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Lizard host abundances and climatic factors explain phylogenetic diversity and prevalence of blood parasites on an oceanic island

Rodrigo Megía-Palma[1,2,3] | Gemma Palomar[1,4,5] | Javier Martínez[1] | Bernardo Antunes[4] | Katarzyna Dudek[4] | Anamarija Žagar[2,3,6] | Nina Serén[2,3,7] | Miguel A. Carretero[2,3,7] | Wiesław Babik[4] | Santiago Merino[8]

[1]Universidad de Alcalá (UAH), Department of Biomedicine and Biotechnology, Parasitology Unit, Alcalá de Henares, Spain

[2]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, Portugal

[3]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal

[4]Institute of Environmental Sciences, Faculty of Biology, Jagiellonian University, Kraków, Poland

[5]Department of Genetics, Physiology, and Microbiology, Faculty of Biological Sciences, Complutense University of Madrid, Madrid, Spain

[6]NIB, National Institute of Biology, Ljubljana, Slovenia

[7]Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, Porto, Portugal

[8]Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain

Correspondence
Rodrigo Megía-Palma, Universidad de Alcalá (UAH), Department of Biomedicine and Biotechnology, Parasitology Unit, Alcalá de Henares E-28805, Spain.
Email: rodrigo.megia@uah.es

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Abstract

Host abundance might favour the maintenance of a high phylogenetic diversity of some parasites via rapid transmission rates. Blood parasites of insular lizards represent a good model to test this hypothesis because these parasites can be particularly prevalent in islands and host lizards highly abundant. We applied deep amplicon sequencing and analysed environmental predictors of blood parasite prevalence and phylogenetic diversity in the endemic lizard *Gallotia galloti* across 24 localities on Tenerife, an island in the Canary archipelago that has experienced increasing warming and drought in recent years. Parasite prevalence assessed by microscopy was over 94%, and a higher proportion of infected lizards was found in warmer and drier locations. A total of 33 different *18s* rRNA parasite haplotypes were identified, and the phylogenetic analyses indicated that they belong to two genera of Adeleorina (Apicomplexa: Coccidia), with *Karyolysus* as the dominant genus. The most important predictor of between-locality variation in parasite phylogenetic diversity was the abundance of lizard hosts. We conclude that a combination of climatic and host demographic factors associated with an insular syndrome may be favouring a rapid transmission of blood parasites among lizards on Tenerife, which may favour the maintenance of a high phylogenetic diversity of parasites.

KEYWORDS
Adeleorina, Canary Islands, climate change, *Gallotia galloti*, NGS

1 | INTRODUCTION

The evolutionary patterns of animal populations on oceanic islands often diverge from the mainland because the ecological conditions on islands are different (e.g., Olesen & Valido, 2003). Repeated (convergent) evolution of traits across independent islands can result from natural selection in a phenomenon known as 'insular syndrome' (IS) (Blount et al., 2018; Cooper & Uy, 2017; Novosolov et al., 2013). Some of the animal traits often related to the IS are gigantism or dwarfism, increased melanism, shift towards herbivory, and slower life history with longer lifespan (Bolnick et al., 2010; Buglione et al., 2019; Castanet & Báez, 1991; Raia et al., 2010; Schwarz & Meiri, 2017; Stadler et al., 2022). Examples of this evolutionary syndrome are found across animal taxa (Adler & Levins, 1994; Covas, 2012; Goltsman et al., 2005), including lizards (Buglione et al., 2019; Raia et al., 2010; Rotger et al., 2022; Schwarz & Meiri, 2017; Stadler et al., 2022). A frequent convergent feature in lizard populations across oceanic islands is also their abundance that is generally one order of magnitude higher than in the mainland (e.g., Buckley & Jetz, 2007). This difference is the likely result of multiple factors, namely a low predation pressure and a low interspecific competition on islands (e.g., MacArthur et al., 1975; Rotger et al., 2022).

One negative consequence of the high abundance of lizards is an increase in the intraspecific competition. This can be compensated by (i) an expansion of the lizards' ecological niche breadth on those islands with relatively high resource availability (Stadler et al., 2022), and (ii) some degree of interlocal emigration rate of less competitive or younger lizards towards regions with lower adult densities (Oppliger et al., 1999).

Insular syndrome may also affect parasites that often switch their infective strategy becoming more generalist on islands and infecting hosts that are more phylogenetically distant from those in the mainland (Fecchio et al., 2019; Gupta et al., 2019; Pérez-Rodríguez, Ramírez, et al., 2013; but see Tomé et al., 2018). Moreover, blood parasites native to the islands can be less virulent to insular hosts and, perhaps for this reason, highly abundant on some islands (García-Ramírez et al., 2005; Garrido & Pérez-Mellado, 2013; Magnanou & Morand, 2006; Megía-Palma, Arregui, et al., 2020; Schall, 1986; Tomás et al., 2022). Recent research found that host density, island age, and vector prevalence are important predictors of blood parasite prevalence across insular populations of lizards (Ferreira et al., 2023; Fornberg & Semegen, 2021). High parasite prevalence might be explained by high transmission rates in highly dense host populations (Arakelyan et al., 2019; Buckley & Jetz, 2007). While some island parasites can exhibit relatively lower genetic diversity compared to mainland (Magnanou & Morand, 2006; Pérez-Rodríguez, Ramírez, et al., 2013), others show the opposite trend (e.g., intestinal coccidia: Illera et al., 2015; helminths: Jorge et al., 2018; hematic coccidia: Tomé et al., 2018, 2019). Thus, overall, implications of IS for the evolution of insular populations of parasites are still poorly understood (Padilla et al., 2017).

