# Host associations and turnover of haemosporidian parasites in manakins (Aves: Pipridae)

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SUMMARY

Parasites of the genera *Plasmodium* and *Haemoproteus* (Apicomplexa: Haemosporida) are a diverse group of pathogens that infect birds nearly worldwide. Despite their ubiquity, the ecological and evolutionary factors that shape the diversity and distribution of these protozoan parasites among avian communities and geographic regions are poorly understood. Based on a survey throughout the Neotropics of the haemosporidian parasites infecting manakins (Pipridae), a family of Passerine birds endemic to this region, we asked whether host relatedness, ecological similarity and geographic proximity structure parasite turnover between manakin species and local manakin assemblages. We used molecular methods to screen 1343 individuals of 30 manakin species for the presence of parasites. We found no significant correlations between manakin parasite lineage turnover and both manakin species turnover and geographic distance. Climate differences, species turnover in the larger bird community and parasite lineage turnover in non-manakin hosts did not correlate with manakin parasite lineage turnover. We also found no evidence that manakin parasite lineage turnover among host species correlates with range overlap and genetic divergence among hosts. Our analyses indicate that host switching (turnover among host species) and dispersal (turnover among locations) of haemosporidian parasites in manakins are not constrained at this scale.

Key words: Avian malaria, community assembly, host switching, host turnover, parasite community, parasite diversity.

## INTRODUCTION

Parasite assemblage structure can change through local colonization and extinction of individual lineages, which depend on several attributes of hosts (Poulin, 1997). For example, the geographic range of the host has been shown to positively influence parasite richness: host species with larger ranges would presumably be exposed to, and colonized by, more parasite species over evolutionary time (Poulin, 1997, 2007). Indeed, this pattern has been found among several types of parasites and

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assemblages in different host taxa (Poulin, 1997, 2007; Kamiya *et al*. 2014). The effects of ecological and evolutionary processes on parasite assemblages can be revealed, to some degree, by comparing parasite assemblages among host species and/or among localities, and correlating variation in assemblage similarity with ecological and evolutionary factors. Comparing assemblages across host species, the extent of geographic overlap and phylogenetic relatedness of hosts may influence parasite assemblages. Davies and Pedersen (2008) found evidence for both these factors in the greater similarity of pathogen assemblages between more closely related primates and between primates sharing more of their geographic ranges. In multi-host vector-borne pathogens, comparisons of parasite assemblages across localities are also worthwhile, as turnover may result from, for example, climate and habitat differences (which are most likely to affect parasites through their ectothermic, moisture-dependent vectors), and host assemblage turnover (e.g. Ishtiaq *et al*. 2010; Svensson-Coelho and Ricklefs, 2011). Finally, assemblage similarity of free-living organisms is expected to decrease with increasing geographic distance (Nekola and White, 1999; Soininen *et al*. 2007), which has also been demonstrated in some assemblages of parasitic organisms (Poulin, 2003; Krasnov *et al*. 2005; Svensson-Coelho and Ricklefs, 2011).

Haemosporida of the genera *Plasmodium* and *Haemoproteus* are vector-borne protozoan parasites that complete asexual reproduction in their avian hosts (Valkiūnas, 2005). These parasites are nearly worldwide in distribution, abundant and diverse in most bird orders and families, and infect a wide range of invertebrate dipteran vectors (Valkiūnas, 2005; Santiago-Alarcon *et al*. 2012*a*). The prevalence, distribution, and diversity of these blood parasites vary among biogeographical regions (Valkiūnas, 2005), altitude (Galen and Witt, 2014; González *et al*. 2014), host life history traits (Fecchio *et al*. 2013; Svensson-Coelho *et al*. 2013; Lutz *et al*. 2015; Matthews *et al*. 2016), habitat (Mendes *et al*. 2005; Loiseau *et al*. 2010, 2012), bioclimatic conditions (Oakgrove *et al*. 2014), and can also be affected by urbanization and land use (Evans *et al*. 2009; Hernández-Lara *et al*. 2017). Usually, multiple species of these intracellular parasites coexist locally and exhibit varying levels of host specificity, ranging from infecting a single host to several distantly related hosts (Waldenström *et al*. 2002; Fecchio *et al*. 2013; Svensson-Coelho *et al*. 2013; Drovetski *et al*. 2014; Ellis *et al*. 2015). Although some avian malaria lineages might have diverged within a single-host population (Pérez-Tris *et al*. 2007), diversification by host switching appears to be common throughout the evolutionary history of this group of parasites (Ricklefs *et al*. 2004, 2014; Lauron *et al*. 2015). These factors listed above may play significant roles in structuring avian malaria parasite assemblages, either within a single-host population or within a more diverse local host community.

Using the mitochondrial cytochrome *b* (cyt *b*) gene to delineate parasite lineages, we describe the distribution and diversity of *Plasmodium* and *Haemoproteus* in their manakin hosts (Aves: Pipridae) across Central and South America. We focused on this endemic Neotropical bird family as a model system for three reasons: (1) its phylogeny has been relatively well studied (Ohlson *et al*. 2013), allowing for detailed investigation of how parasites are related to the evolutionary histories of their hosts; (2) the geographic distributions and diversity of manakins are characterized by high temperature and precipitation (Anciães and Peterson, 2009), which may promote high diversity and prevalence of blood parasites through climate influence on vector density and diversity; and (3) manakins are known by their polygynous breeding system, complex courtship displays and strong sexual dimorphism. The clustering of individuals during mating might result in increased exposure of manakins to haemosporidian vectors (Tella, 2002; Fecchio *et al*. 2011) and, under the expectation of significant parasite impact on secondary sexual traits of males (Hamilton and Zuk, 1982), one would predict that manakins are heavily parasitized.

Here, we first asked whether haemosporidian parasite diversity in manakins exhibits turnover among individual host species, and whether this turnover can be explained by the extent of geographic overlap between species and by the degree of phylogenetic relatedness among species. Second, we tested whether turnover in parasite assemblages of the manakin community among sites across Amazonia is related to: (a) geographic distance, (b) turnover in the manakin assemblage, (c) environmental differences and (d) turnover in the bird community of species other than manakins.

