Parasitology

cambridge.org/par

The global biogeography of avian haemosporidian parasites is characterized by local diversification and intercontinental dispersal

Vincenzo A. Ellis[1], Eloisa H. R. Sari[1], Dustin R. Rubenstein[2], Rebecca C. Dickerson[3], Staffan Bensch[1] and Robert E. Ricklefs[4]

[1]Department of Biology, Molecular Ecology and Evolution Lab, Lund University, Lund, Sweden; [2]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA; [3]College of Veterinary Medicine, University of Missouri, Columbia, MO 65211, USA and [4]Department of Biology, University of Missouri-St. Louis, St. Louis, MO 63121, USA

Research Article

Cite this article: Ellis VA, Sari EHR, Rubenstein DR, Dickerson RC, Bensch S, Ricklefs RE (2019). The global biogeography of avian haemosporidian parasites is characterized by local diversification and intercontinental dispersal. *Parasitology* **146**, 213–219. https://doi.org/10.1017/S0031182018001130

Received: 6 March 2018
Revised: 28 May 2018
Accepted: 4 June 2018
First published online: 16 July 2018

Key words:
Avian malaria; biogeography; emerging infectious disease; Haemosporida; parasite dispersal; pathogens

Author for correspondence:
Vincenzo A. Ellis, E-mail: vincenzoaellis@gmail.com

Abstract

The biogeographic histories of parasites and pathogens are infrequently compared with those of free-living species, including their hosts. Documenting the frequency with which parasites and pathogens disperse across geographic regions contributes to understanding not only their evolution, but also the likelihood that they may become emerging infectious diseases. Haemosporidian parasites of birds (parasite genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon*) are globally distributed, dipteran-vectored parasites. To date, over 2000 avian haemosporidian lineages have been designated by molecular barcoding methods. To achieve their current distributions, some lineages must have dispersed long distances, often over water. Here we quantify such events using the global avian haemosporidian database MalAvi and additional records primarily from the Americas. We scored lineages as belonging to one or more global biogeographic regions based on infection records. Most lineages were restricted to a single region but some were globally distributed. We also used part of the cytochrome *b* gene to create genus-level parasite phylogenies and scored well-supported nodes as having descendant lineages in regional sympatry or allopatry. Descendant sister lineages of *Plasmodium*, *Haemoproteus* and *Leucocytozoon* were distributed in allopatry in 11, 16 and 15% of investigated nodes, respectively. Although a small but significant fraction of the molecular variance in cytochrome *b* of all three genera could be explained by biogeographic region, global parasite dispersal likely contributed to the majority of the unexplained variance. Our results suggest that avian haemosporidian parasites have faced few geographic barriers to dispersal over their evolutionary history.

Introduction

Emerging infectious diseases are caused by parasites and pathogens that appear in new areas of the world, or in new host species, and can represent serious threats to biodiversity and human health (Daszak *et al.*, 2000). For example, the fungal pathogen of bats *Pseudogymnoascus destructans* (white-nose syndrome), recently appeared in eastern North America, possibly *via* human introduction from Europe, and has devastated bat populations there (Frick *et al.*, 2010, 2015). Many similar negative effects of pathogens on evolutionarily naïve hosts have been documented (e.g. West Nile Virus impact on birds after introduction to North America (LaDeau *et al.*, 2007); the emergence of the chytrid fungus *Batrachochytrium dendrobatidis* as a major amphibian pathogen (James *et al.*, 2015), etc.). Despite the importance of determining where emerging infectious diseases originate, the biogeography of few major taxonomic groups of parasites and pathogens has been documented (Gaunt *et al.*, 2001; Morand and Krasnov, 2010; Summerell *et al.*, 2010; Pagenkopp Lohan *et al.*, 2016). Biogeographic analyses of whole clades may help reveal the frequency and geography of natural parasite and pathogen dispersal and provide information in support of modelling and prediction of emerging infectious diseases. Such analyses might also indicate the relative contribution of divergence in allopatry, as opposed to different hosts, in generating pathogen diversity.

Avian haemosporidian parasites (order Haemosporida) of the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* are widespread in birds on all continents except Antarctica (Valkiūnas, 2005). These parasites are transmitted by dipteran vectors [*Plasmodium* by mosquitos (Culicidae), *Haemoproteus* by biting midges (Ceratopogonidae) and hippoboscid flies (Hippoboscidae), and *Leucocytozoon* by black flies (Simuliidae) (Valkiūnas, 2005)], in which the parasites develop and undergo sexual reproduction. Individual species of parasite often infect a broad range of avian host species (Hellgren *et al.*, 2009; Ricklefs *et al.*, 2014) and many parasite lineages have switched frequently to new avian hosts over the course of their evolutionary history (Ricklefs *et al.*, 2004, 2014;

CAMBRIDGE UNIVERSITY PRESS

Alcala *et al.*, 2017). The introduction of avian haemosporidian parasites to Hawaii led to widespread declines and likely extinctions of forest birds, demonstrating the potential of these parasites to become emerging infectious diseases in naïve host populations (van Riper *et al.*, 1986; Beadell *et al.*, 2006). Genetic barcoding methods have revealed thousands of avian haemosporidian genetic lineages (Bensch *et al.*, 2009) which, in many cases, seem to constitute true biological species (Bensch *et al.*, 2004; Outlaw and Ricklefs, 2014; Hellgren *et al.*, 2015).

