southern Spain (Muñoz et al., 2012). In addition, these species are potentially involved in the transmission of *Plasmodium* (Ferraguti et al., 2013), which together with the high abundance recorded in the studied area suggest that mammophilic mosquitoes may still favour the transmission of avian *Plasmodium* to birds. Finally, we found negative relationships between mosquito evenness and both *Plasmodium* prevalence and diversity. This fact could be due to a differential competence of mosquitoes cohabiting in the area, which may play a differential role in the transmission of avian *Plasmodium* with respect to their relative abundance. Furthermore, according to previous molecular studies, *Plasmodium* lineages are often generalist in terms of their vectors (Clark et al., 2014; Ferraguti et al., 2013; Kimura et al., 2010; Tolle, 2009 but see Gager et al., 2008). These studies are, however, based on the presence of parasite DNA, but potential quantitative interspecific differences in parasite loads are currently unknown. Quantitative differences in vector competence for different *Plasmodium* lineages should be studied in future to identify the causes of the observed pattern.

The vertebrate community also contributed to explain parasite prevalence and diversity. It is widely accepted that pathogen diversity is spatially correlated with host biodiversity (Lafferty, 2012; Wood et al., 2014), wherein an increase in host diversity may be linked with dilution or amplification of diseases (Huang, Yu, Van Langevelde, & De Boer, 2017; Ostfeld & Keesing, 2012; Randolph & Dobson, 2012). As predicted, we found *Plasmodium* richness positively related with bird evenness, supporting an increase in the number of parasite clades circulating in house sparrows as bird richness and diversity increased in the area. Thus, contrary to the dilution effect predictions, *Plasmodium* parasites were never negatively associated to host richness nor diversity, suggesting the occurrence of an amplification rather than a dilution effect. Moreover, Ishtiaq et al. (2010) found that the richness of bird species affected parasite richness more than the species richness of mosquitoes. Likewise, bird diversity was correlated to parasite diversity, supporting the hypothesis that high host richness might provide more niches to the different parasite lineages (Lacorte et al., 2013). Our results not only support this possibility but also that even abundances may favour the richness of *Plasmodium* lineages infecting birds.

Surprisingly, we did not find support for the urbanization effect on *Plasmodium* variables, which does not support a differential exposure hypothesis of these parasites, as previously found (Bichet et al., 2014). While in some cases animals living in urban habitats may be protected from infectious diseases, there have been reports of increased transmission of pathogens in urban areas (Bradley & Altizer, 2007). At this point, it is worth noting the dual role of anthropization on host communities and the incidence of infectious diseases. Indeed, urbanization can drastically affect wildlife populations due to the high amount of pollutants that might weaken the avian immune system and increase their susceptibility to infectious diseases (Fair & Myers, 2002; Hawley, Hallinger, & Cristol, 2009; Snoeijs et al., 2005). Nevertheless, these same urbanization factors can also reduce parasite prevalence in birds from urban habitats (Evans et al., 2009; Geue & Partecke, 2008).

In spite of the large sample size included in this study, our results are limited by the fact that *Plasmodium* was only analysed in a single host. Avian *Plasmodium* lineages may vary in their ability to infect different species (Palinauskas, Valkiūnas, Bolshakov, & Bensch, 2008; Zhang et al., 2014), and some parasite morphospecies are thought to be host restricted (Iezhova, Valkiūnas, & Bairlein, 2005). The two most abundant lineages found in this study, belonging to different clades, were already described in 116 (SGS1) and 10 (COLL1) different host species (according to MalAvi; accessed 27 November 2017, see Bensch et al., 2009), supporting that these lineages are generalist and not restricted to house sparrows, possibly affecting the bird community of the study areas. However, our approach allowed us to deal with the problem of differential detection associated with heterogeneous sample size among host species (see Loiseau et al., 2012), although the latter approach limits the isolated lineages to those from a single host species.

To conclude, we present evidence that biotic and abiotic factors play an important role in *Plasmodium* transmission. We show that it is essential to develop integrative studies, focusing in all the players affecting the dynamics of vector-borne diseases to gain a more comprehensive understanding of the ecology of vector-borne pathogens in natural ecosystems. While vectors and hosts are both necessary links in parasite transmission dynamics, the environmental context plays a determinant role in regulating the regional incidence and diversity of pathogens.