## MATERIALS AND METHODS

### *Sample collection*

We obtained blood (92% of all samples), or muscle/liver tissue (8%) from 1343 individual birds of 30 species of manakins sampled in four biomes: Amazonia (1027 birds, 24 species), Lowland Tropical Forest (233 birds, four species), Cerrado (57 birds, seven species) and Atlantic Rain Forest (26 birds, one species) (Fig. 1). The birds were netted during different time periods, seasons and/or years. Blood was collected by brachial venipuncture with disposable sterile needles from netted birds. Muscle and liver samples were taken during specimen preparation. All blood samples were stored in 95% ethanol or lysis buffer until DNA extraction. Tissue samples were stored in absolute

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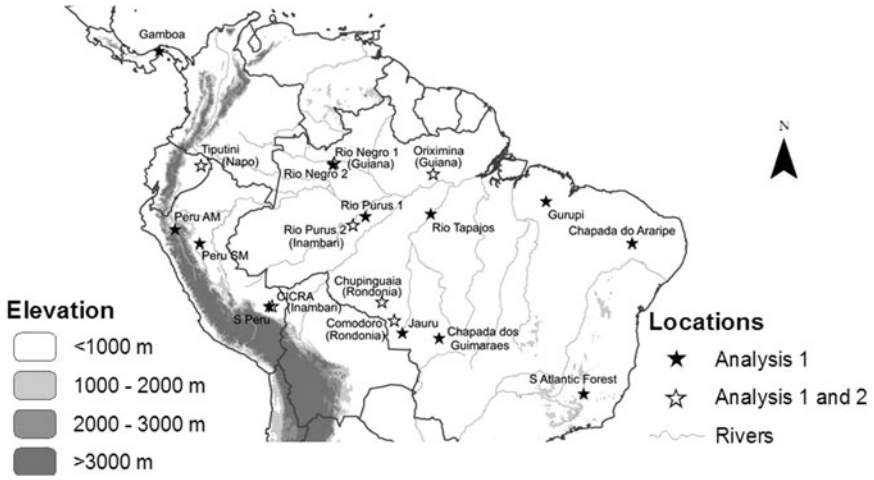


Fig. 1. Map of sampling localities included in this study. White and black stars represent sites incorporated for analysis 1 (parasite lineage turnover among manakin species). White stars represent localities incorporated in analysis 2 (parasite lineage turnover among localities). Endemic area of Amazonia is shown in parenthesis.

ethanol or flash frozen in liquid nitrogen. All samples were collected under appropriate permits in Brazil, Ecuador, Panama and Peru.

### *Parasite detection*

To screen total DNA samples for presence of *Plasmodium* and *Haemoproteus*, we adopted three molecular protocols by using parasite-specific primers targeting a fragment of cyt *b*. Information for detailed laboratory methods, primers names, and PCR conditions can be found in Fallon *et al*. (2003), Hellgren *et al*. (2004), Bell *et al*. (2015)]. These screening methods have similar effectiveness to detect haemosporidian parasites (Bell *et al*. 2015).

### *Phylogenetic relationships of parasites*

Sequences were edited and the 56 unique haplotypes recovered from manakins were aligned in Geneious v. 7.03 (Biomatters, Ltd., Auckland, New Zealand). For some sequences, the outer reactions amplified using the protocol of Svensson-Coelho *et al*. (2013) were then sequenced instead for the nested products. Because different cyt *b* regions were sequenced by different laboratories, overlap was not complete and thus coverage at individual nucleotide sites across the alignment ranged from 3 to 45 known characters per site (median 36, quartile range 16–45). The shortest sequence was 448 bases long; thus, no sequence included in our alignment was missing more than 46% of the examined sites. The complete alignment lacked data at 35% of the sites. Simulation studies have demonstrated that up to 50% missing data does not pose a problem for assigning placement in phylogenies (Wiens, 2003; Wiens and Morrill, 2011). Nonetheless, after estimating an initial maximum-likelihood (ML) phylogeny including all haplotypes, we collapsed shallow clades and repeated the ML analysis, including the one haplotype per clade with more sequence data. If several haplotypes within a clade were of equal length, one was chosen at random for the phylogeny Ohlson *et al*. (2013). We refer to collapsed clades as putative evolutionary lineages (Svensson-Coelho *et al*. 2013). Grouping haplotypes in this manner may result in loss of information about geographical or host specificity of parasites: therefore, we examined each lineage more closely in median-joining haplotype networks visualized by the program Network (available at fluxus-engineering.com, Bandelt *et al*. 1999). All ML analyses were performed in RA×ML BlackBox (Stamatakis *et al*. 2008), applying the default general time reversible (GTR) + gamma model of evolution and running 100 bootstrap replicates.

In a final ML analysis, we incorporated our 39 putative evolutionary lineages and 102 haemosporidian cyt *b* sequences analysed in Borner *et al*. (2016). Prior to analysis, ends were trimmed to where at least two sequences overlapped to result in a total of 1070 sites being compared. We used the five *Leucocytozoon* lineages incorporated in the phylogeny of Borner *et al*. (2016) as an outgroup. After analysis, the phylogeny was pruned using the command 'drop.tip' in the package ape (Paradis *et al*. 2004) in R (R Core Team, 2016) to include only lineages recovered from manakins. To understand the host specificity of the parasite lineages recovered from manakins, we matched parasite lineages to host species association based on data from the local bird communities from which we obtained manakin samples (Fig. 2).

### *Turnover of malaria parasites*

To examine factors potentially influencing the structure of avian malaria parasite assemblages, either

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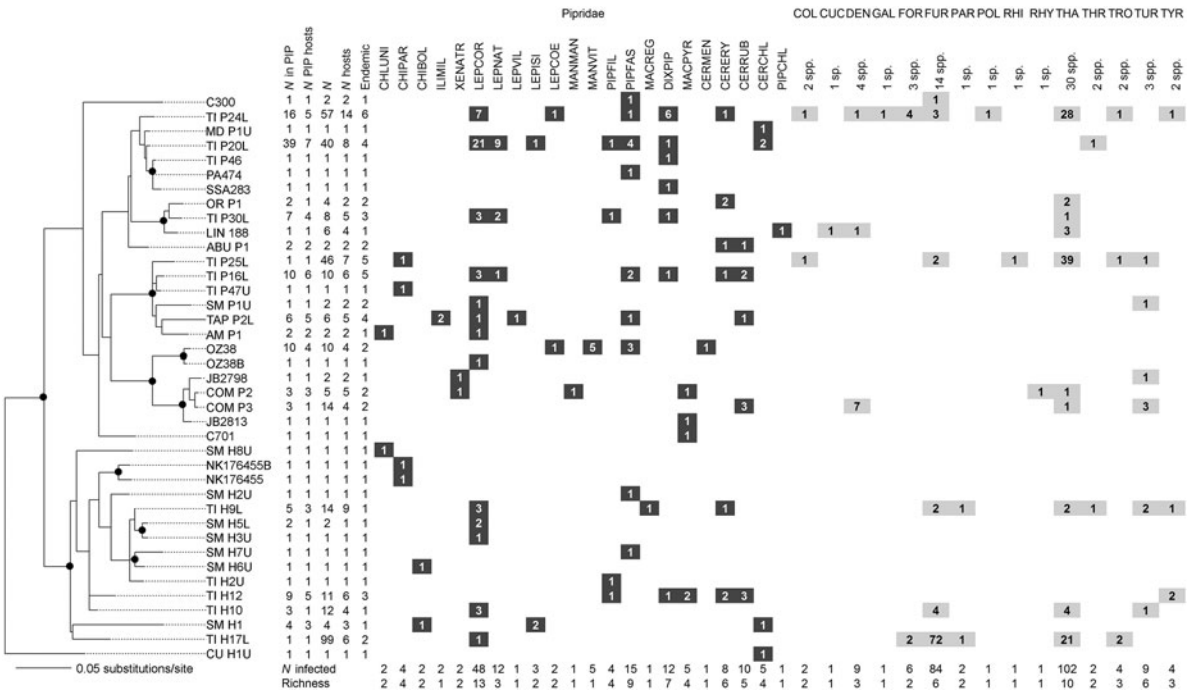