The geographic distributions of haemosporidian parasites have been investigated in the context of the migration patterns of their avian hosts. For example, in a survey of resident and migratory birds at a stop-over site in Nigeria, Waldenström *et al.* (2002) identified phylogenetic clades of parasite lineages that might have been transmitted either in Europe, in Africa or in both continents. A similar study of avian haemosporidian parasites of birds in the Americas found similar regional specialization but less phylogenetic signal in parasite transmission areas (Ricklefs *et al.*, 2017). Indeed, differences in distributions among haemosporidian genera have been linked to the probability that the parasites infect migratory host species (Hellgren *et al.*, 2007). However, some avian haemosporidian parasites, such as the lineage GRW04 (morphological species *Plasmodium relictum*) – the parasite that contributed to the decline of Hawaii's avifauna (Beadell *et al.*, 2006) – have nearly global distributions that cannot be attributed to natural avian migration patterns and might be related to human introductions of birds and vectors to novel areas (Soares *et al.*, 2017). Still other haemosporidians may have dispersed large distances without the help of humans and outside of typical bird migration routes. For example, Ricklefs and Fallon (2002) explicitly investigated the regional distributions of avian haemosporidian parasites and found many examples of related lineages restricted to more than one biogeographic region. Similarly, Beadell *et al.* (2006) identified an African and a Eurasian parasite nested within a well-supported clade of mostly New World parasite lineages, suggesting long-distance, overwater dispersal events in the evolutionary history of those parasites. Additional patterns likely representing long-distance dispersal events can be identified from other avian haemosporidian phylogenies (e.g. Ewen *et al.*, 2012; Cornuault *et al.*, 2013; Murdock *et al.*, 2015).

The mechanisms by which long-distance dispersal of avian haemosporidian parasites may have occurred (i.e. *via* avian or dipteran hosts, natural or human-mediated) are unclear. An analysis of the molecular substitution rate of extant haemosporidian parasites indicates that these parasites may have diversified across mammals, birds and reptiles within the last 20 million years, and across birds and reptiles in the last 10 million years (Ricklefs and Outlaw, 2010), although this estimate is controversial (Bensch *et al.*, 2013; Pacheco *et al.*, 2018). However, regardless of the rate of haemosporidian evolution, frequent overwater, long-distance dispersal events are indicated by the present-day global distribution of most major clades. Current parasite distributions reveal many examples of closely related haemosporidian lineages occupying disparate geographic localities, and several lineages appear to have nearly global distributions, providing the strongest evidence of long-distance dispersal.

Here, we investigated the phylogenetic relationships, historical biogeography, and current distributions of presently known avian haemosporidian parasites. Our goal was to place the geographic distributions of these parasites in an evolutionary context and to quantify global patterns of dispersal. Understanding the global biogeography of these parasites is an important step in determining the likelihood that lineages may disperse between regions and become emerging infectious diseases in the future.

Materials and methods

Data

We downloaded a 479 bp fragment of the cytochrome *b* gene from all parasite lineages in the MalAvi database (http://mbio-serv2.mbioekol.lu.se/Malavi/; Bensch *et al.*, 2009) belonging to the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* on 13 September 2017 (MalAvi v.2.3.2). Several of the MalAvi sequences probably represent variations on a single lineage because they differed by one or a few ambiguous base pairs only. We randomly selected one sequence from each repeated haplotype and removed the others using the 'clean_alignment' function in the R package *malaviR* (Ellis *et al.*, 2017). We then compared this group of parasite lineages with lineages defined in several published studies from RE Ricklefs' laboratory (e.g. Ricklefs *et al.*, 2014; Ellis *et al.*, 2015) and one unpublished survey (Table S1). We only compared sequences with complete or nearly complete overlap in the 479 bp gene fragment. We found 62 lineages that were identical among the MalAvi and Ricklefs databases (Table S2), and for those we retained the MalAvi names. We identified an additional 47 lineages that were not found in MalAvi (Table S3); all new lineages and alternative lineages names have been submitted to MalAvi.

We then added geographic information to lineages in the MalAvi database that were missing information by consulting original publications (Table S4) and using the Ricklefs database (Table S5). We identified geographic information for 861 *Plasmodium* lineages (out of 875 in the full alignment), 938 *Haemoproteus* lineages (out of 950) and 653 *Leucocytozoon* lineages (out of 673). Lineages were assigned to one or more of 11 biogeographic regions (Europe, North Africa and the Middle East, South Sahara, Asia, Oceania, Australia and New Zealand, North America, Central America, South America, Hawaii and Antarctica; Supplementary Fig. S1) following the current classifications in MalAvi.

Phylogenetic analyses

For each parasite genus, we created a maximum likelihood phylogenetic tree based on the cytochrome *b* sequences using the software RAxML Blackbox (Stamatakis *et al.*, 2008) with a γ model of rate heterogeneity and bootstrap support values for the nodes (Supplementary Figs S2–S4). Most nodes in these trees were unresolved, so we identified nodes with bootstrap support $\geqslant 0.8$ and with geographic information for all descendant lineages. We excluded one deep node in the *Haemoproteus* phylogeny that had 52 descendant lineages and multiple biogeographic regions on either side of the node making it difficult to classify as allopatric or sympatric (see below), and different than the rest of the nodes that were mostly shallow on the phylogeny. This left for the analysis 100 nodes for *Plasmodium*, 142 nodes for *Haemoproteus* and 96 nodes for *Leucocytozoon* (Tables S6 and S7), the majority of which were shallow (mean number of descendant lineages per node for *Plasmodium* was 3.94 ± 0.45 S.E.; *Haemoproteus*, 3.85 ± 0.30; *Leucocytozoon*, 3.82 ± 0.47). We scored these nodes as having sister lineages distributed in sympatry or in allopatry (Supplementary Fig. S5). For nodes with three or more descendant lineages, we conservatively classified sister lineages as being in sympatry if at least one lineage on one side of a node was found in the same geographic area as any lineage on the other side of the node. Such coarse-grain geographic classifications might misrepresent some short-distance allopatric events as sympatric events. However, we were primarily interested in identifying long-distance allopatric dispersal and we expected that uneven sampling across smaller geographic scales and across studies could produce false short-distance allopatric events. We therefore chose the coarse-grain classifications in

https://doi.org/10.1017/S0031182018001130 Published online by Cambridge University Press

MalAvi, while acknowledging the shortcomings of this approach. Finally, we determined whether allopatric nodes connected biogeographic regions that fall along three prominent avian migratory flyways, the Nearctic–Neotropical flyway, the Palaearctic–Afrotropical flyway and the Asian–Australasian flyway (Newton, 2007).