ACKNOWLEDGEMENTS

This study was funded by project P11-RNM-7038 from the Junta de Andalucía, project CGL2012-30759 and CGL2015-65055-P from the Spanish Ministry of Economy and Competetion, EDENEXT (FP7-261504 EDENext) and from the European Regional Development Fund (FEDER). Funds were also partially provided by RNM118 and RNM153 from Junta de Andalucía. Information on remote sensing variables was obtained with the financial support of the project CGL2006-02247/BOS. M.F. and J.M.P. were partially supported by a FPU grant and a Juan de la Cierva contract, respectively. J.M.P. was partially supported by a 2017 Leonardo Grant for Researchers and Cultural Creators, BBVA Foundation. The Foundation accepts no responsibility for the opinions, statements and contents included in the project and/or the results thereof, which are entirely the responsibility of the authors. We are grateful for the logistical support provided by the Laboratorio de SIG y Teledetección, Estación Biológica de Doñana, CSIC (LAST-EBD). Alberto Pastoriza, Manolo Lobón, Manolo Máñez, Oscar González, Carlos Moreno, Cristina Pérez, Esmeralda Pérez, Juana Moreno Fernandez and Antonio Magallanes Martín de Oliva for their help with bird and mosquito capture and identification. Isabel Martín and Laura Gómez helped in the laboratory. We are grateful to all the landowners and to Consejeria de Medio Ambiente for allowing us to work on their properties. Two anonymous reviewers provided valuable comments in a previous version of the manuscript. Mosquito and bird trapping were carried out with all the necessary permits issued by the regional Department of the Environment (Consejería de Medio Ambiente, Junta de Andalucía). Entomological surveys and bird sampling on private land and in private residential areas were conducted with all the necessary permits and consent, and in the presence of owners. The CSIC Ethics Committee approved the experimental procedures on 9 March 2012. This study did not affect any endangered or protected species.

AUTHORS' CONTRIBUTIONS

M.F., J.M.P., R.S. and J.F. conceived and designed the experiments; M.F., J.M.P., D.R. and S.R. collected samples and performed the experiments; M.F., J.M.P., S.B., D.V. and J.F. carried out the data analysis; J.F. and R.S. contributed to the reagents/materials/analysis tools. M.F., J.M.P., S.B., D.V., D.R., S.R., R.S. and J.F. wrote the paper.

DATA ACCESSIBILITY

The data associated with new lineage information described in this manuscript are accessible from GenBank (KX438373-KX438378).

ORCID

Martina Ferraguti http://orcid.org/0000-0001-7481-4355

REFERENCES

Agrawal, A., & Gopal, K. (2013). Application of diversity index in measurement of species diversity. In A. Agrawal & K. Gopal (Eds.), *Biomonitoring of water and waste water* (pp. 41–48). New Delhi, India: Springer.

Balenghien, T., Vazeille, M., Grandadam, M., Schaffner, F., Zeller, H., Reiter, P., ... Bicout, J. D. (2008). Vector competence of some French Culex and Aedes mosquitoes for West Nile Virus. *Vector-Borne Zoonotic Disease*, *8*, 589–595. https://doi.org/10.1089/vbz.2007.0266

Balls, M. J., Bodker, R., Thomas, C. J., Kisinza, W., Msangeni, H. A., & Lindsay, S. W. (2004). Effect of topography on the risk of malaria infection in the Usambara Mountains, Tanzania. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, *98*, 400–408. https://doi.org/10.1016/j.trstmh.2003.11.005

Bartoń, K. (2015). Package 'MuMIn': Multi-model inference. *R Package Version*, *1*, 1.

Beerntsen, B. T., James, A. A., & Christensen, B. M. (2000). Genetics of mosquito vector competence. *Microbiology and Molecular Biology Reviews*, *64*, 115–137. https://doi.org/10.1128/MMBR.64.1.115-137.2000

Bensch, S., Hellgren, O., & Pérez-Tris, J. (2009). MalAvi: A public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. *Molecular Ecology Resources*, *9*, 1353–1358. https://doi.org/10.1111/j.1755-0998.2009.02692.x

Bichet, C., Sorci, G., Robert, A., Julliard, R., Lendvai, A. Z., Chastel, O., ... Loiseau, C. (2014). Epidemiology of *Plasmodium relictum* infection in the house sparrow. *Journal of Parasitology*, *100*, 59–65. https://doi.org/10.1645/12-24.1

Bouma, M. J., & Rowland, M. (1995). Failure of passive zooprophylaxis: Cat tle ownership in Pakistan associated with a higher prevalence of malaria. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, *89*, 351–353. https://doi.org/10.1016/0035-9203(95)90004-7

Bradley, C. A., & Altizer, S. (2007). Urbanization and the ecology of wildlife diseases. *Trends in Ecology & Evolution*, *22*, 95–102. https://doi.org/10.1016/j.tree.2006.11.001

Buckland, S. T. (2006). Point transect surveys for songbirds: Robust methodologies. *The Auk*, *123*, 345–357. https://doi.org/10.1642/0004-8038(2006)123[345:PSFSRM]2.0.CO;2

Cardon, M., Loot, G., Grenouillet, G., & Blanchet, S. (2011). Host characteristics and environmental factors differentially drive the burden and pathogenicity of an ectoparasite: A multilevel causal analysis. *Journal of Animal Ecology*, *80*, 657–667. https://doi.org/10.1111/j.1365-2656.2011.01804.x

Clark, N. J., Clegg, S. M., & Lima, M. R. (2014). A review of global diversity in avian haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): New insights from molecular data. *International Journal for Parasitology*, *44*, 329e338.