Fig. 2. ML tree of cyt *b* lineages recovered in manakins. Bootstrap support of ⩾70 is indicated with circles on nodes. The analysis incorporated data from Borner *et al*. (2016) and was subsequently pruned (see text). Lineages from TI P24L to C701 group significantly with other *Plasmodium* lineages. Lineages SM H8U to TI H17L group significantly within the *Haemoproteus* clade. Infections from all manakin species are highlighted in dark grey (species codes can be found in Table 1) and other non-manakin species are highlighted in light grey. We also indicate the number of individual non-manakin species (per family) exhibiting infection of a given parasite lineage and the number of species per host family from which the parasite was recovered. In columns on the left, we list number of individuals infected in Pipridae, number of manakin host species utilized, total number of individual host recovered in all sites and hosts combined (including non-manakins), the total number of host species utilized (including non-manakins), and list of the number of endemic areas from which a parasite was recovered (maximum possible = 10). Finally, in rows we list number of individuals infected and number of parasite lineages harboured per host species or family for non-manakins (Richness).

among manakin species (Analysis 1) or spatially among local assemblages of manakin species (Analysis 2), we used Mantel and partial Mantel tests (Mantel, 1967; Manly, 2007) to obtain correlations and associated significance values. To estimate malaria lineage turnover both between manakin species and among manakin assemblages, we used the Jaccard similarity index (Jaccard, 1912; Magurran, 2004). To obtain an index that increases with increasing dissimilarity, we subtracted the original Jaccard index from one as follows:

$$\jmath = \frac{(b+c)}{(a+b+c)}, \qquad (1)$$

where $a$ is the number of shared species between two assemblages, and $b$ and $c$ are the numbers unique to each assemblage. In all analyses, our operational taxonomic units are manakin species and parasite lineages.

To test for a relationship between parasite turnover among host species and either host phylogenetic relatedness or geographic range overlap, we selected only manakin species in which five or more individuals harboured identified parasite infections ($n = 9$ species; Fig. 1). We used $\jmath$ to assess turnover between all manakin species pairs. We obtained pairwise host genetic distance from DNA sequences of four genes (ND2, Myoglobin, G3PDH and ODC) from Ohlson *et al*. (2013). We estimated raw pairwise distances and averaged these across the four genes. We obtained geographic range maps of all nine manakin species in our sample from BirdLife International (available from http://www.birdlife.org/datazone/info/spcdownload) and calculated proportional range overlap as ½ (overlap/range size A + overlap/range size B) following Davies and Pedersen (2008).

In the second analysis, in which we sought correlates of turnover in the parasite community among locations, we estimated $\jmath$ not among host species, but among localities. For this analysis, we tested whether malaria turnover among Pipridae assemblages correlates with: (1) turnover of the malaria assemblage of all host species sampled; (2) climatic factors; (3) geographic distance; (4) turnover of the hosts (i.e. of manakin species); or (5) turnover of the overall host assemblage (mostly passerines). At each locality in the study, we sampled non-manakin species following the same protocols for sample collection and identification of infections

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reported above for manakins. We included only localities in which at least five infections within Pipridae and five infections in the rest of the host assemblage were identified ($n = 7$ localities in Amazonia with between 91 and 1901 birds sampled, primarily passerines). We refer to the non-manakin bird assemblage as the 'larger community' to distinguish it from parasite assemblages within host species (Esch *et al*. 1990).

For climate, we obtained 19 bioclimatic variables and elevation from WorldClim (available from http://www.worldclim.org/; Hijmans *et al*. 2005) at a 1 min resolution in DIVA-GIS (available from http://www.diva-gis.org/). We extracted principal components (PCs) from a correlation matrix of these variables, and saved those with an eigenvalue >1. This resulted in three PCs that explained 97% of the variation. Finally, we calculated the Euclidean distances among sites based on these three PCs. We obtained geographic distances in km in DIVA-GIS. Distances between localities are range from 190 km (Comodoro-Brazil and Chupinguaia-Brazil) to 2110 km (Comodoro-Brazil and Tiputini-Ecuador). Finally, we estimated $\beta$ of the host species assemblages, first for Pipridae only and then for the remaining species. We used the packages vegan (Oksanen *et al*. 2010), ape (Paradis *et al*. 2004), maptools (Bivand *et al*. 2015), PBSmapping (Schnute *et al*. 2015) and rgdal (Bivand *et al*. 2014) in R to calculate all distance matrices.

We estimated both Mantel and partial Mantel correlations (where we test the dependent and one independent variable while controlling for the remaining independent variables) using the package ecodist (Goslee and Urban, 2007) for R. In all analyses involving our dependent variable (lineage turnover of manakin parasites), we used a one-tailed test. We predicted manakin parasite lineage turnover among host species to correlate negatively with host range overlap and positively with host genetic distance (analysis 1); we predicted manakin parasite lineage turnover among localities to correlate positively with parasite compound community dissimilarity, geographic distance, Pipridae species turnover, climatic dissimilarity and non-Pipridae species turnover.

## RESULTS

### *Haemosporidian prevalence and diversity of lineages in manakins*

We analysed 1343 manakins of 30 species sampled across Brazil, Ecuador, Panama and Peru (Fig. 1). Samples were taken from a dataset comprised 5896 individual birds screened for haemosporidian parasites. We detected 146 infections in 22 manakin species with a prevalence of 10·9% (Table 1). Infections varied among host species, ranging from 0 to 50% (Table 1).