Molecular variation among biogeographic regions

We were also interested in how much of the molecular variation among parasite lineages could be explained by biogeographic regions. Accordingly, we restricted the lineages to those occurring in only one biogeographic region (the vast majority of lineages; see Fig. 1) and calculated the raw genetic distances among those lineages (separately for each genus) based on their cytochrome *b* sequences using the 'dist.dna' function in the R package *ape* (Paradis *et al.*, 2004). We then tested whether biogeographic region could explain any of the variation in the genetic distance matrices using the 'adonis' function in the R package *vegan* (Oksanen *et al.*, 2017), which performs a permutational analysis of variance (ANOVA) on distance matrices equivalent to an 'analysis of molecular variance' (Excoffier *et al.*, 1992). We ran 999 permutations per test. All analyses were run with R v.3.4.0 (R Core Team, 2017) and graphics were produced using the R packages *ggplot2* (Wickham, 2009) and *phytools* (Revell, 2012).

Results

Although the majority of the lineages in each genus were recovered from hosts in a single biogeographic region (Fig. 1), some lineages were globally distributed (Table S8; however, no lineages were found in Antarctica). For example, the *Plasmodium* lineage GRW04 was found in all regions except Antarctica, and the *Plasmodium* lineage GRW06 was found in eight regions (only missing from Hawaii, Central America and Antarctica). The most broadly distributed *Haemoproteus* lineage (PYERY01) was recovered from birds in six biogeographic regions (Europe, North Africa and the Middle East, South Sahara, North America, Central America and South America) and the most broadly distributed *Leucocytozoon* lineage (SFC8) occurred in four regions (Europe, North Africa and the Middle East, South Sahara and Asia). Overall, 12% of *Plasmodium* lineages (100/861), 15% of *Haemoproteus* lineages (139/938) and 7% of *Leucocytozoon* lineages (47/653) were distributed in more than one biogeographic region.

Among the well-supported nodes in the phylogenetic analysis, most descendant sister lineages were distributed in the same biogeographic region (89/100 *Plasmodium* nodes, 119/142 *Haemoproteus* nodes and 82/96 *Leucocytozoon* nodes were sympatric). Although these sympatric nodes were heterogeneously distributed among biogeographic regions (likely representing heterogeneous sampling), the distributions differed among the parasite genera ($\chi^2 = 76.3$, D.F. = 16, $P < 0.001$; Fig. 2). Specifically, sympatric nodes in the *Plasmodium* phylogeny were most often found connecting lineages in South America ($\chi^2 = 122.3$, D.F. = 8, $P < 0.001$), whereas sympatric *Haemoproteus* nodes were most often found connecting lineages in Europe, South Sahara and South America ($\chi^2 = 39.3$, D.F. = 8, $P < 0.001$). Additionally, sympatric nodes in the *Leucocytozoon* phylogeny were most often found connecting lineages in Asia, North America, Europe and South Sahara ($\chi^2 = 59.9$, D.F. = 8, $P < 0.001$). Neither the *Plasmodium* nor the *Leucocytozoon* phylogenies had sympatric nodes connecting lineages in Central America. In most cases, sympatric nodes connected descendant sister lineages occupying a single region. However, some sympatric nodes connected sister lineages that occur in more than one region (two *Plasmodium* nodes and 11 *Haemoproteus* nodes; Tables S6 and S7). For example, node 1030 in the *Plasmodium* phylogeny connects two lineages, PESA01 and NYCNYC01, both of which have been reported from both North America and South America.

A substantial proportion of the nodes connected descendant sister lineages distributed in allopatry, i.e. different continental regions; 11% of *Plasmodium* nodes (11/100), 16% of *Haemoproteus* nodes (23/142) and 15% of *Leucocytozoon* nodes (14/96). Many of these allopatric sister lineages were separated by considerable distances. As expected, many allopatric sister lineages were distributed in regions that fall along known avian migratory flyways, however some were not (Table S9, Figs 3 and 4).

We also tested how much of the molecular variation among parasite lineages could be explained by biogeographic region using ANOVA for distance matrices. Biogeographic region explained a small but significant fraction of the variation in genetic distances among lineages for all three parasite genera (*Plasmodium* $F_{8,752} = 3.76$, $R^2 = 0.04$, $P = 0.001$; *Haemoproteus* $F_{8,790} = 5.72$, $R^2 = 0.05$, $P = 0.001$; *Leucocytozoon* $F_{6,599} = 5.54$, $R^2 = 0.05$, $P = 0.001$). However, the vast majority of the variation remained unexplained by region, emphasizing the global-scale homogenization of haemosporidian lineages by long-distance dispersal.

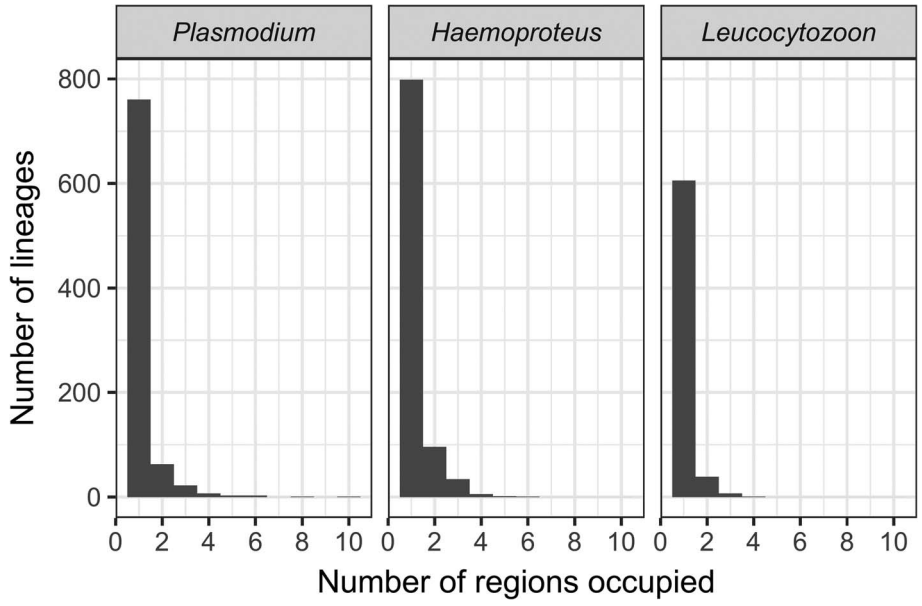

Fig. 1. Frequency distributions of the number of biogeographic regions (11 total regions) occupied by parasite lineages in each genus. The majority of lineages were found in a single region, but several, especially in *Plasmodium*, were globally distributed (see list of lineages distributed in more than one region in Table S8).