Tenerife (Canary Islands) is an island located in the northern Atlantic subtropical region (28°26′ N, 16°58′ W). It covers an area of 2034.38 km^2 and harbours an increasing human population of 1,048,306 residents (ISTAC, 2022; https://www3.gobiernodecanarias.org/istac/). This human pressure may raise up yearly to six million, tourism considered. With the Teide volcano in the centre of the island, Tenerife peaks at 3718 m asl. Its intricate geography promotes strong heterogeneity in climate regimes and habitats within distances of few kilometres (Del Arco et al., 2006; Salces-Castellano et al., 2020). Moreover, there is evidence supporting predictions of sustained warming on the island with a mean increase of 0.09°C per decade over the period 1944–2010, with a stronger increase in the period between 1970 and 2010 and in the high mountain areas above the stratocumulus layer (Martín et al., 2012). In addition, a significant decrease in precipitation frequency and intensity was observed in the northern areas of Tenerife, leading to more frequent droughts (García-Herrera et al., 2003).

Despite their relatively low dispersal ability, terrestrial reptiles have colonized the Canary Islands. This includes lacertid lizards of genus *Gallotia* (Squamata: Lacertidae: Gallotinae) that are endemic to this archipelago and is the result of a single colonization event, likely 17–20 million years ago (Cox et al., 2010). The host study species, *Gallotia galloti*, naturally occurs on La Palma and Tenerife. It plays a prominent role as fruit disperser in xeric habitats of Tenerife (Valido & Nogales, 1994) and is relatively long-living (9–11 years; Castanet & Báez, 1991; Serén et al., 2023). Populations attain densities of 3500 lizards/ha on eastern lava flows of Tenerife (de los Santos & de Nicolás, 2008). They are widespread but vary in density across most habitats of the island, where they show some degree of genetic structuring into western and eastern lineages as well as across a latitudinal ecotone in the North of Tenerife (Thorpe & Richard, 2001). Furthermore, those lizards in the northeasternmost part of the island (Anaga region) had the highest genomic diversity based on an analysis of more than 276 k SNPs in *G. galloti* sampled across Tenerife, whereas those in its southernmost region had the lowest (Brown et al., 2016).

Contrary to those lacertids occurring in the continent that are parasitized by apicomplexan blood protozoans of two orders, Adeleorina and Coccidiasina (Megía-Palma et al., 2018, 2023), *G. galloti* is only parasitized by Adeleorina (Megía-Palma, Arregui, et al., 2020; Megía-Palma, Jiménez-Robles, et al., 2020; Tomé et al., 2018). Adeleorine parasites undergo asexual reproduction (schizogony) in the lizards' blood red cells, and both asexual and sexual reproduction cycles in mite vectors (Bannert et al., 1995; Fain &

Bannert, 2000). Micro- (male) and macrogametocyte (female) parasite stages can be found in the blood of the lizards. These are the sexual stages and require arriving at the gut of a hematophagous mite where they fuse and form a motile phase called sporokinete (Telford, 2009). The infection in lizards occurs when they swallow an infected mite. Sporokinetes of the genus *Karyolysus* form an oocyst by a single germinal center that is released in a mite (definitive host). In contrast, the genus *Hepatozoon* is characterized by producing a large polysporocystic oocyst (Telford, 2009). The mite genus *Ophionyssus* (Acari: Macronyssidae) is the known vector, where adeleorine parasites encyst as sporocysts (Haklová-Kočíková et al., 2014; Reichenow, 1919). A single mite species of this genus, *Ophionyssus galloticolus*, is known as *G. galloti* (Fain & Bannert, 2002).

Thermal and humidity conditions at microgeographic scale over distances of only a few kilometres have been found to explain genetic richness, distribution, and/or prevalence of some blood parasites (Gonzalez-Quevedo et al., 2014; Padilla et al., 2017; Pérez-Rodríguez, Fernández-González, et al., 2013). As such, we predict that a high genetic diversity of blood parasites in *G. galloti* will be favoured on Tenerife, an island with a combination of heterogenous climate and dense host populations. The latter might favour a high transmission rate that, in turn, would cushion the expected negative selection of the host immune system on parasites (Dietz, 1988; Ewald, 1983; Råberg & Stjernman, 2012). We implemented a deep amplicon sequencing technique to comprehensively assess the phylogenetic diversity of the community of adeleorine blood parasites in the blood of lizards and investigated whether a set of abiotic and biotic factors can explain the observed variation in parasite prevalence and phylogenetic diversity across Tenerife. We hypothesized that a combination of (i) host traits (e.g., vector intensity and lizard abundance), (ii) blood parasite intensity, and (iii) climatic conditions will influence the α-diversity of blood parasites (Arneberg et al., 1998; Song & Proctor, 2020). We also expect that (iv) a high current lizard connectivity on Tenerife may promote low ß-diversity of their blood parasites (lack of geographic structuring) (Pérez-Rodríguez et al., 2014). Additionally, (v) we predict that parasite prevalence will be highest in the most arid environments of the island where high intensities of blood parasites in lizards were previously detected and may represent a biomarker of environmental stress (Megía-Palma, Arregui, et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Sampling

We captured *G. galloti* lizards in 24 localities across the diverse habitats, climates, and elevation of Tenerife in the summer of 2017 and 2018 (Figure 1). We registered GPS coordinates and elevation at each locality (GPSMAP 64s, Garmin, Kansas, USA) (Table S1). We used pitfall traps ($N = 15–30$ per site) baited with tomato. Traps were set in the field, ~10 m apart one from another, between 11:00 and 13:30, which is the lizards' daily peak of activity period (Bohórquez-Alonso et al., 2011). They were checked every 15 min for the presence of lizards (Megía-Palma et al., 2016; Megía-Palma, Arregui, et al., 2020). We measured the snout-to-vent length (SVL) of the lizards using a ruler (precision = 1 mm). We used a 10× magnifying lens to count mites on the lizards. We captured all lizards from a single location within a single day and released them at the point of capture within 24 h.