We recovered 39 haemosporidian cyt *b* lineages: 23 within the genus *Plasmodium* and 16 within the genus *Haemoproteus* (Fig. 2). Fifteen lineages infecting manakins were also found in other bird families (Fig. 2). Twenty-four lineages were found only in manakins, but at this stage we cannot claim that they are all specific to manakins, since we did not sample all the communities where these manakin hosts were caught. However, some rare lineages were found exclusively in manakins within well-sampled bird communities. For example, lineage C701L was found in only a single fiery-capped manakin (*Machaeropterus pyrocephalus*) individual in our Peru site, where we also screened 717 birds belonging to 115 species. The lineage P16L found exclusively in six manakin species across four areas of endemism in Amazonia and Cerrado represents the most widespread and specialized lineage of manakin parasite.

### *Turnover of lineages*

Among Pipridae host species, malaria parasite lineage turnover ranged from 0·0 to 0·43 (mean $0{\cdot}12 \pm 0{\cdot}11$ S.D.; Table 2). This variation did not correlate with either manakin species range overlap or genetic divergence between hosts (Fig. 3). Among Amazonian localities, malaria lineage turnover ranged from 0·0 to 0·40 (mean $0{\cdot}16 \pm 0{\cdot}12$ S.D.; Table 3). This variation did not correlate with manakin species turnover, geographic distance, climate difference, species turnover in the larger bird community or lineage turnover of parasites recovered from non-manakin species (Fig. 4). Some independent variables were significantly correlated with each other, although the correlation coefficient never exceeded 0·6 (Table 4).

## DISCUSSION

We investigated broad ecological and evolutionary factors that may shape the diversity and distribution of haemosporidian parasites in manakins across the Neotropics. In our analyses, we found low to moderate levels of lineage turnover across manakin species and localities. However, none of the seven factors that we tested explained variation in malaria parasite lineage turnover in this host family.

A diminishing proportion of shared parasites among host communities with increasing geographic distance has been found in several host–parasites systems such as helminthes of freshwater fish and mammals (Poulin, 2003), mites and fleas from small mammals (Krasnov *et al*. 2005; Vinarski *et al*. 2007), trematodes from marine molluscs (Thieltges *et al*. 2009) and malaria parasites from birds across island archipelagoes (Ishtiaq *et al*. 2010; Svensson-Coelho and Ricklefs, 2011). Our results do not agree with these previous findings.

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Table 1. Blood parasite prevalence (pooled *Plasmodium* and *Haemoproteus*) in manakins

| | | Individuals | |
|---|---|---|---|
| Manakin species | Abbreviation | Analysed | Infected (%) |
| *Lepidothrix isidorei* | LEPISI | 6 | 3 (50·0) |
| *Lepidothrix vilasboasi* | LEPVIL | 3 | 1 (33·3) |
| *Chloropipo unicolor* | CHLUNI | 6 | 2 (33·3) |
| *Xenopipo atronitens* | XENATR | 7 | 2 (28·6) |
| *Ceratopipra rubrocapilla* | CERRUB | 38 | 10 (26·3) |
| *Lepidothrix nattereri* | LEPNAT | 46 | 12 (26·1) |
| *Machaeropterus pyrocephalus* | MACPYR | 20 | 5 (25·0) |
| *Piprites chloris*[a] | PIPCHL | 5 | 1 (20·0) |
| *Ceratopipra chloromeros* | CERCHL | 28 | 5 (17·9) |
| *Lepidothrix coronata* | LEPCOR | 277 | 48 (17·3) |
| *Chiroxiphia boliviana* | CHIBOL | 13 | 2 (15·4) |
| *Pipra fasciicauda* | PIPFAS | 116 | 15 (12·9) |
| *Dixiphia pipra* | DIXPIP | 130 | 12 (9·2) |
| *Lepidothrix coeruleocapilla* | LEPCOE | 23 | 2 (8·7) |
| *Ceratopipra erythrocephala* | CERERY | 99 | 8 (8·1) |
| *Ilicura militaris* | ILIMIL | 26 | 2 (7·7) |
| *Manacus vitellinus* | MANVIT | 67 | 5 (7·5) |
| *Manacus manacus* | MANMAN | 15 | 1 (6·7) |
| *Chiroxiphia pareola* | CHIPAR | 85 | 4 (4·7) |
| *Pipra filicauda* | PIPFIL | 106 | 4 (3·8) |
| *Machaeropterus regulus* | MACREG | 29 | 1 (3·5) |
| *Ceratopipra mentalis* | CERMEN | 102 | 1 (1·0) |
| *Antilophia bokermanni* | ANTBOK | 27 | 0 |
| *Antilophia galeata* | ANTGAL | 15 | 0 |
| *Chiroxiphia linearis* | CHILIN | 31 | 0 |
| *Cryptopipo holochlora* | CRYHOL | 1 | 0 |
| *Heterocercus linteatus* | HETLIN | 12 | 0 |
| *Lepidothrix iris* | LEPIRI | 1 | 0 |
| *Neopelma pallescens* | NEOPAL | 6 | 0 |
| *Tyranneutes stolzmanni* | TYRSTO | 3 | 0 |
| Total | | 1343 | 146 (10·9) |

Species of birds are organized by prevalence.
[a] No longer Pipridae.

Table 2. Manakin malaria parasite lineage turnover estimated by the Jaccard index [equation (1)] among nine host species. Species names can be found in Table 1

| | LEPCOR | LEPNAT | MANVIT | PIPFAS | DIXPIP | MACPYR | CERCHL | CERRUB |
|---|---|---|---|---|---|---|---|---|
| LEPNAT | 0·23 | | | | | | | |
| MANVIT | 0 | 0 | | | | | | |
| PIPFAS | 0·22 | 0·2 | 0·11 | | | | | |
| DIXPIP | 0·25 | 0·43 | 0 | 0·23 | | | | |
| MACPYR | 0 | 0 | 0 | 0 | 0·1 | | | |
| CERCHL | 0·06 | 0·17 | 0 | 0·08 | 0·1 | 0 | | |
| CERRUB | 0·13 | 0·14 | 0 | 0·17 | 0·2 | 0·13 | 0 | |
| CERERY | 0·19 | 0·13 | 0 | 0·15 | 0·3 | 0·11 | 0 | 0·38 |

One plausible explanation for this is that haemosporidian dispersal in continental ecosystems is not as constrained as it is in insular ecosystems. For example, the turnover of haemosporidian parasites across bird populations in eastern North America (Ellis *et al*. 2015) and high degree of similarity in diptera vectors species across landscapes with different land use in Mexico (Abella-Medrano *et al*. 2015; Hernández-Lara *et al*. 2017) demonstrate the capability of these parasites to disperse within regions and to switch between avian hosts. Here, we show similarly low turnover of haemosporidia across a large geographic region in the Neotropics.

