Factors affecting the distribution of haemosporidian parasites within an oceanic island

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Abstract

Understanding how different ecological and evolutionary processes influence the distribution of pathogens within the environment is important from many perspectives, including for wildlife epidemiology, evolutionary ecology and conservation. The simultaneous use of ecological and evolutionary frameworks together can enhance our conceptual understanding of host-parasite interactions, however such studies are rare in the wild. Using samples from 12 bird species caught across all habitats existing on an oceanic island, we evaluated how environmental variables, parasites host specificity, and parasite phylogenetic relationships determine the distribution and prevalence of haemosporidians (*Haemoproteus*, *Plasmodium* and *Leucocytozoon*) in the wild living avifauna. Differences were found in the prevalence of *Plasmodium,* but not *Leucocytozoon*, strains between habitats. The warmest temperature best predicted *Plasmodium* prevalence in the low altitude habitats, which had the highest incidence of *Plasmodium*. The prevalence of *Leucocytozoon* lineages was associated with natural factors, i.e. rainfall, temperature and habitat, but the two most important predictors (from model averaging) for models of *Leucocytozoon* were anthropogenic: poultry farms and distance to a water reservoir. We found no relationship between local (Tenerife) versus global host range indexes (which assess the diversity of hosts that a parasite is observed to infect), thus global generalist lineages do not behave in the same way on Tenerife (i.e. they infected less avian hosts than was expected). Phylogenetic analysis revealed that the most abundant haemosporidians on Tenerife grouped with lineages found in African host species. Our data indicate that climatic and anthropogenic factors, plus proximity to the African mainland, are the main factors influencing the presence and distribution of avian haemosporidians on Tenerife. Future climate projections for the archipelago foresee significant temperature increases, which would, given our results, increase rates of *Plasmodium* infection in bird species in all habitats. Such patterns could be of concern if they increase mortality rates in the unique avifauna of these islands.

Keywords: avian haemosporidian, Canary Islands, community level, environmental variables, host

specificity, oceanic islands, parasite biogeography.

1. Introduction

Knowledge of the factors that shape parasite distributions in space and across host species is key to understanding how host-parasite interactions influence ecological and evolutionary processes (Anderson and May, 1978; May and Anderson, 1978; Fallon et al., 2003). Such information is especially relevant to predicting spatial variation in infection risk and to unravelling host-parasite coevolution (Apanius et al., 2000; Ricklefs et al., 2004; Wilder et al., 2015; Gonzalez-Quevedo et al., 2016). The prevalence and heterogeneous distribution of haemosporidian parasites (protozoan parasites from the genera *Haemoproteus*, *Plasmodium* and *Leucocytozoon*, which are blood parasites that infect vertebrates around the globe) in wild animals make them a useful model for understanding how pathogen distributions vary in and among geographical locations (Ellis et al., 2015).

Parasite distributions within and among hosts can be affected by the evolutionary history of a given host-parasite relationship (Dybdahl and Storfer, 2003; Poulin and Mouillot, 2004; Szöllősi et al., 2011). Long co-evolutionary relationships may mean that host-specific parasites (specialists) after adapting to a single host's immune system, achieve higher prevalence than parasites capable of infecting multiple than one host species (i.e. generalist parasites). This predicted outcome is known as the "Trade-off" hypothesis (Poulin, 1988; Poulin and Mouillot, 2004). However, it is also plausible to predict the opposite pattern: i.e. generalist parasites due to their ability to colonise new hosts reach higher prevalence than specialist parasites, a hypothesis known as the "Niche-breadth" hypothesis (Brown, 1984). Interestingly, both host specialism and generalism appear to be successful strategies for parasites in terms of colonising new areas (e.g. Drovetski et al., 2014; Medeiros et al., 2014). In the case of specialists associating with an abundant and widespread host, the specialist parasites will colonise new areas as the successful host colonises new areas (Lima and Bensch, 2014). The host ranges of parasite lineages often provide insight into the geographic origin of the parasites and the limits of their transmission. For example, the number of geographical areas occupied by a parasite strain seems to be related to their host specificity and abundance, such as has been showed to occur with forest birds of northwestern Africa and northwestern Iberian Peninsula (Mata et al., 2015). Finally, phylogenetic constraints will also affect prevalence if the degree of specialization of a parasite lineage is phylogenetically dependent (e.g. Hellgren et al., 2009; Loiseau et al., 2012, but see Szöllősi et al., 2011). For example, phylogenetically related parasites may show similar prevalence because of their related life cycles and transmission pathways (Kaiser et al., 2010).