2.2 | Blood parasite prevalence

Adult individuals captured in 2017 and 2018 were considered for the analysis of parasite prevalence assessed by microscopy ($n_{\text{blood smears}} = 620$), according to a minimum snout-to-vent length (SVL) of 100 mm for adult males ($n = 296$) and 80 mm for adult

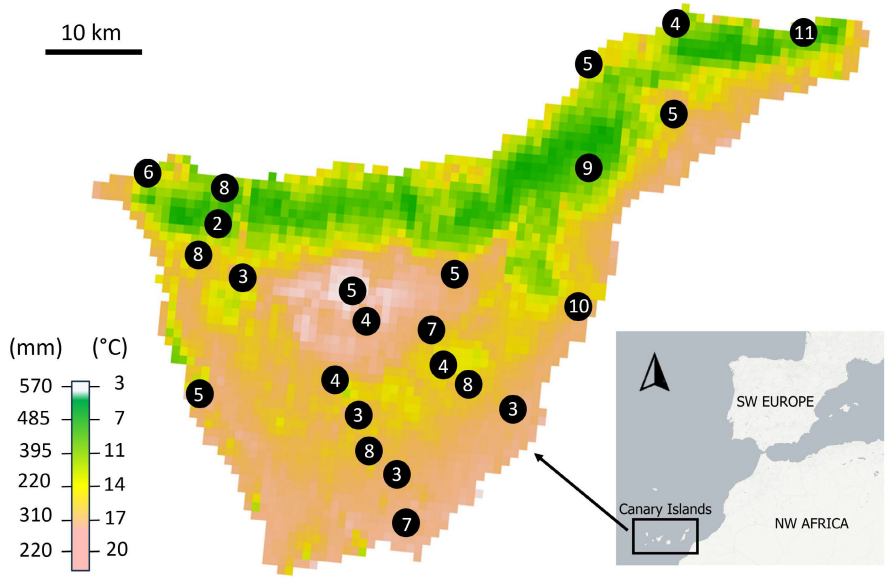

FIGURE 1 Climatic model of Tenerife where pixels represent square areas at 30 arc sec of resolution (~1 km^2). The coloured scale on the left indicates mean precipitation (mm) and mean temperature (°C) based on 30 years of climatic data. Blood parasite prevalence in *G. galloti* is higher in warm, drier regions. Black circles indicate the distribution of sampling locations and number of parasite haplotypes found. Further details of specific *18S* haplotypes found per site in Figure S6.

females ($n = 324$) (see Salvador, 2015). We collected a blood sample (~5 μL) from the coccygeal vein of these lizards using sterile needles and Na-heparinized capillary tubes (75 × 1.15 mm, Brand, Wertheim, Germany) (Megía-Palma, Arregui, et al., 2020). A blood droplet was smeared onto a microscope slide that was later stained with Giemsa 1:10 in phosphate buffer pH 7.2 and used to diagnose blood parasites by the examination of 5000 blood cells per individual at 1000× magnification in a light microscope BX41 (Olympus, Tokyo, Japan) (Megía-Palma, Arregui, et al., 2020). A lizard was considered infected when at least one parasite was observed in the microscope, and we calculated parasite prevalence as the proportion of lizards infected assessed by microscopy per sex and locality (Rózsa et al., 2000).

2.3 | Molecular and phylogenetic analyses of blood parasites

We preserved another drop of blood in Whatman paper (FTA® Classic Card, WB12 0205; GE Healthcare UK Limited, Buckinghamshire, UK) for molecular analyses. Total genomic DNA was extracted from a total of 247 individuals (median = 10, range = 4–12 per locality), following the protocol described in Megía-Palma et al. (2013). Samples used for parasite DNA analysis were chosen based on the presence of blood parasites in the corresponding blood smear, and all were positive following molecular methods (Megía-Palma et al., 2023).

18S rRNA gene is a standard marker to investigate genetic diversity and phylogenetic relationships in the Adeleorina (Megía-Palma et al., 2023). It shows a repetitive arrangement within the genome and the presence of different alleles within this locus can represent multiple haplotypes within a single species, not necessarily representing individual parasites (e.g., Prajapati et al., 2011). We designed the following primers for the amplification of a 450 bp fragment of *18s* rRNA aimed to detect parasites in the order Adeleorina: Kar18S_NGS_f 5′-CAGTAAAACTGCAAATGGCTC-3′ and Kar18S_NGS_r 5′-ACTTGCCCTCCAATTGATAC-3′. Different combinations of barcodes were used for each lizard host to allow the assignment of reads to individual hosts following Illumina sequencing.