Cornet, S., Bichet, C., Larcombe, S., Faivre, B., & Sorci, G. (2014). Impact of host nutritional status on infection dynamics and parasite virulence in a bird-malaria system. *Journal of Animal Ecology*, *83*, 256–265. https://doi.org/10.1111/1365-2656.12113

De Laet, J., & Summers-Smith, J. (2007). The status of the urban house sparrow Passer domesticus in North-Western Europe: A review. *Journal of Ornithology*, *148*, S275–S278. https://doi.org/10.1007/s10336-007-0154-0

Diuk-Wasser, M. A., Brown, H. E., Andreadis, T. G., & Fish, D. (2006). Modelling the spatial distribution of mosquito vectors for West Nile virus in Connecticut, USA. *Vector-Borne & Zoonotic Diseases*, *6*, 283–295. https://doi.org/10.1089/vbz.2006.6.283

Dobson, A., Cattadori, I., Holt, R. D., Ostfeld, R. S., Keesing, F., Krichbaum, K., ... Hudson, P. J. (2006). Sacred cows and sympathetic squirrels: The importance of biological diversity to human health. *PLoS Medicine*, *3*, e231. https://doi.org/10.1371/journal.pmed.0030231

Drovetski, S. V., Aghayan, S. A., Mata, V. A., Lopes, R. J., Mode, N. A., Harvey, J. A., & Voelker, G. (2014). Does the niche breadth or trade-off hypothesis explain the abundance–occupancy relationship in avian Haemosporidia? *Molecular Ecology*, *23*, 3322–3329. https://doi.org/10.1111/mec.12744

Dubiec, A., Podmokła, E., Zagalska-Neubauer, M., Drobniak, S. M., Arct, A., Gustafsson, L., & Cichoń, M. (2016). Differential prevalence and diversity of haemosporidian parasites in two sympatric closely related non-migratory passerines. *Parasitology*, *143*, 1–10.

Estrada-Peña, A., Ostfeld, R. S., Peterson, A. T., Poulin, R., & de la Fuente, J. (2014). Effects of environmental change on zoonotic disease risk: An ecological primer. *Trends in Parasitology*, *30*, 205–214. https://doi.org/10.1016/j.pt.2014.02.003

Evans, K. L., Gaston, K. J., Sharp, S. P., McGowan, A., Simeoni, M., & Hatchwell, B. J. (2009). Effects of urbanisation on disease prevalenceand age structure in blackbird *Turdus merula* populations. *Oikos*, *118*, 774–782. https://doi.org/10.1111/j.1600-0706.2008.17226.x

Faeth, S. H., Warren, P. S., Shochat, E., & Marussich, W. A. (2005). Trophic dynamics in urban communities. *BioScience*, *55*, 399–407. https://doi.org/10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2

Fair, J. M., & Myers, O. B. (2002). The ecological and physiological costs of lead shot and immunological challenge to developing western bluebirds. *Ecotoxicology*, *11*, 199–208. https://doi.org/10.1023/A:1015474832239

Faraji, A., Egizi, A., Fonseca, D. M., Unlu, I., Crepeau, T., Healy, S. P., & Gaugler, R. (2014). Comparative host feeding patterns of the Asian tiger mosquito, *Aedes albopictus*, in urban and suburban Northeastern USA and implications for disease transmission. *PLoS Neglected Tropical Diseases*, *8*, e3037. https://doi.org/10.1371/journal.pntd.0003037

Fecchio, A., Pinheiro, R., Felix, G., Faria, I. P., Pinho, J. B., Lacorte, G., … Weckstein, J. (2017). Host community similarity and geography shape the diversity and distribution of haemosporidian parasites in Amazonian birds. *Ecography*, https://doi.org/10.1111/ecog.03058.

Felsenstein, J. (1981). Evolutionary trees from DNA sequences: A maximum likelihood approach. *Journal of Molecular Evolution*, *17*, 368–376. https://doi.org/10.1007/BF01734359

Ferraguti, M., Martínez-de la Puente, J., Muñoz, J., Roiz, D., Ruiz, S., Soriguer, R., & Figuerola, J. (2013). Avian *Plasmodium* in *Culex* and *Ochlerotatus* mosquitoes from southern Spain: Effects of season and host-feeding source on parasite dynamics. *PLoS ONE*, *8*, e66237. https://doi.org/10.1371/journal.pone.0066237