Evidence for that malaria parasite community structure relates to that of birds is mixed. Whereas Svensson-Coelho and Ricklefs, (2011) found no evidence for the predicted positive association between bird and malaria assemblage

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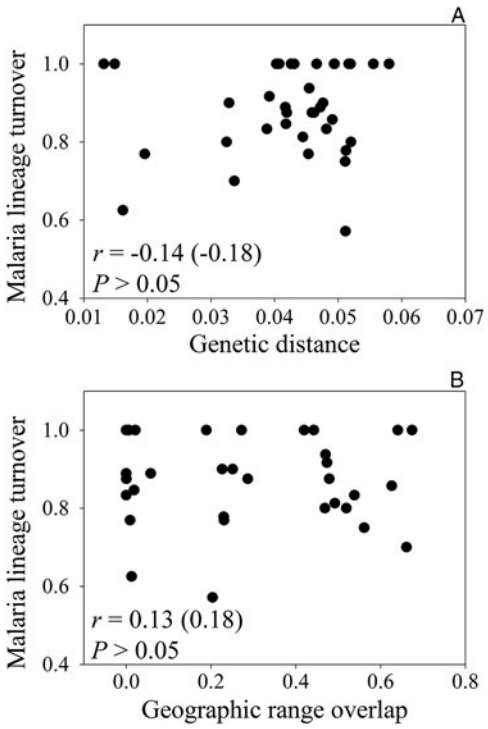


Fig. 3. Lineage turnover in avian malaria assemblages among nine manakin host species in relation to host genetic distance (A) and geographic range overlap (B). Mantel correlation coefficients ($r$) and one-tailed significance thereof ($P$) are reported. Partial Mantel test, where we control for the second independent variable, are presented in parentheses.

dissimilarity across islands in the Caribbean, Ellis *et al*. (2015) did in their continental system in eastern North America. Here, we found no evidence for such an association. This is true both when considering only the manakin assemblage and when considering the larger bird assemblage. An explanation for the lack of such association is that the distribution of haemosporidia is constrained by vector distribution. Although we have no information about vectors in our study region, Ishtiaq *et al*. (2008) argued that the movement of avian malaria lineages between southwest Pacific Islands might be restricted by the lack of distributional overlaps of competent vector species.

A positive correlation between parasite sharing and host geographical overlap is expected because opportunities for host shifting should increase where a non-infected potential host species occurs in sympatry with an actual host species (Fenton and Pedersen, 2005; Davies and Pedersen, 2008; Ricklefs *et al*. 2014). Indeed, this has been found for several types of parasites and pathogens in wild primates and humans (Davies and Pedersen, 2008). However, here we show that turnover among local assemblages of haemosporidian parasites of manakins is largely insensitive to host range overlap, 19 bioclimatic variables, and the dissimilarity of alternative hosts (i.e. non-manakin).

Environmental factors have been shown to affect the prevalence, distribution and alpha diversity (Gonzalez-Quevedo *et al*. 2014; Oakgrove *et al*. 2014; Olsson-Pons *et al*. 2015), but not beta diversity of avian malaria parasites (Svensson-Coelho and Ricklefs, 2011; Ellis *et al*. 2015). Malaria parasites are never subjected to the external environment directly, but they do pass through an ectothermic vector as part of their life cycle. At that time, they may be indirectly exposed to the external environment. For example, lower temperature not only constraints the sporogonic development of these parasites, but also reduces the activity of its mosquito vectors (Valkiūnas, 2005), which consequently could influence transmission and prevalence. Our study, however, is set in a tropical ecosystem, where temperature and moisture are unlikely to limit parasite transmission. Hence, the slight variation in climate across sites may have no consequence for Amazonian haemosporidians.

The lack of an association between malaria lineage turnover and all independent dissimilarity variables examined here supports the idea that local coevolution between avian hosts and avian malaria parasites, as well as local vector ecology, are more important in structuring malaria assemblages than distance–decay relationships (Svensson and Ricklefs, 2011; Scordato and Kardish, 2014). Additionally, transmission of multi-host pathogens, such as avian malaria, seems to be driven mostly by heterogeneity in host–parasite compatibility (Medeiros *et al*. 2013), thereby making external factors (other potential host species, climate, geography, etc.) less influential. External factors may nonetheless influence malaria assemblages to some degree, which would explain the significant associations recovered in some studies (e.g. Ishtiaq *et al*. 2010; Ellis *et al*. 2015)

Host switching has been shown to be a central event in the diversification of haemosporidians in New World passerine (Ricklefs *et al*. 2014) and non-passerine birds (Santiago-Alarcon *et al*. 2014) and is reflected in patterns recovered in this study in that 15 of 39 (38%) lineages recovered from manakins are also found in non-manakin hosts. The diversity of bird families within Amazonia and movement of haemosporidian lineages among these families must have played a role in forming the high diversity within this group of parasites in the Neotropics. The definitive hosts (i.e. vectors from the families Ceratopogonidae and Culicidae, respectively) of both *Haemoproteus* and *Plasmodium* have been poorly studied with regard to distribution, density and feeding preferences, and, in most cases, competent parasite vectors have not been identified (Santiago-Alarcon *et al*. 2012*a*). Recent studies on feeding preferences of blood-sucking diptera have revealed low preference for specific bird species, suggesting that vectors do not present barriers between bird and parasite encounters (e.g. Santiago-Alarcon

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Table 3. Manakin malaria parasite lineage turnover estimated by the Jaccard index [equation (1)] among seven Amazonian localities (Fig. 1). Comparisons within two endemic areas are highlighted in different shades of grey

| | Tiputini | CICRA | Rio Negro | Oriximiná | Rio Purus | Chupinguaia |
|---|---|---|---|---|---|---|
| CICRA | 0·2 | | | | | |
| Rio Negro | 0·14 | 0·25 | | | | |
| Oriximiná | 0·15 | 0·29 | 0·4 | | | |
| Rio Purus | 0·08 | 0·14 | 0 | 0 | | |
| Chupinguaia | 0·17 | 0·33 | 0·2 | 0·25 | 0·33 | |
| Comodoro | 0·19 | 0·08 | 0 | 0 | 0·13 | 0·13 |