PCR was performed in 25 μL volume and consisted of 12.5 μL of Multiplex PCR kit (Qiagen, Hilden, Germany), 9.25 μL of distilled water, 2 μL of DNA extraction, and 0.625 μL of F and R primers (final concentration of 0.25 μM). PCR conditions were the following: 95°C for 15 min, 40 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 70 s, followed by 72°C for 5 min. Amplification was performed in triplicates to reduce the effect of PCR amplification on total number of reads per parasite haplotype. The three PCR products per individual were pooled together and visualized in agarose gel. All individuals were combined equimolarly based on intensity of bands in the gel, and the pooled sample was purified using Zymo DNA Clean and Concentrator (Zymo). Illumina adapters were added following the protocol of NEBNext Ultra II DNA Library Prep Kit modified according to the PCR Free Protocol for NEBNext Library Prep for Illumina. After adapter ligation, library was purified twice with AMPure XP beads (0.8×). High-throughput sequencing (2 × 300 bp) was carried out on MiSeq platform (Illumina, San Diego, USA). Identification of parasite haplotypes present in each *Gallotia* individual was performed using the adjustable clustering method implemented in AmpliSAS (Sebastian et al., 2016). Briefly, forward and reverse reads were assembled and de-multiplexed into individuals based on matching of tag sequences. Then, reads were clustered based on similarity with a maximum number of clusters of 60 and filtered based on length (432–468 bp), minimum depth (100), and minimum frequency (0.0025). The resulting haplotypes were cross-checked against the NCBI database to exclude genetic material not belonging to adeleorine parasites and confirmed that the primers used, and the deep amplicon sequencing technique implemented, only amplified the targeted parasites. In order to visualize the genetic relationships between parasite haplotypes, we constructed a haplotype network using a median-joining algorithm implemented in the software PopART 1.7 (Leigh & Bryant, 2015), and we also performed phylogenetic analyses with 128 sequences from Genbank database coding for *18S* rRNA to build a phylogenetic tree of Adeleorina. The final alignment contained 161 sequences, including the 33 sequences newly obtained in the present survey (for further details on the phylogenetic methods, see Data S1).

2.4 | Phylogenetic diversity indices of the blood parasite community

To assess the genetic diversity of the parasite community, a measure that considers the phylogenetic distance between parasite haplotypes was used. For each population, two α phylogenetic diversities based on Hill's numbers were estimated (Chao et al., 2014) using hill_phylo from R package 'hillR' (Li, 2018). These two measures differed in the q parameter (0 or 1). While $q = 0$ assigns equal weight to all variants and diversity corresponds to the number of different haplotypes (i.e., richness), $q = 1$ weights variants according to their frequency and diversity corresponds to the exponential of Shannon's diversity index (see Palomar et al., 2021 for further details). For these calculations, a neighbour joining tree of the haplotypes and the frequencies of each haplotype within each lizard were used. The median values of the α phylogenetic diversities, instead of the mean, were used in all the analyses of phylogenetic diversity because data showed an aggregated distribution (Figure S1) and median scores are better descriptors in this case (Rózsa et al., 2000).

2.5 | Validation of climatic factors

We used climatic data from the WorldClim 2.0 database, which provides 19 bioclimatic variables that represent average values of 30 years at a 1 km^2 resolution (Fick & Hijmans, 2017). We kept eight bioclimatic variables that significantly correlated with real temperature and humidity data collected on 18 random localities of Tenerife during July 2018 (see Supplementary Methods in Appendix S1 for further details). In addition, we calculated climatic slopes for

the period 1980–2010 based on climatic data downloaded from CHELSA-TraCE21k (Karger et al., 2021) of yearly mean, minimum and maximum temperature, and mean precipitation as a measure of the intensity of climate change (see Figure S2) that yielded additional four bioclimatic variables. We then summarized the information on these 12 bioclimatic variables using principal component analysis. We also included elevation in this calculation to account for other environmental factors that could vary altitudinally along with climate. We obtained two principal components (PCs) that, after a varimax normalization of factor rotation, summarized 88.7% of the climatic variability (see Data S1). Climatic PC1 was negatively correlated with maximum temperature of the warmest month and mean temperature of both the driest and warmest quarter. It was also positively correlated with precipitation of both the driest month and quarter and both mean and maximum temperature change slopes for the period 1980–2010. Climatic PC2 was negatively correlated with standard deviation of temperatures (seasonality), temperature annual range, and elevation. It was also positively correlated with the minimum temperature of the coldest month and the minimum temperature change slope for the period 1980–2010 (Table S2).

2.6 | Validation of lizard abundance estimates

Lizard counts (number of lizards in the pitfall traps) were performed in 2017 and 2018 within a temperature range of 24–28°C on sunny warm days. We calculated lizard abundance estimates by dividing the number of lizards trapped during the first sampling hour by the number of traps used (Megía-Palma, Arregui, et al., 2020). We validated this methodology by repeating lizard abundance estimates under the same weather conditions in 14 localities in the summer of 2021. We performed a pairwise (repeated measures) analysis that compared lizard abundance estimates between 2017–2018 and 2021 per locality. We also performed a pairwise correlation test between sampling campaigns. For this analysis, we had a total sample size of 791 lizards captured in the years 2017, 2018, and 2021. Lizard abundance estimates calculated for the same 14 localities did not significantly differ between sampling campaigns ($F_{1, 13}=0.24$, $p=.62$). Furthermore, the pairwise correlation of lizard abundance estimates between sampling campaigns was highly significant ($p=.008$, $r=.67$; Figure S3). Assuming that lizard abundances remain stable across years, this indicated that this approach is a reliable methodology that can consistently estimate lizard host abundance in this system.

2.7 | Accounting for spatial autocorrelation

We tested whether parasite prevalence estimated by microscopy and indices of phylogenetic diversity show spatial autocorrelation on Tenerife using Moran's I matrix, where the null hypothesis equals the spatial independency of the data (Legendre & Legendre, 1998). There was no justification to control the models for spatial autocorrelation because α-diversity (for $q=0$, SD = 0.041, $p=.768$; and for $q=1$, SD = 0.045, $p=.943$), median of the number of blood parasite haplotypes (SD = 0.050, $p=.072$), and parasite prevalence estimated by microscopy (SD = 0.025, $p=.637$) showed spatial independence (Dormann et al., 2007).