Ferraguti, M., Martínez-de la Puente, J., Roiz, D., Ruiz, S., Soriguer, R., & Figuerola, J. (2016). Effects of landscape anthropization on mosquito community composition and abundance. *Scientific Reports*, *6*, 29002. https://doi.org/10.1038/srep29002

Figuerola, J. (1999). Effects of salinity on rates of infestation of waterbirds by haematozoa. *Ecography*, *22*, 681–685. https://doi.org/10.1111/j.1600-0587.1999.tb00517.x

Foley, D. H., Torres, E. P., Mueller, I., Bryan, J. H., & Bell, D. (2003). Host-dependent *Anopheles flavirostris* larval distribution reinforces the risk of malaria near water. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, *97*, 283–287. https://doi.org/10.1016/S0035-9203(03)90143-X

Fourcade, Y., Keišs, O., Richardson, D. S., & Secondi, J. (2014). Continental-scale patterns of pathogen prevalence: A case study on the corncrake. *Evolutionary Applications*, *7*, 1043–1055. https://doi.org/10.1111/eva.12192

Gager, A. B., Del Rosario Loaiza, J., Dearborn, D. C., & Bermingham, E. (2008). Do mosquitoes filter the access of Plasmodium cytochrome b lineages to an avian host? *Molecular Ecology*, *17*, 2552–2561. https://doi.org/10.1111/j.1365-294X.2008.03764.x

Geue, D., & Partecke, J. (2008). Reduced parasite infestation in urban Eurasian blackbirds (*Turdus merula*): A factor favoring urbanization? *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, *86*, 1419–1425. https://doi.org/10.1139/Z08-129

Gilioli, G., & Mariani, L. (2011). Sensitivity of *Anopheles gambiae* population dynamics to meteo-hydrological variability: A mechanistic approach. *Malaria Journal*, *10*, 294. https://doi.org/10.1186/1475-2875-10-294

Gonzalez-Quevedo, C., Davies, R. G., & Richardson, D. S. (2014). Predictors of malaria infection in a wild bird population: Landscape-level analyses reveal climatic and anthropogenic factors. *Journal of Animal Ecology*, *83*, 1091–1102. https://doi.org/10.1111/1365-2656.12214

Gutiérrez-López, R., Gangoso, L., Martínez-de la Puente, J., Fric, J., López-López, P., Mailleux, M., … Figuerola, J. (2015). Low prevalence of blood parasites in a long-distance migratory raptor: The importance of host habitat. *Parasites & Vectors*, *8*, 189. https://doi.org/10.1186/s13071-015-0802-9

Gutiérrez-López, R., Martínez-de la Puente, J., Gangoso, L., Soriguer, R. C., & Figuerola, J. (2015). Comparison of manual and semi-automatic DNA extraction protocols for the barcoding characterization of hematophagous louse flies (Diptera: *Hippoboscidae*). *Journal of Vector Ecology*, *40*, 11–15. https://doi.org/10.1111/jvec.12127

Gutiérrez-López, R., Martínez-de la Puente, J., Gangoso, L., Yan, J., Soriguer, R. C., & Figuerola, J. (2016). Do mosquitoes transmit the avian malaria-like parasite Haemoproteus? An experimental test of vector competence using mosquito saliva. *Parasites & Vectors*, *9*, 609. https://doi.org/10.1186/s13071-016-1903-9

Hawley, D. M., Hallinger, K. K., & Cristol, D. (2009). Compromised immune competence in free-living tree swallows exposed to mercury. *Ecotoxicology*, *18*, 499–503. https://doi.org/10.1007/s10646-009-0307-4

Hechinger, R. F., & Lafferty, K. D. (2005). Host diversity begets parasite diversity: Bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London Series B*, *272*, 1059–1066. https://doi.org/10.1098/rspb.2005.3070

Hellgren, O., Bensch, S., & Malmqvist, B. (2008). Bird hosts, blood parasites and their vectors – Associations uncovered by molecular analyses of black fly blood meals. *Molecular Ecology*, *17*, 1605–1613. https://doi.org/10.1111/j.1365-294X.2007.03680.x

Higgs, S., & Beaty, B. J. (2005). Natural cycles of vector-borne pathogens. In W. C. Marquardt (Ed.), *Biology of disease vectors* (pp. 167–186). Burlington, NY: Elsevier Academic Press.

Huang, Z. Y. X., Van Langevelde, F., Estrada-Peña, A., Suzán, G., & De Boer, W. F. (2016). The diversity–disease relationship: Evidence for and criticisms of the dilution effect. *Parasitology*, *143*, 1075–1086. https://doi.org/10.1017/S0031182016000536

Huang, Z. Y., Yu, Y., Van Langevelde, F., & De Boer, W. F. (2017). Does the dilution effect generally occur in animal diseases? *Parasitology*, *144*, 823–826. https://doi.org/10.1017/S0031182016002572

Iezhova, T. A., Valkiūnas, G., & Bairlein, F. (2005). Vertebrate host specificity of two avian malaria parasites of the subgenus Novyella: *Plasmodium nucleophilum* and *Plasmodium vaughani*. *Journal of Parasitology*, *91*, 472–474. https://doi.org/10.1645/GE-3377RN

Ishtiaq, F., Clegg, S. M., Phillimore, A. B., Black, R. A., Owens, I. P., & Sheldon, B. C. (2010). Biogeographical patterns of blood parasite lineage diversity in avian hosts from southern Melanesian islands. *Journal of Biogeography*, *37*, 120–132.