In addition to phylogenetic relatedness and host-specificity, climatic and landscape features have been highlighted as important in determining prevalence and transmission in haemosporidians (Wood et al., 2007; Mordecai et al., 2013; Pérez-Rodríguez et al., 2013a). Such findings are explained by the environmental conditions that vectors and pathogens need to complete their life cycles (Guthmann et al., 2002; LaPointe et al., 2010; 2012). For example, temperature and water availability across altitudinal gradients appear to be important in explaining haemosporidians infection patterns (Zamora-Vilchis et al., 2012; Atkinson et al., 2014), because both factors play an important role in vector larval development (Mordecai et al., 2012; Okanga et al., 2013). However, the picture may be complicated by anthropogenic factors (Altman and Byers, 2014). For example, humans greatly affect the distribution of water across the landscape (Smith et al., 2002), which can then shape both host and vectors distributions (Smit et al., 2007; Smit and Grant, 2009). Importantly, animal husbandry appears to be a key factor governing the distribution of parasites because domestic animal populations, or the effect of their farming on the local habitat, can create disease hotspots (Patz et al., 2000; Carrete et al., 2009; Gonzalez-Quevedo et al., 2014).

Habitat effects on avian haemosporidian assemblages have been analysed mostly at the local scale, or using single species or restricted subsets of the species in the avian community. Such studies have provided evidence for climatic, geographical, and anthropogenic factors explaining the distribution, prevalence, and richness of avian haemosporidians (Sehgal et al., 2011; Pérez-Rodríguez et al., 2013; Gonzalez-Quevedo et al., 2014; Fairfield et al., 2016). However, we have a limited knowledge of how habitat and environmental changes can determine distribution of avian haemosporidians at the community level (Loiseau et al., 2012, Laurance et al., 2013; Oakgrove et al., 2014). Oceanic islands are useful places to study ecology, evolutionary biology and biogeography due to their relative simplicity in terms of biodiversity and ecological interactions (Emerson, 2002). For the aforementioned reasons, oceanic islands are also excellent scenarios to assess haemosporidian parasite assemblages, and study the factors determining their distributions and prevalence within and among islands (Cornuault et al., 2013; Ricklefs et al., 2016). Despite improvements in our knowledge of parasite diversity and establishment in relation to island biogeography (e.g. Ishtiaq et al., 2010; Svensson-Coelho and Ricklefs, 2011; Illera et al., 2015), little is known about the relative importance of different ecological factors in determining the prevalence and distribution of parasites within such ecosystems. This information is especially important for oceanic islands, which are often biodiversity hotspots, where predictions on future global climate change foresee a significant loss of biodiversity (Wetzel et al., 2012; Harter et al., 2015).

The Canary Islands is a volcanic archipelago of seven main islands, spanning a total area of ca. 7,500 km^2, in the Atlantic close to the northern-eastern African continent (Fig. 1). The easternmost (Fuerteventura) and westernmost (La Palma) islands are situated about 100 and 460 km off the African coast, respectively and there is an east-west island age gradient with the oldest islands being Fuerteventura (≈ 20 million years) and the youngest El Hierro (≈ 1.2 m.y.). The Canary Islands have become a focus for ecology, evolutionary and biogeography studies (e.g. Juan et al., 2000; Illera et al., 2012, 2016; Spurgin et al., 2014; Stervander et al., 2015). Most studies on avian pathogens in the Canary Islands have been performed on individual host species (e.g. Illera et al., 2008; Spurgin et al., 2012; Pérez-Rodríguez et al., 2013b; Barrientos et al., 2014; Gutiérrez-López et al., 2015; Illera et al., 2015). However, single species approaches make it difficult to draw general and comprehensive interpretations about host-parasite relationships, especially when contrary results are obtained. For instance, Pérez-Rodríguez et al. (2013b) found a reduction in parasite richness and diversity in blackcaps (*Sylvia atricapilla*) across the Macaronesian islands compared with the mainland, but no impoverishment was found in the spectacled warbler (*Sylvia conspicillata*) (Illera et al., 2015).

Therefore, studies at the community level are necessary to understand the general mechanisms that structure parasite communities in ecosystems (Olsson-Pons et al., 2015). The Canary Islands with its diversity of ecosystems and rich endemic biota provides an excellent system in which to do this.

Here, we use an island community dataset of parasite infection across terrestrial bird species to investigate the relative effects of habitat, parasite host-specificity, and parasite phylogenetic relationships on the distribution and prevalence of avian haemosporidians. We focus on the island of Tenerife because, 1) it is the largest (2,034 km^2) and highest (3,718 m a.s.l.) island in the Canary Islands, and 2) it contains an exceptional ecosystem diversity (see below) across which to disentangle the factors influencing the distribution and prevalence of haemosporidians parasites at the community level. Our specific aims are as follows. First, to assess the prevalence of haemosporidian lineages across the avian assemblages in the different habitats on Tenerife (see below). Second, to evaluate the importance of environmental variables such as climatic (i.e. temperature and precipitation), anthropogenic and topographical features in determining prevalence across different habitats and host species. Here we hope that the varying combination of these factors across habitats may allow us to unravel their relative effects and improve our understanding of haemosporidian prevalence across habitats (Pérez-Rodríguez et al., 2013). Third, to examine the host specificity of lineages detected on Tenerife and compare them with those detected globally with the final aim of understanding how host-specificity may influence parasite prevalence or distribution. We predict that generalist lineages observed around the world will be also be generalists on Tenerife, and therefore we expect to find a positive association between both indexes. In addition, a positive association between the number of hosts a parasite infects and individuals infected would suggest that parasite lineages capable of infecting multiple hosts will be more abundant, supporting the ‘Niche breadth’ hypothesis. A negative relationship (i.e. specialist parasites infecting single hosts but many individuals) would support the “Trade-off” hypothesis. Fourth, to assess phylogenetic relationships between parasite lineages to understand how their evolutionary history may influence the parasite lineage composition in terms of prevalence and habitat specificity. Here we predict to find more African than European lineages (in terms of richness) infecting Canarian birds, due to the proximity of Tenerife to the African mainland. Analysing an avian multi-host, multi-parasite community will help us to unravel the relative importance of evolutionary and ecological factors determining the prevalence and distribution of the parasites.