2.8 | Ecological relationships

We analysed parasite prevalence estimated by microscopy of paired males and females per locality that indicated no sexual differences ($F_{1, 23}=2.22$, $p=.15$). Therefore, we calculated a pooled parasite prevalence for males and females from the data assessed by microscopy ($n=620$) and used it in the subsequent analyses. The prevalence data fit well with a general linear model. We set as predictors the factor year (2017 and 2018) and the two climatic components (PC1 and PC2) as continuous predictors. We also included in the model the median scores of mite intensities (i.e., vectors) and the estimates of lizard abundances as covariates. The number of lizards microscopically screened per locality was included as a weighing term in the model.

The interlocal variations of both parasite phylogenetic diversity α-indices ($q=0$ and $q=1$) were best fitted to generalized linear models with quasibinomial error distribution and linked to a logit function (Westby et al., 2019). The resulting model residuals did not conform to parametric expectations and, thus, in a second approach, non-parametric univariate Spearman's correlations were used to test whether lizard abundance estimates, PC1_climate, PC2_climate, and median scores of both mite and blood parasite local intensities (magnifying glass and microscope counts, respectively), correlated with the α-indices of parasite diversity. The threshold of significance for these correlations was Bonferroni-corrected to 0.01 in order to reduce type I error. Since this approach did not consider all the factors simultaneously but one by one, a proxy of the α-diversity for $q=0$ was calculated—the median prevalence of parasite haplotypes found per individual lizard. This latter metric was best fitted to a general linear model with Gaussian distribution model that included year, lizard abundance estimates, PC1_climate and PC2_climate, and median intensities of both mites and blood parasites as predictors. The number of samples molecularly analysed per locality was included as weighing term in this model. A test based on variance inflation factors (VIF; Schroeder et al., 1990) indicated a low autocorrelation of the variables (all VIFs < 2).

We used the R package 'MuMIn' to implement a multimodel inference approach in the analysis of the models of parasite prevalence assessed by microscopy and the median prevalence of parasite haplotypes found per individual lizard (Barton, 2018). For this, we considered sufficiently informative all the models with ΔAICc ≤4 (Burnham & Anderson, 2004). We used model averaging to get a final model and calculate the relative importance of each predictor. For this, we considered only the models that included the effect (i.e., conditional average) to calculate the significance ($\alpha<.05$) of the predictors, their *z*-standardized ß coefficient, and their standard error. The resulting final models were cross-validated using a k-fold split of

3 in the R package 'DAAG' (Maindonald et al., 2015). Finally, we calculated the percentage of the variance explained by each significant predictor by means of their sum of squares.

2.9 | Geographic patterns of parasite community genetic structure

To evaluate the spatial processes that determine the genetic structure of parasite community, we compared the genetic distance of parasites between populations with geographic resistance and environmental distances (Figure S4). Regarding genetic distance, we used three indexes: the phylogenetic β-diversity instead of F_{ST} for two main reasons: (i) it considers the phylogenetic relationship between the haplotypes, and (ii) it allows the evaluation of diversity and richness using the same formula (only changing q parameter from 1 to 0), thanks to Hill numbers (R package 'hillR'; Li, 2018). Furthermore, we included absolute genetic divergence, Dxy, calculated with DnaSP (Rozas et al., 2017), which represents the average number of nucleotide substitutions per site between populations, ranging from 0 (where populations have identical allele frequencies) to infinity (where populations do not share any alleles). For geographic patterns, we used Euclidean geographic distance (Wright, 1943), topographic and environmentally informed least cost paths (McRae, 2006; Wang, 2020), and local environment dissimilarity, independent from geographic distance (Wang & Bradburd, 2014). To test if geographic resistance and environmental dissimilarity predicted genetic distances, we used the multiple matrix regression with randomization approach (MMRR; Wang, 2013). For details, see Supplementary Methods in Appendix S1 and Figure S4.

3 | RESULTS

3.1 | Mites and blood parasite prevalence

We found a 68.44% mite vector prevalence (mean ± standard error = 62.89 ± 5.37 mites per infested lizard), and an overall 94.2% parasite prevalence assessed by microscopy (n = 620) across lizard populations on Tenerife (Figure S5). All populations exhibited >75% parasite prevalence, except the one located on the top of the volcano at 3600 m asl (Cone of Teide, Figure S5). The multimodel inference approach produced seven models with ΔAICc ≤4 (Table 1a), and the final model resulting from their average indicated that PC1_climate (importance = 1.00; z = 3.63, p < .001) and lizard abundance estimates (importance = 0.75; z = 2.06, p = .039) had important effects on parasite prevalence. However, the k-fold cross-validation of this final model dropped lizard abundance estimates and confirmed the negative effect of PC1_climate (estimate = −0.09 ± 0.02; $F_{1, 21}$ = 23.92, p < .001). Thus, parasite prevalence was higher in hotter and more arid localities, namely where maximum temperature of the warmest month and the mean temperature of both the driest and warmest quarter were the highest, and precipitations of the driest month and quarter were the lowest. However, in these locations, the raise (positive slope) of both mean and maximum temperature changes was less intense in the period 1980–2010 than compared to other localities (see Table S2 for the interpretation of PC1_climate).

TABLE 1 Model selection for (a) parasite prevalence assessed by microscopy and (b) median prevalence of parasite haplotypes per lizard assessed by deep amplicon sequencing.

