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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 wildlife epidemiology, evolutionary ecology and conservation. The simultaneous use of ecological and evolutionary frameworks 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, parasite 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, Canary Islands) versus global host range indices (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 those increase mortality rates in the unique avifauna of these islands.

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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 borne 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).

[☆] Note: Nucleotide sequence data reported in this paper is available in GenBank under accession number KX002266.

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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; Szöllösi 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 more than one host species (i.e. generalist parasites). This predicted outcome is known as the “Trade-off” hypothesis (Poulin, 1998; 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 shown to occur in the forest birds of northwestern Africa and the Iberian Peninsula (Mata et al., 2015). Finally, phylogenetic constraints will also affect prevalence if the degree of specialisation of a parasite lineage is phylogenetically dependent (e.g. Hellgren et al., 2009; Loiseau et al., 2012) (but also see Szöllösi et al., 2011). For example, phylogenetically related parasites may show similar prevalence due to 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 haemosporidian 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 vector 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., 2013a,b; Gonzalez-Quevedo et al., 2014; Fairfield et al., 2016). However, we have limited knowledge of how habitat and environmental changes can determine the 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 of 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 km², in the Atlantic Ocean close to the northeastern African continent (Fig. 1). The easternmost (Fuerteventura) and westernmost (La Palma) islands are situated approximately 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 (m.y.)) and the youngest El Hierro (≈1.2 m.y.). The Canary Islands have become a focus for ecological, evolutionary and biogeographical 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, 2015; Spurgin et al., 2012; Pérez-Rodríguez et al., 2013b; Barrientos et al., 2014; Gutiérrez-López 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 (i) it is the largest (2,034 km²) and highest (3,718 m above sea level (a.s.l.)) island in the Canary Islands, and (ii) 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., 2013a,b). 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 also be generalists on Tenerife, and therefore we expect to find a

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