2. Materials and methods

2.1. Study area and sampling

Tenerife supports five well defined vegetation habitats related to geographic orientation and altitude: coastal, thermophilous, laurel woodlands, pine forests, and alpine habitat (del-Arco et al., 2006a). Dispersed xerophytic shrubs occurring in the lowlands represent the coastal habitat. At higher altitudes (300-550 m a.s.l.) a type of Mediterranean forest termed thermophilous woodland exists, characterised by dispersed patches of endemic palms and trees. On northern slopes (550–1100 m a.s.l.), evergreen laurel forest, the most humid habitat in Tenerife, exists, consisting of ca 20 tree species. Above these forests a monospecific conifer forest (1,100-2,000 m a.s.l.) of Canary island pine (*Pinus canariensis*) dominates. Finally, alpine habitat occurs above 2000 m a.s.l with dispersed leguminous shrubs dominating the vegetation. This last habitat is characterised by low annual rainfall and extreme contrasts in day/night temperatures (with minimum values below -16ºC).

Birds were sampled using mist nets during May and August of 2011 from 19 localities spanning the geography of each habitat within Tenerife. With such a design we ensured that we sampled all the environmental variability within each habitat class. Most of the sampled bird species are not habitat specialists and can be found in all habitats and altitudes on Tenerife (Martín & Lorenzo, 2001). Individuals were captured in four localities per habitat, except in the alpine habitat where only three localities were sampled due to its smaller area (Fig. 1). All birds were ringed with unique aluminium rings from the Spanish authority, and classified as juveniles or adults based on feather moult pattern (post-juvenile moult was partial, whereas the post-breeding moult in adults was complete, authors unpublished data). Blood samples (*c*. 20-40 µl) were taken by brachial venipuncture and stored at room temperature in 1.5 ml screw-capped vials filled with 1ml of absolute ethanol and kept at room temperature. After sampling, individual birds were released in the same place they were trapped.

2.2 Molecular procedures

DNA was extracted from blood using a modified salt method (Richardson et al., 2001). The molecular technique described by Griffiths et al. (1998) was used to confirm sex of the bird and verify the quality of DNA samples. Avian haemosporidian parasites (*Haemoproteus*, *Plasmodium* and *Leucocytozoon*) were screened for using a nested polymerase chain reaction (PCR) method described by Hellgren et al. (2004), which amplifies a 479 base pair (bp) fragment of the mitochondrial cytochrome *b* gene. PCR runs were performed including two positive and two negative controls, and the reagents and conditions followed Spurgin et al. (2012). The entire procedure was replicated twice to check repeatability on all samples to ensure the accuracy of results. When results were not in agreement a third PCR was performed, and only results that amplified twice were considered positives (Spurgin et al., 2012). Amplicons (only one positive per sample) were sequenced on an ABI Prism 3730 genetic analyser using the conditions described in Illera et al. (2015).

2.3. Data analysis

2.3.1. Parasite prevalence

The prevalence of each parasite lineage per host species was calculated as the proportion of individuals of that species infected by that lineage. All prevalence comparisons were done separately for each parasite genus (*Haemoproteus*, *Plasmodium*, and *Leucocytozoon*).

2.3.2. Environmental variables

We selected 14 environmental variables that may be related to haemosporidian parasite prevalence based on previous studies (Carrete et al., 2009; Gonzalez-Quevedo et al., 2014): Vegetation habitat (HABITAT), mean annual temperature (MEANTEMP), minimum temperature of the coldest month (MINTEMP), maximum temperature of the warmest month (MAXTEMP), temperature seasonality (TEMPSEAS), mean temperature of the wettest quarter (MT_WETTQUAR), mean temperature of the driest quarter (MT_DRIQUAR), mean temperature of the warmest quarter (MT_WARMQUAR), mean temperature of the coldest quarter (MT_COLDQUAR), average monthly precipitation (PRECIP), and altitude (ALT). In addition, we included the distance to artificial water reservoirs (DISTWATER), distance to livestock farms (DISTFARM) or, alternatively, distance to poultry farms (DISTPOUL). DISTPOUL was used as an alternative predictor to DISTFARM to investigate the specific influence of poultry farms as potential reservoirs for avian haemosporidians as opposed to general farm characteristics (Gonzalez-Quevedo et al., 2014). DISTWATER was included in the analyses because artificial water reservoirs are the main source of water in Tenerife where natural standing bodies of water are scarce. All environmental variable calculations were carried out in ArcGIS version 10 and R (R Development Core Team, 2011). Climatic variables were obtained from the WorldClim database (Hijmans et al., 2005) at a resolution of 30 arc seconds (1 km). ALT was calculated at a resolution of 90 m from digital elevation models obtained from the Shuttle Radar Topography Mission Digital Elevation Database version 4.1 (Consortium for Spatial Information, www.cgiar-csi.org). Sampling point distance from water (DISTWATER), farm (DISTFARM) and poultry farm (DISTPOUL) was calculated using ‘proximity’ tool implemented in ArcGIS 10. Polygon layers for the characteristic in question were obtained from the census of farms made by the government of Tenerife (http://www.tenerife.es/planes/). All environmental variables were continuous except HABITAT which was categorical. Distance variables were log-transformed prior to fitting models.