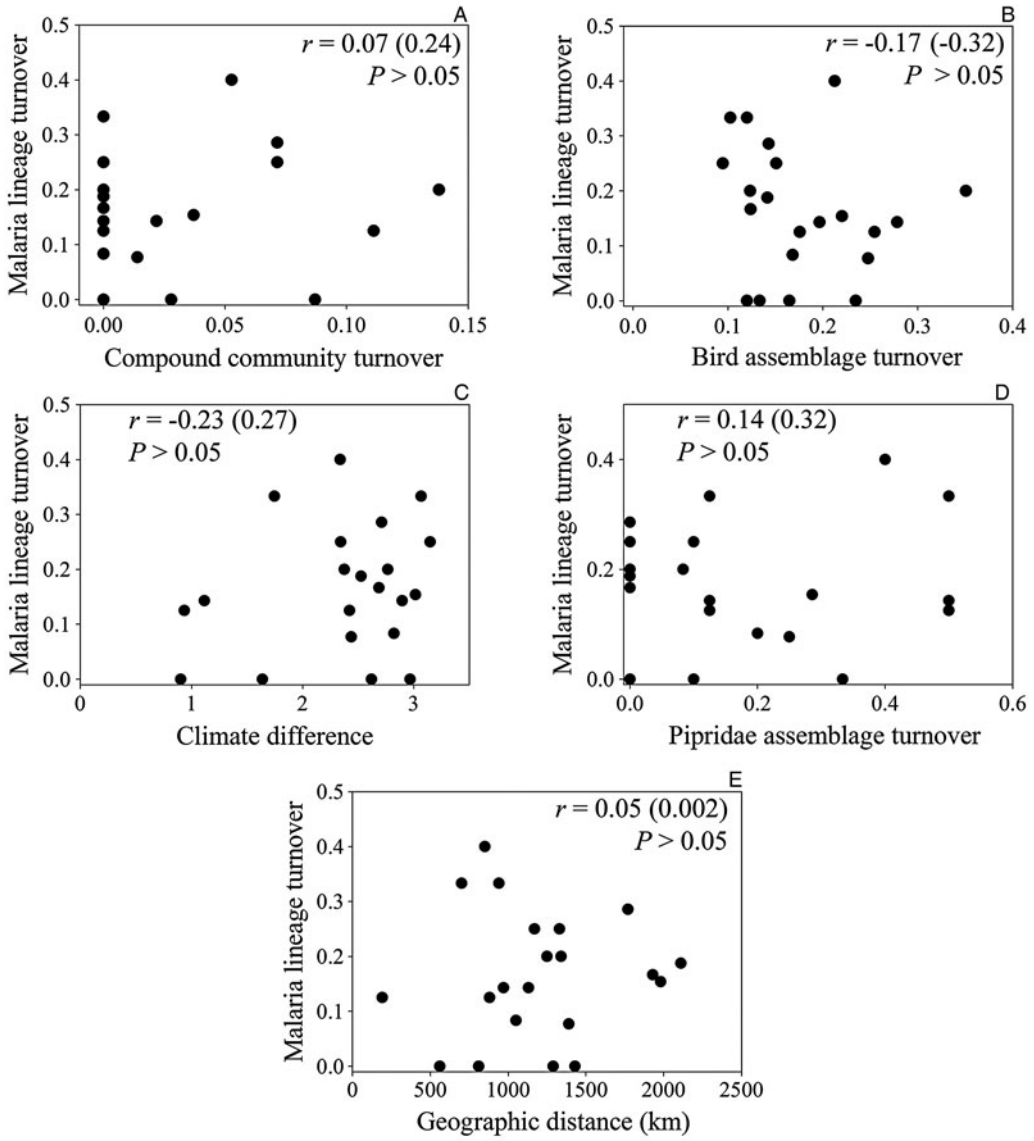


Fig. 4. Lineage turnover in avian malaria assemblages among seven Amazonian localities in relation to: turnover of malaria lineages in non-manakin species (A); turnover among the non-manakin bird assemblages (B); climatic differences (C); turnover among manakin assemblages (D); and geographic distance (E). Mantel correlations and significance thereof are reported. Partial Mantel correlations (*r*), in which the remaining four independent variables are controlled for, are shown in parentheses.

*et al*. 2012*b*; Medeiros *et al*. 2015; Ferreira *et al*. 2016). Further investigation into parasite vector distribution, host specificity and transmission will undoubtedly help to determine whether haemosporidian lineages track the diversity of their definitive hosts or of their intermediate hosts across Neotropical region.

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Table 4. Correlations between independent variables used in calculating among-locality turnover of avian malaria parasites of Pipridae. Independent variables considered are: (1) parasite assemblage turnover within the rest of the bird assemblage (CdC); (2) climatic differences (Clim); (3) geographic distance (Geo); (4) Pipridae assemblage turnover (Pip); and (5) turnover of the larger avian assemblage (Bird). Two-tailed *P* values are reported

| | *R* | *P* |
|---|---|---|
| CdC ~ Clim | −0·05 | 0·821 |
| CdC ~ Geo | −0·11 | 0·618 |
| Clim ~ Geo | 0·58 | 0·004 |
| Pip ~ Bird | 0·33 | 0·136 |
| Pip ~ Geo | −0·49 | 0·009 |
| Bird ~ Geo | 0·21 | 0·393 |

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REFERENCES

**Abella-Medrano, C. A., Ibáñez-Bernal, S., MacGregor-Fors, I. and Santiago-Alarcon, D.** (2015). Spatiotemporal variation of mosquito diversity (Diptera: Culicidae) at places with different land-use types within a neotropical montane cloud forest matrix. *Parasites & Vectors* **8**, 487.

**Anciães, M. and Peterson, A. T.** (2009). Ecological niches and their evolution among Neotropical manakins (Aves: Pipridae). *Journal of Avian Biology* **40**, 591–604.

**Bandelt, H.-J., Forster, P. and Röhl, A.** (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* **16**, 37–48.

**Bell, J. A., Weckstein, J. D., Fecchio, A. and Tkach, V. V.** (2015). A new real-time PCR protocol for detection of avian haemosporidians. *Parasites & Vectors* **8**, 383.

**Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R. and Rouault, E.** (2014). rgdal: Bindings for the Geospatial Data Abstraction Library. version 0.9-1.http://www.gdal.org, https://r-forge.r-project.org/projects/rgdal/

**Bivand, R., Lewin-Koh, N., Pebesma, E., Archer, E., Baddeley, A., Bibiko, H.-J., Brey, S., Callahan, J., Carrillo, G., Dray, S., Forrest, D., Friendly, M., Giraudoux, P., Golicher, D., Gómez-Rubio, V., Hausmann, P., Hufthammer, K. O., Jagger, T., Luque, S., MacQueen, D., Niccolai, A., Perpiñán-Lamigueiro, O., Short, T., Snow, G., Stabler, B., Stokely, M. and Turner, R.** (2015). maptools: Tools for Reading and Handling Spatial Objects. version 0.8-34. http://r-forge.r-project.org/projects/maptools/

**Borner, J., Pick, C., Thiede, J., Kolawole, O. M., Kingsley, M. T., Schulze, J., Cottontail, V. M., Wellinghausen, N., Schmidt-Chanasit, J., Bruchhaus, I. and Burmester, T.** (2016). Phylogeny of haemosporidian blood parasites revealed by a multi-gene approach. *Molecular Phylogenetics and Evolution* **94**, 221–231.