(a) Model – Parasite prevalence assessed by microscopy	df	logLik	AICc	ΔAICc	Weight
PC1_environ + lizard abundance estimates + Year	5	20.9	−28.4	0	0.36
PC1_environ + lizard abundance estimates	4	18.6	−27.1	1.3	0.19
PC1_environ	3	16.6	−26	2.38	0.11
PC1_environ + Year	4	17.5	−24.9	3.49	0.06
PC1_environ + PC2_environ + lizard abundance estimates + Year	6	20.9	−24.9	3.51	0.06
Mite_median + PC1_environ + lizard abundance estimates + Year	6	20.9	−24.8	3.61	0.06
PC1_environ + PC2_environ	4	17.4	−24.6	3.72	0.06
(b) Model – Parasite haplotypes per lizard assessed by DAS	**df**	**logLik**	**AICc**	**ΔAICc**	**Weight**
Lizard abundance estimates + Year	4	−18.1	46.2	0	0.27
Mite_median + Lizard abundance estimates + Year	5	−17.4	48	1.81	0.11
PC1_environ + Lizard abundance estimates + Year	5	−17.9	49.1	2.85	0.06
Microscopic intensity blood parasites + Lizard abundance estimates + Year	5	−18	49.3	3.1	0.06
PC2_environ + Lizard abundance estimates + Year	5	−18	49.4	3.17	0.06
Year	3	−21.3	49.9	3.64	0.04
Lizard abundance estimates	3	−21.5	50.1	3.89	0.04

Abbreviations: DAS, deep amplicon sequencing; df, degrees of freedom; logLik, log likelihood.

3.2 | Genetic structure and phylogenetic diversity of parasites

Amplicon sequencing provided a mean ± standard error of 3986 ± 83 reads per lizard. A total of 33 parasites *18s* rRNA haplotypes were found in the blood samples of the 247 lizards analysed (Table S3). The median ± standard error parasite haplotype richness per locality was 5.0 ± 0.50 (range = 2 in San José de Los Llanos – 11 in Benijo; Figure 1 and Figure S6), whereas the mean ± SE parasite haplotype richness per lizard was 2.1 ± 0.08 (range = 1–9). The haplotype network showed three groups of parasite haplotypes (Figure 2). In its left part, 26 haplotypes formed a subnetwork separated from the haplotype Gg31 (in the middle) by at least eight mutations (blue group in Figure 2). In the right part, haplotypes from Gg32 to Gg37 formed another subnetwork separated from haplotype Gg31 by at least 15 mutations (red group in Figure 2). This pattern was consistent with the results of the phylogenetic analyses because the tree showed that 27 out of the 33 haplotypes grouped within a clade of parasites of the genus *Karyolysus* (Apicomplexa: Coccidia: Adeleorina) (Figure S7). This clade included parasites from the western Mediterranean, North Africa, and Macaronesia found in reptile hosts (Maia et al., 2011, 2012; Megía-Palma et al., 2023; Tomé et al., 2018, 2019) and 26 haplotypes from left haplotype subnetwork and Gg31 (blue group in Figure 2). As in the haplotype network, the haplotype Gg31 appeared separated from the rest but within *Karyolysus*, although its phylogenetic relationships with the closest sequences were uncertain due to the low intranodal support. Five more parasite haplotypes within this subnetwork (Gg5, Gg14, Gg19, Gg23, and Gg26) were detected in nine or more localities. Two of them, Gg14 and Gg23, were detected in most localities (20 and 24 localities, respectively) (Figure 2). Gg23 was detected in 90.3% (i.e., 223/247) of the lizards analysed (Table S3). *Karyolysus* was thus detected in the 24 localities and 100% of the lizards molecularly analysed. The remaining haplotypes detected (red group in Figure 2) grouped within the genus *Hepatozoon* (Figure S7). Parasites of the latter genus were found in 7.28% (18/247) of lizards and in 25% (6/24) of localities across Tenerife. Two of these haplotypes (Gg32 and Gg34) were consistently detected in lizard hosts in four localities, in Anaga, northernmost east part of Tenerife, Valle de Arriba nearby Teno, northeastern most part of the island, La Esperanza, centre, and Cruz de Tea, south (Figure S6). Their overall prevalence was low because they were only detected in nine and seven lizards, respectively. Co-infections of *Hepatozoon* and *Karyolysus* were limited (7.28%), and they were mostly explained by the co-infection of *Karyolysus* Gg23 and *Hepatozoon* Gg37 haplotypes.

The median scores for the three indices of parasite diversity (q0, q1, and median prevalence of parasite haplotypes found per individual lizard) were identical when they were calculated for *Karyolysus* alone or for *Karyolysus* + *Hepatozoon*. Non-parametric analyses showed that both α-diversities ($q = 0$ and $q = 1$) of blood parasites were positively correlated with lizard abundance estimates (Table 2). Blood parasite haplotypes were more phylogenetically diverse in localities of Tenerife with higher lizard host abundances.

The model of median prevalence of parasite haplotypes found per individual lizard allowed a more complex analysis that produced seven models with ΔAICc ≤4 (Table 1b) and indicated important effects of year (importance = 0.94, $z = 2.24$, $p = .025$) and lizard abundance estimates (importance = 0.93, $z = 2.14$, $p = .032$). However, a cross-validation of a final model with the two predictors did not include year ($F_{1, 21} = 3.99$, $p = .059$) and confirmed the