For each haemosporidian genus the influence of environmental variables on prevalence was assessed using Generalised Linear Mixed Models (GLMMs) with haemosporidian genus presence/absence in individual birds as the response variable and locality as random effect with a binomial error distribution. Overdispersion of residuals was checked for and not detected. We implemented a model selection approach (Burnham and Anderson, 2001) to compare the relative fit of competing models, using Akaike's information criterion (AIC) as the measure of model fit. First we compared AICs for single-predictor models to assess the relative importance of each one. Prior to running multi-predictor models, colinearity between each pair of predictor variables was evaluated using pairwise bivariate correlations in PASW Statistics version 18 (SPSS Inc. 2009, Chicago, IL, USA). When a pair of variables reached a correlation coefficient > 0.7, only the variable with the lowest single-predictor AIC (i.e. the highest fit) was included in the multi-predictor model. After excluding highly correlated variables we ran all combinations of predictors and recorded the AIC, ΔAIC (the difference between the best model's AIC and that of the model in question) and the model weight (a relative measure of model fit in comparison to all other models). We considered models with $\Delta AIC \leq 2$ as having sufficient support (Burnham and Anderson, 2004). We also performed model averaging on all models within $\Delta AIC \leq 2$, of the best model, to estimate the relative importance of predictors using the R package MuMIn (Barton, 2013). GLMMs were performed in R (R Development Core Team, 2011).

2.3.3. Phylogenetic analyses and host specificity index

We evaluated the phylogenetic relationships between parasite lineages to infer how their evolutionary history may influence the composition of parasite lineages on Tenerife in terms of prevalence and habitat specificity. Parasite sequences were edited and aligned using BIOEDIT version 7.0.9 (Hall, 1999). A BLAST-search against sequences from GenBank and the MalAvi database for avian malaria (Bensch et al., 2009) was performed to determine whether the parasite lineage had been identified previously. A phylogenetic tree was constructed using all mitochondrial cytochrome *b* sequences obtained in this study together with a group of other selected haemosporidian sequences (n = 26, chosen on the basis of the highest levels of sequence similarity) downloaded from MalAvi database.

Leucocytozoon buteonis (DQ177273) was included as a divergent phylogeographic lineage in the analysis and *Haemoproteus columbae* (GenBank accession number AF495554) was used as outgroup. jModelTest version 0.1.1 (Posada, 2008) was used to find the model of evolution that best fits the data according to the Bayesian information criterion. The General Time Reversible model including rate variation among sites model (GTR + G) was the model selected in jModelTest. Phylogenetic relationships were assessed by Bayesian inference using MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003). Markov chains were run for 10,000,000 generations and trees were sampled every 1000 generations. The first 2,500 trees were discarded as burn-in generations. Two independent runs were performed in order to ensure that posterior probabilities were similar. FigTree v. 1.3.1 (Rambaut, 2009) was used to visualise the tree.

We tested the association between the number of host species and individuals infected by a parasite lineage with a Generalized Linear Model (GLM), with number of individuals infected as the response variable, number of host species infected as explanatory variable and parasite genus as fixed factor. A positive association between host numbers and individuals infected would suggest that those parasite lineages capable of infecting multiple hosts will be more abundant, which would support the ‘Niche breadth’ hypothesis. In contrast, a negative relationship, with parasite lineages only infecting single hosts, would support the “Trade-off” hypothesis. The host range of each parasite lineage was measured using the standardised host specificity index S_{TD}* (Poulin and Mouillot, 2003, 2005). This index takes into account the number of host species a parasite lineage was able to infect and the taxonomic distance among hosts. We calculated the taxonomic distance among hosts counting the number of steps needed to take for reaching their common ancestor (Hellgren et al., 2009). Because we only analysed passerines our taxonomic levels were constrained to species, genera and family. For parasite lineages infecting only one host species we assigned a fixed S_{TD}* value of 1. The host range index was calculated for each parasite lineage, (i) using only data from the current study and, (ii) with data available from the MalAvi database version 2.0.4 (Bensch et al., 2009). This allows us to compare the host specificities of parasites on Tenerife with their host specificities in other parts of their distributions to evaluate if generalist lineages globally act in the same way on Tenerife. Here, we predict that generalist lineages will also be generalists on Tenerife, therefore we expect to find a positive association between both indexes. Our final aim was to understand how host-specificity may influence parasite prevalence or distribution patterns on Tenerife.