https://doi.org/10.1017/S0031182018001130 Published online by Cambridge University Press

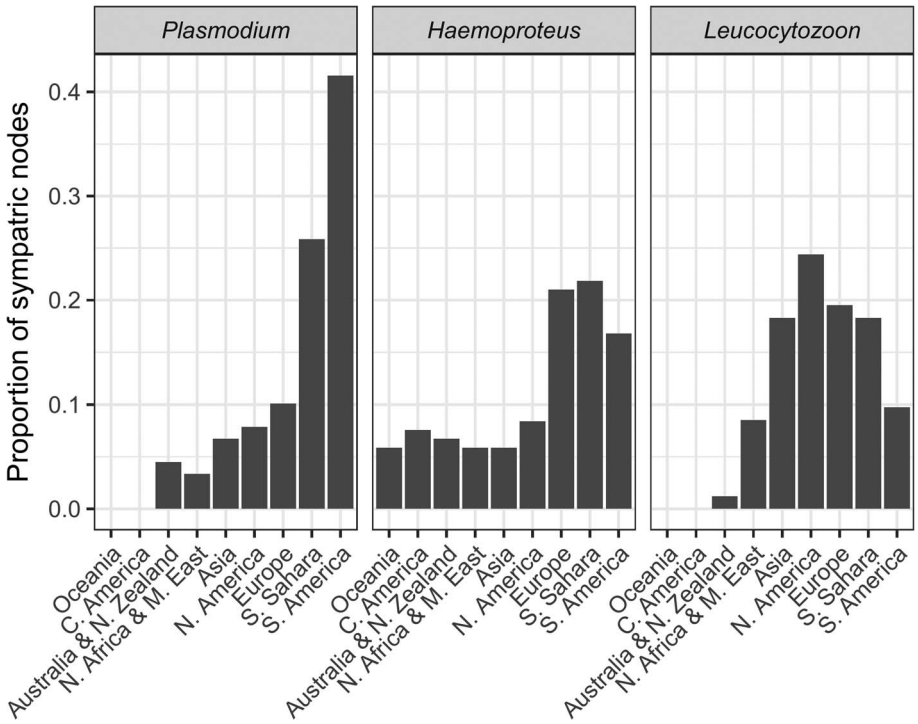

Fig. 2. Relative proportion of sympatric nodes connecting sister lineages by biogeographic region, calculated separately for each parasite genus (i.e. for each parasite genus, the number of nodes connecting sister lineages distributed in a particular biogeographic region divided by the total number of sympatric nodes identified). Sympatric nodes connecting sister lineages in more than one biogeographic region were excluded from this analysis.

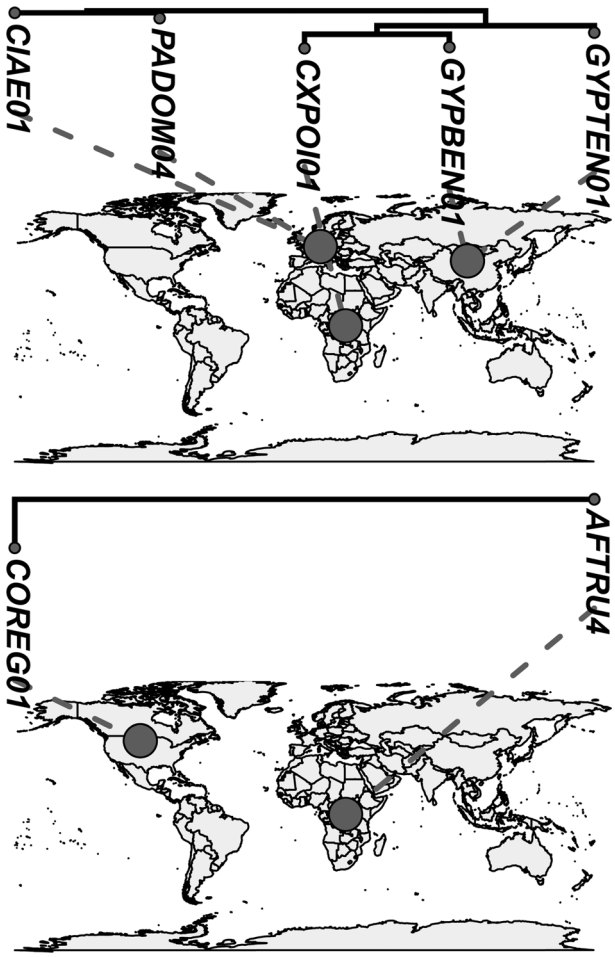

Fig. 3. Examples of allopatric nodes from the *Plasmodium* phylogeny. The top map shows two lineages distributed in Europe that are sister to three lineages distributed in Asia and South Sahara. The bottom map shows an allopatric node connecting two lineages on opposite sides of the Atlantic Ocean (North America and South Sahara).

Discussion

Dispersal of avian haemosporidian parasites appears to have been relatively unimpeded by geographic barriers on a global scale. We found parasite lineages distributed across multiple continents, only weak genetic structure across parasite distributions, and evidence suggesting that 10–15% of speciation events occurred in allopatry with respect to major biogeographic regions. The distributions of several allopatric sister lineages did not fall along regular avian migratory flyways (Table S9, Figs 3 and 4), and it is unlikely that migratory birds could have fully shaped the distributions of the globally distributed lineages. A high dispersal capacity of haemosporidians has been implicit in the literature since avian infections began to be identified molecularly. In an early study, Waldenström *et al.* (2002) identified sister clades of avian haemosporidian parasites distributed allopatrically in Europe and Asia, suggesting historical parasite dispersal events between the continents. At the same time, Ricklefs and Fallon (2002) explicitly investigated the distributions of parasite sister lineages, finding that more diverged lineages were more often found distributed in allopatry and on different host species than less diverged lineages. Hellgren *et al.* (2007) presented further evidence of this pattern, and suggested that it may be more common in *Plasmodium* than in *Haemoproteus*. Furthermore, several studies have documented global distributions of some haemosporidian parasite lineages (e.g. Beadell *et al.*, 2006; Hellgren *et al.*, 2015).