**Davies, T. J. and Pedersen, A. B.** (2008). Phylogeny and geography predict pathogen community similarity in wild primates and humans. *Proceedings of the Royal Society B: Biological Sciences* **275**, 1695–1701.

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

**Ellis, V. A., Collins, M. D., Medeiros, M. C. I., Sari, E. H. R., Coffey, E. D., Dickerson, R. C., Lugarini, C., Stratford, J. A., Henry, D. R., Merrill, L., Matthews, A. E., Hanson, A. A., Roberts, J. R., Joyce, M., Kunkel, M. R. and Ricklefs, R. E.** (2015). Local host specialization, host-switching, and dispersal shape the regional distributions of avian haemosporidian parasites. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 11294–11299.

**Esch, G. W., Bush, A. O. and Aho, J. M.** (1990). *Parasite Communities: Patterns and Processes*. Chapman and Hall, London.

**Evans, K. L., Gaston, K. J., Sharp, S. P., McGowan, A., Simeoni, M. and Hatchwell, B. J.** (2009). Effects of urbanisation on disease prevalence and age structure in blackbird *Turdus merula* populations. *Oikos* **118**, 774–782.

**Fallon, S. M., Ricklefs, R. E., Swanson, B. L. and Bermingham, E.** (2003). Detecting avian malaria: an improved polymerase chain reaction diagnostic. *Journal of Parasitology* **85**, 1044–1047.

**Fecchio, A., Lima, M. R., Silveira, P., Braga, É. M. and Marini, M. Â.** (2011). High prevalence of blood parasites in social birds from a neotropical savanna in Brazil. *Emu* **111**, 132–138.

**Fecchio, A., Lima, M. R., Svensson-Coelho, M., Marini, M. Â. and Ricklefs, R. E.** (2013). Structure and organization of an avian haemosporidian assemblage in a Neotropical savanna in Brazil. *Parasitology* **140**, 181–192.

**Fenton, A. and Pedersen, A. B.** (2005). Community epidemiology in theory and practice: a conceptual framework for classifying disease threats in human and wild populations. *Emerging Infectious Diseases* **11**, 1815–1821.

**Ferreira, F. C., Jr., Rodrigues, R. A., Sato, Y., Borges, M. A. Z. and Braga, É. M.** (2016). Searching for putative avian malaria vectors in a seasonally dry tropical forest in Brazil. *Parasites & Vectors* **9**, 587.

**Galen, S. C. and Witt, C. C.** (2014). Diverse avian malaria and other haemosporidian parasites in Andean house wrens: evidence for regional codiversification by host-switching. *Journal of Avian Biology* **45**, 374–386.

**González, A. D., Matta, N. E., Ellis, V. A., Miller, E. T., Ricklefs, R. E. and Gutiérrez, H. R.** (2014). Mixed species flock, nest height, and elevation partially explain avian haemoparasite prevalence in Colombia. *PLoS ONE* **9**, e100695.

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

**Goslee, S. C. and Urban, D. L.** (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* **22**, 1–19.

**Hamilton, W. D. and Zuk, M.** (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

**Hellgren, O., Waldenström, J. and Bensch, S.** (2004). A new PCR assay for simultaneous studies of *Leucocytozoon, Plasmodium* and *Haemoproteus* from avian blood. *Journal of Parasitology* **90**, 797–802.

**Hernández-Lara, C., González-García, F. and Santiago-Alarcon, D.** (2017). Spatial and seasonal variation of avian malaria infections in five different land use types within a Neotropical montane forest matrix. *Landscape and Urban Planning* **157**, 151–160.

**Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A.** (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.

**Ishtiaq, F., Guillaumot, L., Clegg, S. M., Phillimore, A. B., Black, R. A., Owens, I. P. F., Mundy, N. I. and Sheldon, B. C.** (2008). Avian haematozoan parasites and their associations with mosquitoes across Southwest Pacific Islands. *Molecular Ecology* **17**, 4545–4555.

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

**Jaccard, P.** (1912). The distribution of the flora in the alpine zone. 1. *New phytologist* **11**, 37–50.

**Kamiya, T., O'Dwyer, K., Nakagawa, S. and Poulin, P.** (2014). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews* **89**, 123–134.

**Krasnov, B. R., Shenbrot, G. I., Mouillot, D., Khokhlova, I. S. and Poulin, R.** (2005). Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographical distance or faunal similarity? *Journal of Biogeography* **32**, 633–644.

**Lauron, E. J., Loiseau, C., Bowie, R. C. K., Spicer, G. S., Smith, T. B., Melo, M. and Sehgal, R. N. M.** (2015). Coevolutionary patterns and diversification of avian malaria parasites in African sunbirds (Family Nectariniidae). *Parasitology* **142**, 635–647.

**Loiseau, C., Iezhova, T., Valkiūnas, G., Chasar, A., Hutchinson, A., Buermann, W., Smith, T. B. and Sehgal, R. N. M.** (2010). Spatial variation of haemosporidian parasite infection in African rainforest bird species. *Journal of Parasitology* **96**, 21–29.

**Loiseau, C., Harrigan, R. J., Robert, A., Bowie, R. C. K., Thomassen, H. A., Smith, T. B. and Sehgal, R. N. M.** (2012). Host and habitat specialization of avian malaria in Africa. *Molecular Ecology* **21**, 431–441.

**Lutz, H. L., Hochachka, W. M., Engel, J. I., Bell, J. A., Tkach, V. V., Bates, J. M., Hackett, S. J. and Weckstein, J. D.** (2015). Parasite prevalence corresponds to host life history in a diverse assemblage of Afrotropical birds and haemosporidian parasites. *PLoS ONE* **10**(4), e0121254.

**Magurran, A. E.** (2004). *Measuring Biological Diversity*. Blackwell Science Ltd, Malden, MA, USA.

**Manly, B. F. J.** (2007). *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall/CRC, Boca Raton, FL, USA.

**Mantel, N.** (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**, 209–220.

**Matthews, A. E., Ellis, V. A., Hanson, A. A., Roberts, J. R., Ricklefs, R. E. and Collins, M. D.** (2016). Avian haemosporidian prevalence and its relationship to host life histories in eastern Tennessee. *Journal of Ornithology* **157**, 533–548.