3. Results

3.1. Richness and prevalence of parasites

A total of 1,188 individuals from 18 bird species from the five habitats in Tenerife were screened for haemosporidian infection. The order Passeriformes, with 14 species and 99% of the individuals, was the best sampled bird group in our analysis (Table 1). Overall, *Leucocytozoon* was the dominant parasite genus detected, infecting 159 individuals across nine bird species. *Plasmodium* showed a lower prevalence with 44 infected individuals across nine bird species, while *Haemoproteus* was not detected. Genetic characterisation identified 14 distinct lineages: four for *Plasmodium* and 10 for *Leucocytozoon* (Table 1). All *Plasmodium* sequences were identical to lineages described elsewhere (Bensch et al., 2009). From these, LK06 was the most common lineage, found in 73% of the *Plasmodium* infected individuals (Table 1). The remaining lineages were less common: SYAT05 (18%), SGS1 (7%), and AFTRU5 (2%). From the 10 *Leucocytozoon* lineages found, nine were previously described (CIAE02, PARUS21, REB11, RECOB3, TUMER01, YMWD1, H157, H173 and L_AFR161), while the remaining lineage was identified in the blue tit (*Cyanistes teneriffae*) wild canary (*Serinus canarius*), and blue chaffinch (*Fringilla teydea*) for the first time (CYACA01 GenBank accession number KX002266). The most common *Leucocytozoon* lineage was REB11 (73%), followed by H157 (11%), H173 (7%) and L_AFR161 (3%). The last three *Leucocytozoon* lineages, together with the *Plasmodium* LK06, showed the highest mean number of individuals infected per host species (ranging from 9.67 ± 4.02 to 0.42 ± 0.26 individuals infected, Fig. S1).

Considering only host species where six or more individuals (n = 13 species) were screened (this resulted in 12 species included having > 14 individuals screened, which is considered an acceptable sample size, see below), there was extensive heterogeneity between host species in parasite prevalence, ranging from 0 - 13.1% for *Plasmodium* and 0 - 42.2% for *Leucocytozoon*. Of the non-passerines, we found one sparrowhawk (*Accipiter nisus*), from two individuals sampled, infected with *Leucocytozoon* (CIAE02). This lineage was previously found in other Accipitridae species (Bensch et al., 2009). Because of the low number of infection found in some species (Table 1), only species with a sample size of at least 14 individuals (12 species) were used in the analysis of the influence of environmental variables. Such a number of individuals analysed provides acceptable levels of data for the statistical analyses, since only a sample size below 10 individuals could compromise the accurate detection of prevalence (see Jovani and Tella, 2006 for a review on this matter). The three avian species with the highest prevalence values for *Plasmodium* were the Sardinian warbler (*Sylvia melanocephala*; 13.4%), the blackbird (*Turdus merula*; 13.1%) and the common chaffinch; *Fringilla coelebs* (7.7%). The highest prevalences of *Leucocytozoon*, were in the blue chaffinch (42.2%), the wild canary (26.5%), the Canarian blue tit (24.9%), and the Sardinian warbler (18.5%) (Table 1).

3.2. Parasite distribution

Across all bird species (with ≥ 14 individuals) *Plasmodium* infection was highest in the low altitude habitats of the coastal zone and in the thermophilous woodland (Fig. 2). After assessing colinearity between environmental predictors and relative importance of these in explaining the distribution of parasites, the following six variables were analysed in multi-predictor GLMMs for both *Plasmodium* and *Leucocytozoon*: MT_WARMQUART, DISPOUL, DISTWATER, DISTFARM, PRECIP and HABITAT. Single-predictor GLMM analyses showed that MT_WARMQUAR was the best predictor (positively correlated) of *Plasmodium* infection, whereas DISTPOUL was most strongly positively correlated with *Leucocytozoon* infection (Table S1). In the multi-predictor models, the best model for

Plasmodium included only MT_WARMQUAR (with a model weight of 0.18, an odd ratio of 1.60, and a relative importance of 0.84), and all models with a ΔAIC < 2 contained this predictor (Table 2). All the other predictors had a relative importance below 0.48 (Table 2). Regarding *Leucocytozoon* infection, the best multi-predictor model was the one including all six predictors (with a model weight of 0.25, Table 2). The most important predictor for models of *Leucocytozoon* after model averaging was DISTPOUL with an odd ratio of 1.00 and a relative importance of 0.92, followed by DISTWATER with an odd ratio of 1.00 and a relative importance of 0.88 and HABITAT (0.80). The other three predictors had relative importance below 0.68 (Table 2).

3.3. Phylogenetic relationships and host specificity

Two of the four *Plasmodium* lineages (LK06 and SYAT05) and seven of the nine *Leucocytozoon* detected in passerine hosts (H157, H173, L_AFR161, CYACA01, REB11, RECOB3, and YMWD1) are grouped within African lineages (from hosts either breeding or wintering across pre and sub-Saharan Africa) with high nodal support (Fig. 3, nodes A and B). The other two *Plasmodium* lineages (AFTRU5 and SGS1) are grouped with lineages distributed worldwide (nodes C and D). The remaining two *Leucocytozoon* lineages (PARUS21 and TUMER01) were grouped within European lineages (nodes E and F). The infections observed on Tenerife are clearly dominated by the presence of African lineages (97% of individuals), while the importance of European and global lineages was very limited (3%) (Table 1 and Fig. 3).