Ishtiaq, F., Guillaumot, L., Clegg, S. M., Phillimore, A. B., Black, R. A., Owens, I. P., … Sheldon, B. C. (2008). Avian haematozoan parasites and their associations with mosquitoes across Southwest Pacific Islands. *Molecular Ecology*, *17*, 4545–4555. https://doi.org/10.1111/j.1365-294X.2008.03935.x

Johnson, P. T., Ostfeld, R. S., & Keesing, F. (2015). Frontiers in research on biodiversity and disease. *Ecology Letters*, *18*, 1119–1133. https://doi.org/10.1111/ele.12479

Johnson, P. T., Preston, D. L., Hoverman, J. T., & Richgels, K. L. (2013). Biodiversity decreases disease through predictable changes in host community competence. *Nature*, *494*, 230–233. https://doi.org/10.1038/nature11883

Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. *Nature*, *451*, 990–994. https://doi.org/10.1038/nature06536

Joseph, M. B., Mihaljevic, J. R., Orlofske, S. A., & Paull, S. H. (2013). Does life history mediate changing disease risk when communities disassemble? *Ecology Letters*, *16*, 1405–1412. https://doi.org/10.1111/ele.12180

Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014). Host diversity drives parasite diversity: Meta-analytical insights into patterns and causal mechanisms. *Ecography*, *37*, 689–697. https://doi.org/10.1111/j.1600-0587.2013.00571.x

Kilpatrick, A. M., Daszak, P., Jones, M. J., Marra, P. P., & Kramer, L. D. (2006). Host heterogeneity dominates West Nile virus transmission. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 2327–2333. https://doi.org/10.1098/rspb.2006.3575

Kimura, M., Darbro, J. M., & Harrington, L. C. (2010). Avian malaria parasites share congeneric mosquito vectors. *Journal of Parasitology*, *96*, 144–151. https://doi.org/10.1645/GE-2060.1

Krama, T., Krams, R., Cīrule, D., Moore, F. R., Rantala, M. J., & Krams, I. A. (2015). Intensity of haemosporidian infection of parids positively correlates with proximity to water bodies, but negatively with host survival. *Journal of Ornithology*, *156*, 1075–1084. https://doi.org/10.1007/s10336-015-1206-5

Krams, I., Cīrule, D., Krama, T., Hukkanen, M., Rytkönen, S., Orell, M., … Tummeleht, L. (2010). Effects of forest management on haematological parameters, blood parasites, and reproductive success of the Siberian tit (*Poecile cinctus*) in northern Finland. *Annales Zoologici Fennici*, *47*, 335–346. https://doi.org/10.5735/086.047.0504

Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S., & Degen, A. A. (2004). Relationship between host diversity and parasite diversity: Flea assemblages on small mammals. *Journal of Biogeography*, *31*, 1857–1866. https://doi.org/10.1111/j.1365-2699.2004.01132.x

Lachish, S., Knowles, S. C., Alves, R., Wood, M. J., & Sheldon, B. C. (2011). Infection dynamics of endemic malaria in a wild bird population: Parasite species-dependent drivers of spatial and temporal variation in transmission rates. *Journal of Animal Ecology*, *80*, 1207–1216. https://doi.org/10.1111/j.1365-2656.2011.01893.x

Lacorte, G. A., Felix, G. M., Pinheiro, R. R., Chaves, A. V., Almeida-Neto, G., Neves, F. S., … Braga, E. M. (2013). Exploring the diversity and distribution of neotropical avian malaria parasites – A molecular survey from southeast Brazil. *PLoS ONE*, *8*, e57770. https://doi.org/10.1371/journal.pone.0057770

Lafferty, K. D. (2012). Biodiversity loss decreases parasite diversity: Theory and patterns. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2814–2827. https://doi.org/10.1098/rstb.2012.0110

Legendre, P. (2008). Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, *1*, 3–8. https://doi.org/10.1093/jpe/rtm001

Leisnham, P. T., & Sandoval-Mohapatra, S. (2011). Mosquitoes associated with ditch-plugged and control tidal salt marshes on the Delmarva Peninsula. *International Journal of Environmental Research and Public Health*, *8*, 3099–3113. https://doi.org/10.3390/ijerph8083099

Lillesand, T., Kiefer, R. W., & Chipman, J. (1994). *Remote sensing and image interpretation*. New York, NY: John Wiley & Sons.