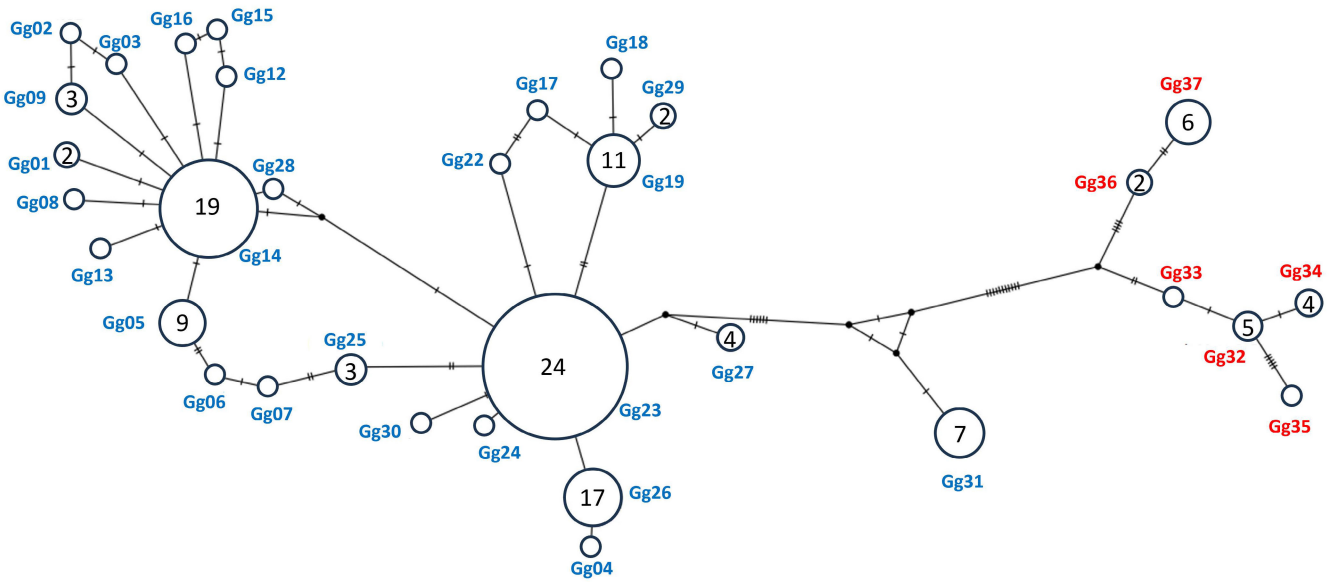

FIGURE 2 Haplotype network showing the relationships of the 33 *18s* rRNA haplotypes of Adeleorine blood parasites found in *Gallotia galloti*. Numbers within circles represent amount of sampling locations where each haplotype was detected. Empty circles represent parasite haplotypes found in single locations. Haplotype names were coloured to identify the two clades of parasites present in the study (blue = *Karyolysus* and red = *Hepatozoon*; see phylogenetic tree in Figure S7). Also see a supplementary version of the network in Figure S8.

TABLE 2 Spearman rank order weighed correlations of median phylogenetic α-diversity ($q=0$ and $q=1$) of blood parasites found in lizard hosts *Gallotia galloti* across Tenerife.

α-diversity ($q=0$)	Sample size	Spearman's *r*	*t*(*N*−2)	*p*-value
Lizard abundance estimates	**247**	**.206**	**3.296**	**.001**
Blood parasites (median intensity)	247	.001	0.019	.985
Mites (median intensity)	247	.029	0.458	.647
PC1_climate	247	.136	2.156	.032
PC2_climate	247	.023	0.363	.716
α-diversity ($q=1$)	**Sample size**	**Spearman's *r***	***t*(*N*−2)**	***p*-value**
Lizard abundance estimates	**247**	**.217**	**3.492**	**<.001**
Blood parasites (median intensity)	247	.035	0.551	.581
Mites (median intensity)	247	−.002	−0.031	.975
PC1_climate	247	.138	2.188	.030
PC2_climate	247	.037	0.584	.560

Note: Significant relationships after Bonferroni correction are shown in bold.

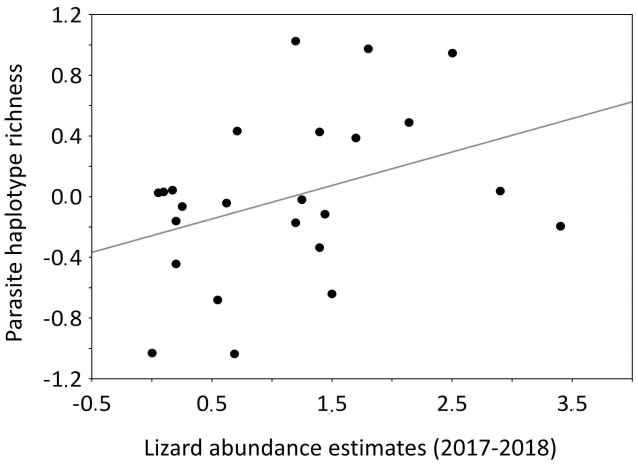

FIGURE 3 Effects plot showing the significant relationship between lizard abundance estimates and the median richness of blood parasite haplotypes across 24 localities on Tenerife. The plot shows residual model values for parasite haplotype richness (see Section 3).

positive and significant effect of lizard abundance estimates on the median prevalence of parasite haplotypes found per individual lizard (estimate = +0.29; $F_{1,\ 21}=7.03$, $p=.015$). Thus, localities with higher abundance of lizards have a higher prevalence of parasite haplotypes found per individual lizard (Figure 3). Lizard abundance estimates explained 21.9% of the observed variance of this metric across Tenerife.

3.3 | Geographic pattern

The comparison between genetic and other distances (Euclidean geographic distance, environmentally informed least cost, and independent from geographic distance) were all non-significant (see Table S4, landscape genetics in Data S1), indicating that the parasite community genetic structure does not seem to depend on geographic distance, topographic and/or local environmental dissimilarities.