Host specificity varied among the haemosporidian lineages found (Fig. 4). Half of the lineages were detected in only a single host species, while the remaining lineages appeared in two or more species (Table 1). Number of individuals infected was positively related to the number of host species infected per haemosporidian lineage ($R^2 = 0.78$, $P < 0.01$), but there was no effect of parasite genus ($P > 0.77$). Considering the data obtained from Tenerife the average standardised host range index S_{TD}* for *Plasmodium* and *Leucocytozoon* was very similar: 3.18 and 3.20, respectively. The most generalist lineages were LK06 (6.72) for *Plasmodium* and REB11 (8.5) for *Leucocytozoon* (Fig. 4).

Other lineages with high values of $S_{TD}*$ were the lineages H157, H173 and L_AFR161, which acted as generalists on Tenerife, but mainly infected endemic taxa (Fig. 4 and Table 1). Considering data available elsewhere, those *Plasmodium* lineages considered to be global generalists, such as SGS1 (global $S_{TD}* = 49$) or SYAT05 (global $S_{TD}* = 13.1$), were only found in two and one bird species, respectively in Tenerife (Fig. 4). Indeed, we did not find a significant relationship between local (Tenerife) versus global values of $S_{TD}*$ ($r = -0.39$, $P = 0.19$).

4. Discussion

The results from our study investigating the distribution of avian haemosporidian blood parasites on Tenerife show that infection prevalence differed between parasite genera (*Haemoproteus*, *Plasmodium*, and *Leucocytozoon*) and habitats, with a distribution primarily dependent on climatic and anthropogenic factors. The highest *Plasmodium* prevalence was found in the lowest and warmest (i.e. coastal zone and thermophilous) habitats. In concordance with this, the environmental variable that best predicted the distribution of *Plasmodium* infection across Tenerife was temperature (mean temperature of the warmest quarter). This finding is logical as *Plasmodium* species need constant temperatures between 13 ºC and 30 ºC to complete their life cycle, with optimal growth reached between 21 ºC to 28 ºC (Fialho and Schall, 1995; LaPointe et al., 2010). On Tenerife, such temperatures are usually reached during the warmest period (mean temperature of 21.6 ºC and 21.1 ºC for the coastal zone and thermophilous woodland, respectively, del-Arco et al., 2006). However, the other habitats on Tenerife (i.e. laurel and pine woodlands, and the alpine zone) often have temperatures well below 20 ºC (del-Arco et al., 2006). Such colder temperatures will retard *Plasmodium* development, thus explaining the low prevalence of parasites in those habitats (Fig. 2).

The best model explaining the distribution of *Plasmodium* infection contained MT_WARMQUAR, but other equally well-supported models ($\Delta AIC < 2$) included the distance to a poultry farm (DISTPOUL) and the distance to water reservoirs (DISTWATER). DISTPOUL was also the most important predictor in determining the distribution of *Leucocytozoon* in Tenerife. The best multi-predictor model for *Leucocytozoon* also included DISTPOUL, DISTWATER, MT_WARMQUAR, HABITAT and PRECIP (rainfall). However, according to the relative importance of each predictor after model averaging of models, two anthropogenic factors had the highest relative importance: DISTPOUL (with a relative importance of 0.92) and DISTWATER (0.88). These data provide a clear example of how specific anthropogenic factors are associated with increased haemosporidian prevalence. In this case, proximity to poultry farms and to artificial water reservoirs appeared to strongly favour *Leucocytozoon* transmission. Similar results have been detected for Berthelot's pipit (*Anthus Berthelotii*) in Tenerife, with poultry farms being associated with elevated *Plasmodium* infection rates (Gonzalez-Quevedo et al., 2014), with interesting subsequent effects on the local structuring of immunogenetic variation (Gonzalez-Quevedo et al., 2016). Elevated levels of infection may be due to increased densities of wild birds, or vectors, around such poultry farms because of the environmental conditions they create (e.g. more food for wild birds, more water for vectors). Alternatively, the poultry themselves could directly act as haemosporidian reservoirs (the lineage SGS1 has been found in jungle fowl), though this has not been confirmed in Tenerife (Gonzalez-Quevedo et al., 2014). The additional association of *Leucocytozoon* with DISTWATER and PRECIP confirms the importance of water in providing suitable habitat for vector larvae development, as has been shown in many previous studies (e.g. Galardo et al., 2009; Lachish et al., 2011; Gonzalez-Quevedo et al., 2014). Finally, for *Leucocytozoon*, the best multi-predictor model included HABITAT. The highest *Leucocytozoon* prevalence levels were reached on Pine and Thermophilous forests and the lowest in the Laurel forest (Fig. 2), which may suggests some kind of habitat specialisation related with the woodland type, which could be explained by constraints in the life cycles of the parasites or their vectors (Pérez-Rodríguez et al., 2013a).