Beyond confirming the potential for haemosporidian parasites to become emerging infectious diseases in the future (and perhaps having been emerging infectious diseases many times in the past), the frequency of long-distance dispersal of haemosporidians has implications for dating the haemosporidian phylogeny using biogeographic calibration points. For example, a monophyletic clade of *Plasmodium* parasites is known to infect the lemurs of Madagascar (Pacheco *et al.*, 2011). This fact led Pacheco *et al.* (2011) to suggest that the last date of terrestrial mammalian colonization of Madagascar (*ca.* 20 million years ago) could be used as the minimum age of lemur *Plasmodium* parasite divergence. However, others have pointed out that the ancestor of lemur

https://doi.org/10.1017/S0031182018001130 Published online by Cambridge University Press

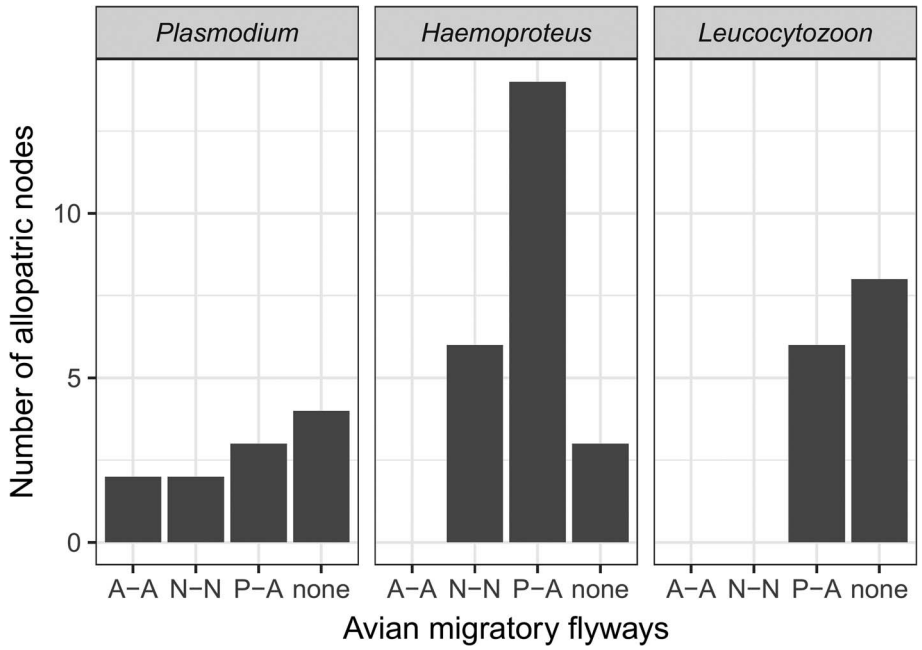

Fig. 4. Allopatric nodes (i.e. those connecting sister lineages distributed in different biogeographic regions) classified by whether they fall along three prominent avian migratory flyways (A–A, Asian–Australasian; N–N, Nearctic–Neotropical; P–A, Palaearctic–Afrotropical) or not. The allopatric nodes that do not connect lineages along those migratory flyways ('none') represent possible trans-oceanic dispersal events (e.g. across the Atlantic Ocean). Full details regarding these nodes can be found in Table S9.

Plasmodium could have arrived more recently *via* mosquito dispersal since vectors may be able to disperse parasites relatively long distances (Bensch *et al.*, 2013). If vectors were able to move the parasites to Madagascar at any time, then divergence of lemur *Plasmodium* from their ancestor could also have happened at any time, rendering that node in the haemosporidian phylogeny impossible to date. Our analysis supports the plausibility of such a scenario (mosquito-mediated dispersal of *Plasmodium*) and casts doubt on the use of that biogeographic event (the cessation of mammalian dispersal to Madagascar) as a calibration point in the haemosporidian phylogeny.

We also found that the geographic distributions of sympatric sister lineages differed among the parasite genera. Sympatric lineages of *Plasmodium* were mostly distributed in South America, while sympatric lineages of *Haemoproteus* were mostly in Europe, South Sahara, and South America, and sympatric lineages of *Leucocytozoon* were mostly in Asia, North America, Europe and South Sahara (Fig. 2). With the data available, we could not determine whether this is a result of differential rates of diversification among biogeographic regions or of differential sampling. One potential bias concerns how lineages are defined. Lineages in MalAvi are defined by single base pair differences, while lineages from the Ricklefs database sometimes incorporate variation in the cytochrome *b* gene. One consequence of this difference in lineage assignment is that the MalAvi lineages are more likely to group into well-supported sister lineages, many of which differ at single nucleotide positions and are more likely to share geographic distributions. Nevertheless, the geographic differences among the parasite genera in a number of sympatric lineages do, to some extent, mirror global patterns of diversity of these parasites (Clark *et al.*, 2014). Furthermore, restricting the data to MalAvi lineages and location information results in a higher proportion of nodes connecting allopatrically distributed sister lineages (17.3% of *Plasmodium* nodes, 21.7% of *Haemoproteus* nodes and 27.7% of *Leucocytozoon* nodes), suggesting that the different approaches to defining lineages did not affect our main conclusion of substantial intercontinental dispersal.