LoGiudice, K., Duerr, S. T., Newhouse, M. J., Schmidt, K. A., Killilea, M. E., & Ostfeld, R. S. (2008). Impact of host community composition on Lyme disease risk. *Ecology*, *89*, 2841–2849. https://doi.org/10.1890/07-1047.1

Loiseau, C., Harrigan, R. J., Robert, A., Bowie, R. C., Thomassen, H. A., Smith, T. B., & Sehgal, R. N. (2012). Host and habitat specialization of avian malaria in Africa. *Molecular Ecology*, *21*, 431–441. https://doi.org/10.1111/j.1365-294X.2011.05341.x

Lyimo, I. N., & Ferguson, H. M. (2009). Ecological and evolutionary determinants of host species choice in mosquito vectors. *Trends in Parasitology*, *25*, 189–196. https://doi.org/10.1016/j.pt.2009.01.005

Manguin, S., & Boëte, C. (2011). *Global impact of mosquito biodiversity, human vector-borne diseases and environmental change*. Rijeka, Croatia: Intech open access Publisher. https://doi.org/10.5772/1831

Martínez-de la Puente, J., Eberhart-Phillips, L. J., Carmona-Isunza, M. C., Zefania, S., Navarro, M. J., Kruger, O., … Figuerola, J. (2017). Extremely low *Plasmodium* prevalence in wild plovers and coursers from Cape Verde and Madagascar. *Malaria Journal*, *16*, 243. https://doi.org/10.1186/s12936-017-1892-y

Martínez-de la Puente, J., Martínez, J., Aguilar, R. D., Herrero, J., & Merino, S. (2011). On the specificity of avian blood parasites: Revealing specific and generalist relationships between haemosporidians and biting midges. *Molecular Ecology*, *20*, 3275–3287. https://doi.org/10.1111/j.1365-294X.2011.05136.x

Martínez-de la Puente, J., Martínez, J., Rivero-de-Aguilar, J., Del Cerro, S., & Merino, S. (2013). Vector abundance determines *Trypanosoma* prevalence in nestling blue tits. *Parasitology*, *140*, 1009–1015. https://doi.org/10.1017/S0031182013000371

Martínez-de la Puente, J., Moreno-Indias, I., Hernández-Castellano, L. E., Argüello, A., Ruiz, S., Soriguer, R., & Figuerola, J. (2012). Host-feeding pattern of *Culex theileri* (Diptera: *Culicidae*), potential vector of *Dirofilaria immitis* in the Canary Islands, Spain. *Journal of Medical Entomology*, *49*, 1419–1423. https://doi.org/10.1603/ME12081

Martínez-de la Puente, J., Ruiz, S., Soriguer, R., & Figuerola, J. (2013). Effect of blood meal digestion and DNA extraction protocol on the success of blood meal source determination in the malaria vector *Anopheles atroparvus*. *Malaria Journal*, *12*, 109. https://doi.org/10.1186/1475-2875-12-109

Marzal, A., Ricklefs, R. E., Valkiūnas, G., Albayrak, T., Arriero, E., Bonneaud, C., … Bensch, S. (2011). Diversity, loss, and gain of malaria parasites in a globally invasive bird. *PLoS ONE*, *6*, e21905. https://doi.org/10.1371/journal.pone.0021905

McClintock, B. T., Nichols, J. D., Bailey, L. L., MacKenzie, D. I., Kendall, W., & Franklin, A. B. (2010). Seeking a second opinion: Uncertainty in disease ecology. *Ecology Letters*, *13*, 659–674. https://doi.org/10.1111/j.1461-0248.2010.01472.x

Mendes, L., Piersma, T., Lecoq, M., Spaans, B., & Ricklefs, R. (2005). Disease-limited distributions? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. *Oikos*, *109*, 396–404. https://doi.org/10.1111/j.0030-1299.2005.13509.x

Merino, S., Barbosa, A., Moreno, J., & Potti, J. (1997). Absence of haematozoa in a wild chinstrap penguin *Pygoscelis antarctica* population. *Polar Biology*, *18*, 227–228. https://doi.org/10.1007/s003000050181

Moens, M. A. J., & Perez-Tris, J. (2016). Discovering potential sources of emerging pathogens: South America is a reservoir of generalist avian blood parasites. *International Journal for Parasitology*, *46*, 41–49. https://doi.org/10.1016/j.ijpara.2015.08.001

Muñoz, J., Ruiz, S., Soriguer, R., Alcaide, M., Viana, D. S., Roiz, D., … Figuerola, J. (2012). Feeding patterns of potential West Nile virus vectors in south-west Spain. *PLoS ONE*, *7*, e39549.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Njabo, K. Y., Cornel, A. J., Sehgal, R. N., Loiseau, C., Buermann, W., Harrigan, R. J., … Smith, T. B. (2009). Coquillettidia (*Culicidae*, Diptera) mosquitoes are natural vectors of avian malaria in Africa. *Malaria Journal*, *8*, 193. https://doi.org/10.1186/1475-2875-8-193

Norris, D. (2004). Mosquito-borne diseases as a consequence of land use change. *EcoHealth*, *1*, 19–24. https://doi.org/10.1007/s10393-004-0008-7

Okanga, S., Cumming, G. S., & Hockey, P. A. (2013). Avian malaria prevalence and mosquito abundance in the Western Cape, South Africa. *Malaria Journal*, *12*, 370.