The parasite lineages that showed the highest prevalence were those with the widest host distributions; i.e. those appearing in three or more species and more than one family (Table 1, Fig. S1). These findings contrast with the 'trade-off' theory that predicts a higher prevalence of specialist than generalist parasites (Futuyma and Moreno, 1988; Garamszegi, 2006). However, these results do support the alternative ‘Niche breadth’ hypothesis (Brown, 1984), which suggests that those parasite lineages capable of infecting multiple hosts will be more abundant and, consequently, expand their range distribution further than host-specific parasites (Drovetski et al., 2014). Remarkably, we did not find a significant association between local (Tenerife) and global (elsewhere) standardised host range indexes, which suggests that generalist lineages recorded around the world do not behave in the same way on Tenerife (i.e. they infected less avian hosts than was expected). We acknowledge that the absence of such an association could be biased on the limited number of species (n = 12) screened on Tenerife, and further studies including more species could, potentially, lead to different results. However, the species studied on Tenerife are the most common and abundant in Tenerife (Martín and Lorenzo, 2001) and represent the majority (12 out of 15) of the common resident passerines on the island we feel confident about the validity of the pattern found on Tenerife.

Our results on prevalence and specificity could be explained by host adaptations to the island environments (i.e. island syndromes) such as density compensation phenomenon (Cody, 1985), and a depauperate genetic variation in hosts (Wikelski et al., 2004; Tella and Carrete, 2008, but see Matson, 2006). According to the density compensation hypothesis, niche expansion of island birds (undergo ecological release) would be associated with higher abundances than their mainland counterparts. Thus, the high avian population densities reached on islands could facilitate the infection of multiple avian species by the same pathogen lineage. Such a situation could enable vectors to use resources (i.e. avian hosts) from which they were barred on the mainland. In contrast, the ‘depauperate genetic variation’ hypothesis suggests that island host populations, which have reduced genetic variation compared to mainland counterparts (Clegg, 2012; Illera et al., 2016), will have less immunogenetic variation (Agudo et al., 2011) and thus be more susceptible to infection by generalist lineages. To understand how the distribution of haemosporidian lineages determine the host abundances could shed light on such matter. However, in a recent study relating haemosporidian parasite abundance and the population abundance of their avian hosts in the Lesser Antilles, Ricklefs and co-workers (2016) found mixed results. Thus, they provided both positive and negative associations between the relative abundance of three avian species with the relative abundance of their haemosporidian lineages. The inverse relationship may suggest a strong and negative influence of parasites on the population density of their hosts but, contrarily, the positive relationship may indicate a stronger immune response in some avian hosts with a limited negative role for the haemosporidian parasites (Ricklefs et al., 2016). Interestingly, those lineages with the ability to infect multiple hosts, as a result of host switching, are also the most likely to colonise new oceanic islands (Beadell et al., 2009). This physiological plasticity to exploit different hosts could result in higher rates of survival and persistence (Richards et al., 2006; Hellgren et al., 2009).

Despite large sample sizes (14 lineages in *ca.* 1,200 birds), we detected low parasite lineage diversity at the community level, with only two lineages responsible for 73% of infections. This suggests that island haemosporidian communities are impoverished compared with mainland communities. At the community level Hellgren et al. (2011) studying the passerine bird community on the oceanic island of São Miguel (Azores) found lower prevalence and richness of haemosporidian compared to their continental counterparts. Lower haemosporidian richness was also documented on selected bird species in other Macaronesian archipelagos (Pérez-Rodríguez et al., 2013, Barrientos et al., 2014, but see Illera et al., 2015) compared to their mainland populations. This lower richness could be a consequence of the colonisation process of hosts where only a subset of individuals (and their parasites) arrive and become established on the islands (MacLeod et al., 2010). However, it may also suggest a scenario with complex interactions among vectors, hosts and environmental features. This last idea is further supported by two results: a) the low prevalence of the *Plasmodium* lineages SGS1 and SYAT05 on Tenerife, two of the most widely distributed haemosporidian lineages globally (Bensch et al., 2009), and, b) the absence of the widespread *Haemoproteus* genus. The absence of *Haemoproteus* could be explained by a limited availability of appropriate vectors in Tenerife, since there is a specific association between the *Haemoproteus* lineages and their dipteran vectors (Martínez-de la Puente et al., 2011). We screened all habitats in Tenerife, habitats that are largely similar to the mainland areas/habitats where these lineages are common. Therefore, our result may indicate that on Tenerife either the abundance of the competent vectors, climatic conditions for transmission or, physiological and behavioural adaptations of the vectors may differ compared to the mainland (Ishtiaq et al., 2008; Martínez-de la Puente et al., 2011; Santiago-Alarcon et al., 2012; Medeiros et al., 2013). Studies on the distribution and abundance of dipteran vectors transmitting haemosporidians in Tenerife are now needed, along with common-garden experiments using different hosts, vectors, and parasites, to disentangle the environmental conditions and specificity of invertebrates transmitting pathogens (Paaijmans et al., 2012).