Understanding how haemosporidian parasites have dispersed across extensive ocean barriers remains a challenge. We consider three scenarios: (1) the natural movement of avian hosts; (2) the natural movement of dipteran vectors; and (3) within-region diversification followed by recent human-mediated transportation of either avian or dipteran hosts. As stated previously, the first scenario is plausible because birds migrate and often carry their haemosporidian parasites with them (Ricklefs and Fallon, 2002; Waldenström *et al.*, 2002; Hellgren *et al.*, 2007; Mendes *et al.*, 2013; Ricklefs *et al.*, 2017). For example, Pérez-Tris and Bensch (2005) sampled several populations of the avian host *Sylvia atricapilla* for haemosporidians in the host's breeding and wintering ranges and found that some parasites present in the breeding range also occurred in the blood of birds in their wintering range. Furthermore, some haemosporidian lineages that infect breeding North American birds have also been recovered on the wintering grounds of their hosts from resident birds in the West Indies (Fallon *et al.*, 2005; Ricklefs *et al.*, 2014). Migrating avian hosts have also been implicated in moving haemosporidian parasites from mainland areas to islands. For example, avian *Plasmodium* in the Galapagos Islands likely arrived *via* a migrating host, the Bobolink (*Dolichonyx oryzivorus*), which regularly stops over in the Galapagos archipelago during its migration (Levin *et al.*, 2013, 2016).

Parasite dispersal events over long distances that do not fall along typical avian migration routes are harder to explain by avian host movement. Few avian species regularly cross the Atlantic Ocean as part of their annual migrations (one of the only passerines known to do this is the northern wheatear, *Oenanthe oenanthe*; Bairlein *et al.*, 2012). However, several species are regular vagrants between Europe and the eastern USA, and these have been implicated in the expansion of the mosquito-vectored West Nile Virus from the Old to the New World (Rappole *et al.*, 2000). Over evolutionary time, vagrant birds may provide ample opportunity for long-distance parasite dispersal, assuming vagrants are exposed to suitable vectors.

The random, passive movement of dipteran vectors might also result in long-distance dispersal by haemosporidian parasites. Kay and Farrow (2000) sampled mosquitos with aerial kite traps up to 310 m in altitude and used prevailing wind speeds to estimate the distance travelled. The authors found that numerous *Aedes*, *Anopheles* and *Culex* mosquitos had travelled an average of 152 km and, accordingly, could have introduced a viral pathogen to Australia. Furthermore, Asahina (1970) collected several mosquito species 500 km at sea, off the coast of Japan. *Culicoides*

https://doi.org/10.1017/S0031182018001130 Published online by Cambridge University Press

biting midges have also been found to travel hundreds of kilometres in wind currents, even over large bodies of water (Burgin *et al.*, 2013). Pettersson *et al.* (2013) captured ornithophilic *Culicoides* biting midges 12 m above the ground in southern Sweden, further suggesting that they may be carried long distances by winds. These results suggest that dipteran vectors could potentially facilitate haemosporidian dispersal over long distances.

A final dispersal scenario involves humans transporting parasites outside of the regions in which they diversified. This has likely happened in the past. The avian malaria parasite GRW04 probably arrived to the Hawaiian Islands with introduced birds and was able to spread due to the presence of the introduced mosquito vector *Culex pipiens quinquefasciatus* (Beadell *et al.*, 2006). Furthermore, Ewen *et al.* (2012) demonstrated that the introduction of haemosporidian parasites to New Zealand likely occurred as a result of the introduction of infected birds from Europe.

Many researchers have documented the geographic spread and host-switching of blood-borne pathogens (Escalante *et al.*, 2005; Kilpatrick *et al.*, 2006), and it is clear that they are often capable of dispersing long distances and switching across large numbers of host species (Peterson, 2008). This also seems to be the case with avian haemosporidian parasites (Ricklefs *et al.*, 2014), which appear to have undergone multiple long-distance dispersal events over their evolutionary history. Future research might address haemosporidian dispersal by (1) screening migrating and vagrant avian hosts, (2) documenting vector dispersal patterns and the potential effect of haemosporidian infection on vector movement (Levin and Parker, 2014), and (3) increasing regional-level sampling of haemosporidian parasites to boost confidence in parasite distributions. Furthermore, as more genetic data are produced, phylogenies should become better resolved (Bensch *et al.*, 2016; Videvall *et al.*, 2017), affording researchers the opportunity to test whether long-distance dispersal events influence the rates of diversification. While most studies of parasite dispersal are undertaken to identify the origins of emerging infectious diseases, additional studies might address the dispersal patterns of entire parasite taxa to better understand the historical context that allows parasites to arise in new areas and infect naïve hosts.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0031182018001130.

Acknowledgements. Discussions with Matthew Medeiros, Alan Fecchio, and members of the Molecular Ecology and Evolution Lab at Lund University and comments from two anonymous reviewers improved the manuscript.

Financial support. We thank the US National Science Foundation and the National Geographic Society for support of fieldwork, and the Curators of the University of Missouri and the Whitney Harris World Ecology Center for funding laboratory work. D.R.R. was supported by the US National Science Foundation (IOS-1121435 and IOS-1257530). V.A.E. was supported by a postdoctoral fellowship from the Carl Tryggers Foundation.

Conflict of interest. None.

Ethical standards. We acknowledge Kenya's National Commission for Science, Technology and Innovation, Kenya's National Environmental Management Authority, the Kenya Wildlife Service and the Mpala Research Centre for enabling this work. This work was approved by Columbia University's IACUC.

References

Alcala N, Jenkins T, Christe P and Vuilleumier S (2017) Host shift and cospeciation rate estimation from co-phylogenies. *Ecology Letters* **20**, 1014–1024.

Asahina S (1970) Transoceanic flight of mosquitoes on the northwest Pacific. *Japanese Journal of Medical Science & Biology* **23**, 255–258.

Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC, Fox JW, Hussell DJT and Schmaljohann H (2012) Cross-hemisphere migration of a 25 g songbird. *Biology Letters* **8**, 505–507.

Beadell JS, Ishtiaq F, Covas R, Melo M, Warren BH, Atkinson CT, Bensch S, Graves GR, Jhala YV, Peirce MA, Rahmani AR, Fonseca DM and Fleischer RC (2006) Global phylogeographic limits of Hawaii's avian malaria. *Proceedings of the Royal Society B: Biological Sciences* **273**, 2935–2944.