Omumbo, J. A., Hay, S. I., Snow, R. W., Tatem, A. J., & Rogers, D. J. (2005). Modelling malaria risk in East Africa at high-spatial resolution. *Tropical Medicine and International Health*, *10*, 557–566. https://doi.org/10.1111/j.1365-3156.2005.01424.x

Ortego, J., & Cordero, P. J. (2010). Factors associated with the geographic distribution of leucocytozoa parasitizing nestling eagle owls (*Bubo bubo*): A local spatial-scale analysis. *Conservation Genetics*, *11*, 1479–1487. https://doi.org/10.1007/s10592-009-9978-x

Ostfeld, R. S., & Keesing, F. (2012). Effects of host diversity on infectious disease. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 157. https://doi.org/10.1146/annurev-ecolsys-102710-145022

Overgaard, H. J., Ekbom, B., Suwonkerd, W., & Takagi, M. (2003). Effect of landscape structure on anopheline mosquito density and diversity in northern Thailand: Implications for malaria transmission and control. *Landscape Ecology*, *18*, 605–619. https://doi.org/10.1023/A:1026074910038

Palinauskas, V., Valkiūnas, G., Bolshakov, C. V., & Bensch, S. (2008). *Plasmodium relictum* (lineage P-SGS1): Effects on experimentally infected passerine birds. *Experimental Parasitology*, *120*, 372–380. https://doi.org/10.1016/j.exppara.2008.09.001

Patz, J. A., Graczyk, T. K., Geller, N., & Vittor, A. Y. (2000). Effects of environmental change on emerging parasitic diseases. *International Journal of Parasitology*, *30*, 1395–1405. https://doi.org/10.1016/S0020-7519(00)00141-7

Pérez-Tris, J., & Bensch, S. (2005). Diagnosing genetically diverse avian malarial infections using mixed-sequence analysis and TA-cloning. *Parasitology*, *131*, 15–23. https://doi.org/10.1017/S003118200500733X

Randolph, S. E., & Dobson, A. D. M. (2012). Pangloss revisited: A critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology*, *139*, 847–863. https://doi.org/10.1017/S0031182012000200

Reisen, W. K. (2010). Landscape epidemiology of vector-borne diseases. *Annual Review of Entomology*, *55*, 461–483. https://doi.org/10.1146/annurev-ento-112408-085419

Reisen, W. K., Meyer, R. P., Tempelis, C. H., & Spoehel, J. J. (1990). Mosquito abundance and bionomics in residential communities in Orange and Los Angeles Counties, California. *Journal of Medical Entomology*, *27*, 356–367. https://doi.org/10.1093/jmedent/27.3.356

Roche, B., Rohani, P., Dobson, A. P., & Guégan, J.-F. (2013). The impact of community organization on vector-borne pathogens. *The American Naturalist*, *181*, 1–11. https://doi.org/10.1086/668591

Roiz, D., Ruiz, S., Soriguer, R., & Figuerola, J. (2015). Landscape effects on the presence, abundance and diversity of mosquitoes in Mediterranean wetlands. *PLoS ONE*, *10*, e0128112. https://doi.org/10.1371/journal.pone.0128112

Saino, N., Møller, A. P., & Bolzern, A. M. (1995). Testosterone effects on the immune system and parasite infections in the barn swallow (Hirundo rustica): An experimental test of the immunocompetence handicap. *Behavioural Ecology*, *6*, 397–404. https://doi.org/10.1093/beheco/6.4.397

Santiago-Alarcón, D., Palinauskas, V., & Schaefer, H. M. (2012). Diptera vectors of avian Haemosporidian parasites: Untangling parasite life cycles and their taxonomy. *Biological Reviews of the Cambridge Philosophical Society*, *87*, 928–964. https://doi.org/10.1111/j.1469-185X.2012.00234.x

Scordato, E. S., & Kardish, M. R. (2014). Prevalence and beta diversity in avian malaria communities: Host species is a better predictor than geography. *Journal of Animal Ecology*, *83*, 1387–1397. https://doi.org/10.1111/1365-2656.12246