4 | DISCUSSION

The results partially conformed to the hypotheses tested. (i) Local abundances of lizards contributed significantly to explaining the observed variation in the phylogenetic diversity of blood parasites on Tenerife. Therefore, ecological contexts with high lizard host abundances may favour a high blood parasite diversity via putative high host–parasite encounter and transmission rates (Dietz, 1988). However, local intensities of neither mites nor (ii) blood parasites significantly explained blood parasite phylogenetic diversity. That is, the blood parasite phylogenetic diversity currently observed in a lizard does not necessarily correlate with its current vector load, or the number of blood parasites counted in the blood at a given time. This lack of correlation could be explained by the fact that these blood parasites produce chronic infections and reproduce asexually in the lizards, thus increasing the number of parasites but not necessarily increasing the haplotype diversity. On the other hand, (iii) climate did not significantly contribute to explaining parasite phylogenetic diversity and (iv) lizard connectivity across Tenerife landscape neither correlated with the genetic structure of blood parasites. Therefore, the results reveal that it is difficult to predict how parasite and host diversities can interact. For example, adeleorine parasites could more easily escape the immune system of lizards in host populations with low genetic diversity (King & Lively, 2012; Lively, 2010). This, in turn, could favour the maintenance of a parasite pool of high phylogenetic diversity. However, parasite phylogenetic diversity does not fit this prediction on Tenerife. While in the south low genetic diversity of lizards (Brown et al., 2016) coincides with high genetic diversity of parasites, in the north both lizard and parasite genetic diversities are high. One possibility in this regard is that parasite phylogenetic

diversity would instead be influenced by vectors, wherein adeleorine parasites reproduce sexually (O'Donoghue, 2017). After the genetic recombination undergone in the vectors, lizards could be favouring a genetic interchange between blood parasite populations via phoresis of vectors carried by the lizards during their dispersal across the island landscape (Oppliger et al., 1999). To test this hypothesis, we encourage future studies to investigate whether the genetic structure of mite vectors could underlie the genetic structure of the blood parasite community (Tomé et al., 2019). Remarkably, (v) climate significantly contributed to explaining the variation in prevalence of blood parasites in *G. galloti* across Tenerife as predicted; a higher proportion of lizards were infected in the more arid regions of the island. The mean prevalence of blood parasites assessed using microscopy was 94.2% and was higher in drier and warmer areas of Tenerife. Lizards may suffer immunosuppression under drought conditions, increasing their susceptibility to infections (Han et al., 2020; Rutschmann et al., 2021). In arid localities of Tenerife, the intensity of infection by blood parasites was also generally high in a previous study (Megía-Palma, Arregui, et al., 2020). This suggests that arid environments represent least hospitable climatic conditions for this lizard (e.g., Herrando-Pérez et al., 2020). This said, we note that 82% of the blood parasites found belong to genus *Karyolysus* (Tomé et al., 2018). In this sense, although our analyses targeted the blood parasite community, any conclusion derived from our ecological analyses applies mostly to this parasite genus because it is the main blood parasite found across all locations and lizards investigated on Tenerife, whereas *Hepatozoon* was only found in 7.28% of the lizards and 25% of the locations.

Previous studies have demonstrated necrotizing inflammatory lesions induced by infection with adeleorine parasites like the ones found here in non-pre-immunized, unnatural reptile hosts (Wozniak et al., 1996). However, studies in lacertids showed only moderate, non-lethal effects of these parasites to the lizard host (Garrido & Pérez-Mellado, 2014; Megía-Palma, Jiménez-Robles, et al., 2020; Oppliger et al., 1996; Oppliger & Clobert, 1997; Sorci et al., 1996). This is also true for lizard hosts of the genus *Gallotia*, where no negative effects of adeleorine parasites, and even positive relationships with other health indicators, have been previously described (García-Ramírez et al., 2005; Megía-Palma et al., 2016). Therefore, it is plausible that blood parasites persist as a chronic infection for several years in lizards on Tenerife. This connects to a second key factor of *G. galloti*; it has a relatively long lifespan (up to 11 years; Serén et al., 2023), which, together with the chronicity of the infection, would favour the accumulation of parasite variants during the lizards' lifetime (e.g., through reinfections; Pokalyuk & Wakolbinger, 2020). This would increase the chances of lizard hosts serving as parasite donors and thus contributing to the conservation of genetic mutants in the parasite pool.

In summary, while climatic factors related with processes of aridification on Tenerife favoured the highest prevalence values of blood parasites in *G. galloti*, lizard abundance seems to favour parasite transmission which, in turn, can promote the maintenance of a high phylogenetic diversity of the blood parasite community.

AUTHOR CONTRIBUTIONS

RM-P, GP, SM, WB, conceived the ideas and designed methodology; RM-P, JM, AŽ, NS, MC, GP, BA, KD produced the data; RM-P analysed the data; RM-P and GP led the writing of the manuscript; SM, JM, WB provided infrastructure and financial resources. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We disclose any actual or potential conflict of interest including any financial, personal, or other relationships with other people or organizations that could inappropriately influence or be perceived to influence our work.

DATA AVAILABILITY STATEMENT

New sequences available in GenBank (OR342828–OR342860) and other metadata at https://data.mendeley.com/datasets/v4w54r7snd/1.

BENEFIT-SHARING STATEMENT

Non-monetary benefits generated: Understanding the ecological factors shaping the distribution, prevalence, and diversity of parasites in island ecosystems is an important matter, because (i) parasites are considered drivers of population regulation in many species, and (ii) many times, the hosts, vectors, and parasites are endemic. Therefore, shedding light on the relationships established among them seems timely and necessary since many human actions may unbalance such interactions with unpredictable results.

ORCID

Rodrigo Megía-Palma https://orcid.org/0000-0003-1038-0468
Bernardo Antunes https://orcid.org/0000-0002-6092-4219
Wiesław Babik https://orcid.org/0000-0002-1698-6615

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