Bensch S, Pérez-Tris J, Waldenström J and Hellgren O (2004) Linkage between nuclear and mitochondrial DNA sequences in avian malaria parasites: multiple cases of cryptic speciation? *Evolution* **58**, 1617–1621.

Bensch S, Hellgren O and Pérez-Tris J (2009) Malavi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome *b* lineages. *Molecular Ecology Resources* **9**, 1353–1358.

Bensch S, Hellgren O, Križanauskienė A, Palinauskas V, Valkiūnas G, Outlaw D and Ricklefs RE (2013) How can we determine the molecular clock of malaria parasites? *Trends in Parasitology* **29**, 363–369.

Bensch S, Canbäck B, DeBarry JD, Johansson T, Hellgren O, Kissinger JC, Palinauskas V, Videvall E and Valkiūnas G (2016) The genome of *Haemoproteus tartakovskyi* and its relationship to human malaria parasites. *Genome Biology and Evolution* **8**, 1361–1373.

Burgin LE, Gloster J, Sanders C, Mellor PS, Gubbins S and Carpenter S (2013) Investigating incursions of Bluetongue Virus using a model of long-distance *Culicoides* biting midge dispersal. *Transboundary and Emerging Diseases* **60**, 263–272.

Clark NJ, Clegg SM and Lima MR (2014) A review of global diversity in avian haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): new insights from molecular data. *International Journal for Parasitology* **44**, 329–338.

Cornuault J, Warren BH, Bertrand JAM, Milá B, Thébaud C and Heeb P (2013) Timing and number of colonizations but not diversification rates affect diversity patterns in hemosporidian lineages on a remote oceanic archipelago. *The American Naturalist* **182**, 820–833.

Daszak P, Cunningham AA and Hyatt AD (2000) Emerging infectious diseases of wildlife – threats to biodiversity and human health. *Science* **287**, 443–449.

Ellis VA, Collins MD, Medeiros MCI, Sari EHR, Coffey ED, Dickerson RC, Lugarini C, Stratford JA, Henry DR, Merrill L, Matthews AE, Hanson AA, Roberts JR, Joyce M, Kunkel MR and Ricklefs RE (2015) Local host specialization, host-switching, and dispersal shape the regional distributions of avian haemosporidian parasites. *Proceedings of the National Academy of Sciences* **112**, 11294–11299.

Ellis VA, Bensch S and Canbäck B (2017) MalaviR: an R interface to MalAvi. R package version 0.1.0. Available at https://github.com/vincenzoaellis/malaviR.

Escalante AA, Cornejo OE, Freeland DE, Poe AC, Durrego E, Collins WE and Lal AA (2005) A monkey's tale: the origin of *Plasmodium vivax* as a human malaria parasite. *Proceedings of the National Academy of Sciences of the USA* **102**, 1980–1985.

Ewen JG, Bensch S, Blackburn TM, Bonneaud C, Brown R, Cassey P, Clarke RH and Pérez-Tris J (2012) Establishment of exotic parasites: the origins and characteristics of an avian malaria community in an isolated island avifauna. *Ecology Letters* **15**, 1112–1119.

Excoffier L, Smouse PE and Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* **131**, 479–491.

Fallon SM, Bermingham E and Ricklefs RE (2005) Host specialization and geographic localization of avian malaria parasites: a regional analysis in the Lesser Antilles. *The American Naturalist* **165**, 466–480.

Frick WF, Pollock JF, Hicks AC, Langwing KE, Reynolds DS, Turner GG, Butchkoski CM and Kunz TH (2010) An emerging disease causes regional population collapse of a common North American bat species. *Science* **329**, 679–682.

Frick WF, Puechmaille SJ, Hoyt JR, Nickel BA, Langwig KE, Foster JT, Barlow KE, Bartonička T, Feller D, Haarsma A-J, Herzog C, Horáček I, van der Kooij J, Mulkens B, Petrov B, Reynolds R, Rodrigues L, Stihler CW, Turner GG and Kilpatrick AM (2015) Disease alters macroecological patterns of North American bats. *Global Ecology and Biogeography* **24**, 741–749.

Gaunt MW, Sall AA, de Lamballerie X, Falconar AK, Dzhivanian TI and Gould EA (2001) Phylogenetic relationships of flaviviruses correlate with their epidemiology, disease association and biogeography. *Journal of General Virology* **82**, 1867–1876.

Hellgren O, Waldenström J, Peréz-Tris J, Ösi ES, Hasselquist D, Krizanauskiene A, Ottosson U and Bensch S (2007) Detecting shifts of transmission areas in avian blood parasites – a phylogenetic approach. *Molecular Ecology* **16**, 1281–1290.

Hellgren O, Perez-Tris J and Bensch S (2009) A jack-of-all-trades and still a master of some: prevalence and host range in avian malaria and related blood parasites. *Ecology* **90**, 2840–2849.

Hellgren O, Atkinson CT, Bensch S, Albayrak T, Dimitrov D, Ewen JG, Kim KS, Lima MR, Martin L, Palinauskas V, Ricklefs R, Sehgal RNM, Valkiūnas G, Tsuda Y and Marzal A (2015) Global phylogeography of the avian malaria pathogen *Plasmodium relictum* based on MSP1 allelic diversity. *Ecography* **38**, 842–850.

James TY, Toledo LF, Rödder D, Silva Leite D, Belasen AM, Betancourt-Román CM, Jenkinson TS, Soto-Azat C, Lambertini C, Longo AV, Ruggeri J, Collins JP, Burrowes PA, Lips KR, Zamudio KR and Longcore JE (2015) Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15 years of amphibian chytridiomycosis research. *Ecology and Evolution* **5**, 4079–4097.

Kay BH and Farrow RA (2000) Mosquito (Diptera: Culicidae) dispersal: implications for the epidemiology of Japanese and Murray Valley Encephalitis Viruses in Australia. *Journal of Medical Entomology* **37**, 797–801.

Kilpatrick AM, Chmura AA, Gibbons DW, Fleischer RC, Marra PP and Daszak P (2006) Predicting the global spread of H5N1 avian influenza. *Proceedings of the National Academy of Sciences* **103**, 19368–19373.