Sehgal, R. N. (2015). Manifold habitat effects on the prevalence and diversity of avian blood parasites. *International Journal for Parasitology: Parasites and Wildlife*, *4*, 421–430.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, *21*, 186–191. https://doi.org/10.1016/j.tree.2005.11.019

Simpson, J. E., Hurtado, P. J., Medlock, J., Molaei, G., Andreadis, T. G., Galvani, A. P., & Diuk-Wasser, M. A. (2012). Vector host-feeding preferences drive transmission of multi-host pathogens: West Nile virus as a model system. *Proceedings of the Royal Society of London B: Biological Sciences*, *279*, 925–933. https://doi.org/10.1098/rspb.2011.1282

Snoeijs, T., Dauwe, T., Pinxten, R., Darras, V. M., Arckens, L., & Eens, M. (2005). The combined effect of lead exposure and high or low dietary calcium on health and immunocompetence in the zebra finch (Taeniopygia guttata). *Environmental Pollution*, *134*, 123–132. https://doi.org/10.1016/j.envpol.2004.07.009

Sol, D., Jovani, R., & Torres, J. (2000). Geographical variation in blood parasites in feral pigeons: The role of vectors. *Ecography*, *23*, 307–314. https://doi.org/10.1111/j.1600-0587.2000.tb00286.x

Svensson, L. (2006). *Identification guide to European passerines*. Thetford, UK: British Trust for Ornithology.

Takken, W., & Verhulst, N. O. (2013). Host preferences of blood-feeding mosquitoes. *Annual Review of Entomology*, *58*, 433–453. https://doi.org/10.1146/annurev-ento-120811-153618

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution*, *30*, 2725–2729. https://doi.org/10.1093/molbev/mst197

Thomas, L., Laake, J. L., Rexstad, E., Strindberg, S., Marques, F. F. C., & Buckland, S. T. (2006). *Distance 6.0. Release 2*. Andrews, UK: Research Unit for Wildlife Population Assessment, University of St.

Tolle, M. A. (2009). Mosquito-borne diseases. *Current Problems in Pediatric and Adolescent Health Care*, *39*, 97–140. https://doi.org/10.1016/j.cppeds.2009.01.001

Valerio, L., Marini, F., Bongiorno, G., Facchinelli, L., Pombi, M., Caputo, B., & Della Torre, A. (2010). Host-feeding patterns of Aedes albopictus (Diptera: Culicidae) in urban and rural contexts within Rome province, Italy. *Vector-Borne and Zoonotic Diseases*, *10*, 291–294. https://doi.org/10.1089/vbz.2009.0007

Valkiūnas, G. (2005). *Avian Malaria Parasites and Other Haemosporidia*. New York, NY: CRC Press.

Ventim, R., Ramos, J. A., Osório, H., Lopes, R. J., Pérez-Tris, J., & Mendes, L. (2012). Avian malaria infections in western European mosquitoes. *Parasitology Research*, *111*, 637–645. https://doi.org/10.1007/s00436-012-2880-3

Vieyra, M. (2006). *A molecular approach to understanding the importance of olfaction in the life history of sea turtles: Turtle olfactory receptor gene phylogeny, allelic diversity and evidence for selection*. Ann Arbor, MI: ProQuest, 299.

Watters, G. T. (1992). Unionids, fishes, and the species-area curve. *Journal of Biogeography*, *19*, 481–490. https://doi.org/10.2307/2845767

Wedekind, C., & Følstad, I. (1994). Adaptive or nonadaptive immunosuppression by sex hormones? *The American Naturalist*, *143*, 936–938. https://doi.org/10.1086/285641

Wood, M. J., Cosgrove, C. L., Wilkin, T. A., Knowles, S. C. L., Day, K. P., & Sheldon, B. C. (2007). Within-population variation in prevalence and lineage distribution of avian malaria in blue tits, *Cyanistes caeruleus*. *Molecular Ecology*, *16*, 3263–3273. https://doi.org/10.1111/j.1365-294X.2007.03362.x

Wood, C. L., Lafferty, K. D., DeLeo, G., Young, H. S., Hudson, P. J., & Kuris, A. M. (2014). Does biodiversity protect humans against infectious disease? *Ecology*, *95*, 817–832. https://doi.org/10.1890/13-1041.1

Zhang, Y., Wu, Y., Zhang, Q., Su, D., & Zou, F. (2014). Prevalence patterns of avian *Plasmodium* and *Haemoproteus* parasites and the influence of host relative abundance in southern China. *PLoS ONE*, *9*, e99501. https://doi.org/10.1371/journal.pone.0099501

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Ferraguti M, Martínez-de la Puente J, Bensch S, et al. Ecological determinants of avian malaria infections: An integrative analysis at landscape, mosquito and vertebrate community levels. *J Anim Ecol*. 2018;87:727–740. https://doi.org/10.1111/1365-2656.12805