**Medeiros, M. C. I., Hamer, G. L. and Ricklefs, R. E.** (2013). Host compatibility rather than vector-host encounter rate determines the host range of avian *Plasmodium* parasites. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20122947.

**Medeiros, M. C. I., Ricklefs, R. E., Brawn, J. D. and Hamer, G. L.** (2015). *Plasmodium* prevalence across avian host species is positively associated with exposure to mosquito vectors. *Parasitology* **142**, 1612–1620.

**Mendes, L., Piersma, T., Lecoq, M., Spaans, B. and Ricklefs, R. E.** (2005). Disease-limited distributions? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. *Oikos* **109**, 396–404.

**Nekola, J. C. and White, P. S.** (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**, 867–878.

**Oakgrove, K. S., Harrigan, R. J., Loiseau, C., Guers, S., Seppi, B. and Sehgal, R. N. M.** (2014). Distribution, diversity and drivers of blood-borne parasite co-infections in Alaskan bird populations. *International Journal for Parasitology* **44**, 717–727.

**Ohlson, J. I., Fjeldså, J. and Ericson, P. G. P.** (2013). Molecular phylogeny of the manakins (Aves: Passeriformes: Pipridae), with a new classification and the description of a new genus. *Molecular Phylogenetics and Evolution* **69**, 796–804.

**Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H.** (2010). vegan: Community Ecology Package. R package version 1.17–0. https://CRAN.R-project.org/package=vegan

**Olsson-Pons, S., Clark, N. J., Ishtiaq, F. and Clegg, S. M.** (2015). Differences in host species relationships and biogeographic influences produce contrasting patterns of prevalence, community composition and genetic structure in two genera of avian malaria parasites in southern Melanesia. *Journal of Animal Ecology* **84**, 985–998.

**Paradis, E., Claude, J. and Strimmer, K.** (2004). APE: analyses of phylogenetics and evolution in R-language. *Bioinformatics* **20**, 289–290.

**Pérez-Tris, J., Hellgren, O., Križanauskienė, A., Waldenström, J., Secondi, J., Bonneaud, C., Fjeldså, J., Hasselquist, D. and Bensch, S.** (2007). Within-host speciation of malaria parasites. *PLoS ONE* **2**, e235.

**Poulin, R.** (1997). Species richness of parasite assemblages: evolution and patterns. *Annual Review of Ecology and Systematics* **28**, 341–358.

**Poulin, R.** (2003). The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *Journal of Biogeography* **30**, 1609–1615.

**Poulin, R.** (2007). *Evolutionary Ecology of Parasites*. Princeton University Press, Princeton, NJ, USA.

**R Core Team**. (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

**Ricklefs, R. E., Fallon, S. M. and Bermingham, E.** (2004). Evolutionary relationships, cospeciation and host switching in avian malaria parasites. *Systematic Biology* **53**, 111–119.

**Ricklefs, R. E., Outlaw, D. C., Svensson-Coelho, M., Medeiros, M. C. I., Ellis, V. A. and Latta, S.** (2014). Species formation by host shifting in avian malaria parasites. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 14816–14821.

**Santiago-Alarcon, D., Havelka, P., Schaefer, H. M. and Segelbacher, G.** (2012*b*). Bloodmeal Analysis Reveals Avian *Plasmodium* Infections and Broad Host Preferences of *Culicoides* (Diptera: Ceratopogonidae) Vectors. *PLoS ONE* **7**, e31098.

**Santiago-Alarcon, D., Palinauskas, V. and Schaefer, H. M.** (2012*a*). Diptera vectors of avian Haemosporidian parasites: untangling parasite life cycles and their taxonomy. *Biological Reviews* **87**, 928–964.

**Santiago-Alarcon, D., Rodríguez-Ferraro, A., Parker, P. G. and Ricklefs, R. E.** (2014). Different meal, same flavor: cospeciation and host switching of haemosporidian parasites in some non-passerine birds. *Parasites & Vectors* **7**, 286.

**Schnute, J. T., Boers, N., Haigh, R., Grandin, C., Chabot, D., Johnson, A., Wessel, P., Antonio, F., Lewin-Koh, N. J. and Bivand, R.** (2015). PBSmapping: Mapping Fisheries Data and Spatial Analysis Tools. version 2.68.68. https://cran.r-project.org/web/packages/PBSmapping/index.html

**Scordato, E. S. and Kardish, M. R.** (2014). Prevalence and beta diversity in avian malaria communities: host species is a better predictor than geography. *Journal of Animal Ecology* **83**, 1387–1397.

**Soininen, J., McDonald, R. and Hillebrand, H.** (2007). The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.

**Stamatakis, A., Hoover, P. and Rougemont, J.** (2008). A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* **57**, 758–771.

**Svensson-Coelho, M. and Ricklefs, R. E.** (2011). Host phylogeography and beta diversity in avian haemosporidian (Plasmodiidae) assemblages of the Lesser Antilles. *Journal of Animal Ecology* **80**, 938–946.

**Svensson-Coelho, M., Blake, J. G., Loiselle, B. A., Penrose, A. S., Parker, P. G. and Ricklefs, R. E.** (2013). Diversity, prevalence, and host specificity of avian *Plasmodium* and *Haemoproteus* in a Western Amazon assemblage. *Ornithological Monographs* **76**, 1–47.

**Tella, J. L.** (2002). The evolutionary transition to coloniality promotes higher blood parasitism in birds. *Journal of Evolutionary Biology* **15**, 32–41.

**Thieltges, D. W., Ferguson, M. A. D., Jones, C. S., Krakau, M., Montaudouin, X., Noble, R. L., Reise, K. and Poulin, R.** (2009). Distance decay of similarity among parasite communities of three marine invertebrate hosts. *Oecologia* **160**, 163–173.

**Valkiūnas, G.** (2005). *Avian Malaria Parasites and other Haemosporidian*. CRC Press, Boca Raton, FL, USA.

**Vinarski, M. V., Korallo, N. P., Krasnov, B. R., Shenbrot, G. I. and Poulin, R.** (2007). Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance, host-species composition or environment. *Journal of Biogeography* **34**, 1691–1700.

**Waldenström, J., Bensch, S., Kiboi, S., Hasselquist, D. and Ottoson, U.** (2002). Cross-species infection of blood parasites between resident and migratory songbirds in Africa. *Molecular Ecology* **11**, 1545–1554.

**Wiens, J. J.** (2003). Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology* **52**, 528–538.

**Wiens, J. J. and Morrill, M. C.** (2011). Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Systematic Biology* **60**, 719–731.