LaDeau SL, Kilpatrick AM and Marra PP (2007) West Nile virus emergence and large-scale declines of North American bird populations. *Nature* **447**, 710–713.

Levin II and Parker PG (2014) Infection with *Haemoproteus iwa* affects vector movement in a hippoboscid fly-frigatebird system. *Molecular Ecology* **23**, 947–953.

Levin II, Zwiers P, Deem SL, Geest EA, Higashiguchi JM, Iezhova TA, JiméNez-UzcáTegui G, Kim DH, Morton JP, Perlut NG, Renfrew RB, Sari EHR, Valkiunas G and Parker PG (2013) Multiple lineages of avian malaria parasites (*Plasmodium*) in the Galapagos Islands and evidence for arrival *via* migratory birds. *Conservation Biology* **27**, 1366–1377.

Levin II, Colborn RE, Kim D, Perlut NG, Renfrew RB and Parker PG (2016) Local parasite lineage sharing in temperate grassland birds provides clues about potential origins of Galapagos avian *Plasmodium*. *Ecology and Evolution* **6**, 716–726.

Mendes L, Pardal S, Morais J, Antunes S, Ramos JA, Perez-Tris J and Piersma T (2013) Hidden haemosporidian infections in Ruffs (*Philomachus pugnax*) staging in Northwest Europe en route from Africa to Arctic Europe. *Parasitology Research* **112**, 2037–2043.

Morand S and Krasnov BR (eds) (2010) *The Biogeography of Host-Parasite Interactions*. New York: Oxford University Press.

Murdock CC, Adler PH, Frank J and Perkins SL (2015) Molecular analyses on host-seeking black flies (Diptera: Simuliidae) reveal a diverse assemblage of *Leucocytozoon* (Apicomplexa: Haemospororida) parasites in an alpine ecosystem. *Parasites & Vectors* **8**, 1–7. doi: 10.1186/s13071-015-0952-9

Newton I (2007) *The Migration Ecology of Birds*. New York: Academic Press.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E and Wagner H (2017) Vegan: community ecology package. R package version 2.4-3. Available at https://CRAN.R-project.org/package=vegan.

Outlaw DC and Ricklefs RE (2014) Species limits in avian malaria parasites (Haemosporida): how to move forward in the molecular era. *Parasitology* **141**, 1223–1232.

Pacheco MA, Battistuzzi FU, Junge RE, Cornejo OE, Williams CV, Landau I, Rabetafika L, Snounou G, Jones-Engel L and Escalante AA (2011) Timing the origin of human malarias: the lemur puzzle. *BMC Evolutionary Biology* **11**, 299.

Pacheco MA, Matta NE, Valkiūnas G, Parker PG, Mello B, Stanley CE, Lentino M, Garcia-Amado MA, Cranfield M, Kosakovsky Pond SL and Escalante AA (2018) Mode and rate of evolution of haemosporidian mitochondrial genomes: timing the radiation of avian parasites. *Molecular Biology and Evolution* **35**, 383–403.

Pagenkopp Lohan KM, Fleischer RC, Carney KJ, Holzer KK and Ruiz GM (2016) Amplicon-based pyrosequencing reveals high diversity of protistan parasites in ships' ballast water: implications for biogeography and infectious diseases. *Microbial Ecology* **71**, 530–542.

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

Pérez-Tris J and Bensch S (2005) Dispersal increases local transmission of avian malarial parasites. *Ecology Letters* **8**, 838–845.

Peterson AT (2008) Biogeography of diseases: a framework for analysis. *Naturwissenschaften* **95**, 483–491.

Pettersson E, Bensch S, Ander M, Chirico J, Sigvald R and Ignell R (2013) Molecular identification of bloodmeals and species composition in *Culicoides* biting midges. *Medical and Veterinary Entomology* **27**, 104–112.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rappole JH, Derrickson SR and Hubálek Z (2000) Migratory birds and spread of West Nile virus in the Western Hemisphere. *Emerging Infectious Diseases* **6**, 319.

Revell LJ (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223.

Ricklefs RE and Fallon SM (2002) Diversification and host switching in avian malaria parasites. *Proceedings of the Royal Society of London B: Biological Sciences* **269**, 885–892.

Ricklefs RE and Outlaw DC (2010) A molecular clock for malaria parasites. *Science* **329**, 226–229.

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

Ricklefs RE, Outlaw DC, Svensson-Coelho M, Medeiros MCI, Ellis VA and Latta S (2014) Species formation by host shifting in avian malaria parasites. *Proceedings of the National Academy of Sciences* **111**, 14816–14821.

Ricklefs RE, Medeiros M, Ellis VA, Svensson-Coelho M, Blake JG, Loiselle BA, Soares L, Fecchio A, Outlaw D, Marra PP, Latta SC, Valkiūnas G, Hellgren O and Bensch S (2017) Avian migration and the distribution of malaria parasites in New World passerine birds. *Journal of Biogeography* **44**, 1113–1123.

Soares L, Marra P, Gray L and Ricklefs RE (2017) The malaria parasite *Plasmodium relictum* in the endemic avifauna of eastern Cuba: Malaria in Cuban avifauna. *Conservation Biology* **31**, 1477–1482.

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

Summerell BA, Laurence MH, Liew ECY and Leslie JF (2010) Biogeography and phylogeography of Fusarium: a review. *Fungal Diversity* **44**, 3–13.

Valkiūnas G (2005) *Avian Malaria Parasites and Other Haemosporidia*. Boca Raton, FL, USA: CRC Press.

van Riper III C, Sandra G, van Riper M, Lee Goff and Marshal Laird (1986) The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* **56**, 327–344.

Videvall E, Cornwallis CK, Ahrén D, Palinauskas V, Valkiūnas G and Hellgren O (2017) The transcriptome of the avian malaria parasite *Plasmodium ashfordi* displays host-specific gene expression. *Molecular Ecology* **26**, 2939–2958.

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

Wickham H (2009) *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag

https://doi.org/10.1017/S0031182018001130 Published online by Cambridge University Press