Phylogenetic analysis revealed that the most successful haemosporidian parasite lineages on Tenerife, in terms of number of lineages and individuals infected, grouped with lineages found in African host species, suggesting that the island's proximity to the African mainland largely explains its parasite lineage composition and abundance. This result is in concordance with the many Palearctic migrants stopping off in the Canary Islands every year (Martín and Lorenzo, 2001). These migrants are likely infected in their African wintering areas (Waldenström et al., 2002; Pérez-Tris and Bensch, 2005), and may bring in new parasites to Tenerife on arrival as they migrate back to Europe. This could explain the over-representation of African parasite lineages on Tenerife, despite the fact that many of the native host bird species are derived from independent colonisation events from Europe or northern neighbour archipelagos (Illera et al., 2012). Global phylogenetic analyses including a larger representation of haemosporidian lineages are now needed to evaluate how robust is the biogeographic pattern here found. Studies on evolutionary independence across haemosporidian parasites at the population level are now needed to understand the reasons behind the prevalence and host plasticity observed here. The use of highly variable nuclear parasite genes, such as merozoite surface protein 1 seems to be a promising approach to shed light on such host-parasite relationships at the population level (Hellgren et al., 2015).

Climatic projections for the Canary Islands through the 21st century point to temperature increases linked to altitude (ranging from 0.5 ºC to 2 ºC), and decreasing precipitation (Expósito et al., 2015) occurring across the islands. Because most of the water that mosquitoes use on the Canary

Islands is a result of human activities, water will not be a limitation for the survival of vectors when rainfall drops in the future. Indeed, human reservoirs may increase in number with warmer climatic conditions. Such a scenario (i.e. warmer habitats and more bodies of standing water) is likely to increase mosquito abundance in all habitats (Beck-Johnson et al., 2013; Ewing et al., 2016), but especially in those at higher altitudes. This may, in turn, increase the rate of *Plasmodium* infection in the birds in those areas, and could cause higher levels of mortality (Yorins and Atkinson, 2000), or fitness effects, for example by reducing life span, fecundity, and/or offspring quality (Asghar et al., 2015, 2016). In contrast, the prevalence of *Leucocytozoon* infection may decrease with the forecast climate change, since high temperature was negative correlated with its prevalence. A further issue is whether the increasingly favourable conditions for *Plasmodium* will result in the increased prevalence of existing lineages such as SGS1, currently at low prevalence in Tenerife but widely distributed elsewhere (Hellgren et al., 2015), or the establishment of new ones. The emergence and establishment of new lineages on Tenerife could be of concern, if these new lineages have higher virulence, and negatively impact the unique avifauna found across the Canary Islands.

Overall, our findings represent an advance in our understanding of mechanisms involved in the parasite distribution at the community level within an oceanic ecosystem, and provide a set of predictors to be evaluated in other oceanic islands. Importantly, our study provides evidence that anthropogenic factors play a large role in shaping the assemblage of haemosporidian parasites on Tenerife, and suggests it may be wise to monitor infection prevalence in and around the poultry farms and bodies of standing water. In addition, long-term monitoring studies of individually marked birds are also needed to understand the effects of chronic infection on host fitness and survival, along with dipteran (vector) habitat surveys to understand the factors determining presence and persistence of blood parasites at local scales.

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Figure legends

Fig. 1. Study area map. A) The geographical position of the Canary Islands in relation to the African and European continents. B) Map of Tenerife (Canary Islands) with colours depicting the distribution of the five habitats studied (light bluish: alpine; light greenish: pine; dark greenish: laurel; orangey: thermophilous; light pinkish: coast). The distribution of vegetation types was based on del Arco et al., (2006b). Sampled localities are marked with black dots. TF: Tenerife.

Fig. 2. Mean prevalence (±SE) of *Plasmodium* and *Leucocytozoon* infection in birds per habitat in Tenerife. The number of individuals sampled per habitat is shown in brackets.

Fig. 3. Bayesian consensus tree based on cytochrome *b* mtDNA sequences of *Plasmodium* and *Leucocytozoon* parasites found to be infecting avian species on Tenerife (this study) and elsewhere (MalAvi data base, Bensch et al., 2009). Sequences found in the present study are marked in bold and highlighted in grey. We have used the terms “Predominantly African, European or worldwide hosts” to simplify the geographic origin where a haemosporidian lineage was mostly recorded to infect a host. Main nodes discussed in the text are shown in capital letters and highlighted in grey. Numbers (and numbers with arrows) above nodes show Bayesian posterior probabilities. *: new parasite lineage described in this study.

Fig. 4. Standardised host specificity index (S_{TD}*) for each parasite lineage, using data from the present study (Local S_{TD}*), and data available from elsewhere (Global S_{TD}*). For parasite lineages infecting only one host species we assigned a fixed S_{TD}* value of 1. †: new parasite lineage described in the present study. Parasite genera are distinguished by the initial names (P: *Plasmodium*. L: *Leucocytozoon*).

Fig. S1. Mean number (+ SE) of individuals infected per haemosporidian lineage and host. Number of host species and families infected per haemosporidian lineage are also provided in brackets.