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Discovering potential sources of emerging pathogens: South America is a reservoir of generalist avian blood parasites[☆]

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ABSTRACT

Generalist pathogens are capable of infecting a wide range of host species, and may pose serious disease emergence threats if accidentally moved outside their native areas. To date little effort has been devoted to identifying geographic areas that may act as reservoirs of generalist pathogens. According to current theory, where host diversity is high, parasite specialisation in one host species may be penalised by reduced host availability, while generalist parasites may benefit from the exploitation of various host species. Therefore natural selection could favor generalist parasites where host diversity is high. Here we explored if, in a highly diverse bird community in Ecuador, a generalist strategy is promoted among local *Haemoproteus* and *Plasmodium* blood-borne parasites compared with similar parasite communities throughout the world. We reconstructed the phylogenetic relationships of every parasite lineage in order to understand the evolution of host specificity in this megadiverse area. We found high levels of host generalisation for both parasite genera, and the mean host range of the *Haemoproteus* community in Ecuador was significantly higher than other parasite communities in other areas outside the Neotropics. Generalist *Haemoproteus* parasites in this bird community had diverse phylogenetic ancestry, were closely related to specialist parasites and were apparently endemic to the Amazon, showing that different parasites have independently evolved into host generalists in this region. Finally we show that *Haemoproteus* communities in Ecuador and South America are more generalist than in temperate areas, making this continent a hotspot of generalist *Haemoproteus* parasites for wild birds.

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1. Introduction

Understanding the evolution and ecology of generalist parasites is crucial to prevent disease outbreaks and to determine hotspots of potential emerging infectious disease (EID) (Woolhouse and Gowtage-Sequeria, 2005; Keesing et al., 2010). Different wildlife species can act as pathogen reservoirs which can form a threat to domestic animals and humans and pose a significant hazard to the conservation of biodiversity (Daszak et al., 2000). A global analysis on the geographical patterns of EID emergence shows that vector-borne diseases and zoonotic pathogens with wildlife origins are more concentrated at lower latitudes, but surveillance efforts have mainly concentrated on temperate areas (Jones et al., 2008). In contrast, a recent study on rodent reservoir species for future zoonotic disease outbreaks found that hotspots are mainly located in temperate areas (Han et al., 2015). For the emergence of

zoonotic EIDs with a wildlife origin, wildlife host species richness is a significant predictor (Jones et al., 2008). Therefore it is especially important to monitor tropical areas and identify hotspots of potential EIDs before their local and large-scale emergence.

The host range of a parasite evolves through natural selection and is determined by different ecological and physiological factors (Combes, 2001). The opportunity of finding the correct hosts is one of the most important ecological factors shaping host specificity (Combes, 2001; Schmid-Hempel, 2011). When a host species is abundant, specialist parasites have an advantage over generalist parasites if specialisation favors host monopolisation. However, if the relative abundance of different host species is low, as usually happens in highly diverse environments, parasite transmission among hosts of the same species can decrease (the dilution effect; Keesing et al., 2006). Under these circumstances, generalist parasites may compensate for reduced compatibility with a single host species if broadening the host range increases the total host encounter rate and disease transmission (the amplification effect; Keesing et al., 2006). Therefore, in highly diverse host communities a generalist strategy of host exploitation may be promoted among

[☆] New nucleotide sequence data reported in this paper are available in the GenBank™ database under accession numbers KT373858–KT373878.

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84 local parasite species, making those important areas to monitor for
85 potential disease outbreak.

86 Avian haemosporidian parasites are a diverse group of parasites
87 which infect most bird species worldwide (Valkiūnas, 2005;
88 Bensch et al., 2009) and are easily moved with host introductions
89 where they have already caused disease emergence problems
90 (van Riper et al., 1986; Schoener et al., 2014). *Haemoproteus* and
91 *Plasmodium* parasites are protozoans that infect red blood cells
92 and organs of birds and are transmitted by biting midges and mos-
93 quitoes, respectively (Valkiūnas, 2005). The MalAvi database
94 (mbio-serv2.mbioekol.lu.se/Malavi/) (Bensch et al., 2009) offers a
95 unique opportunity to study the variation in host specificity in
96 detail as it holds information on more than 1900 unique lineages
97 of avian blood parasites across the world, collected from approxi-
98 mately 250 publications. We have a good knowledge of the degree
99 of host specialisation of these parasites, which is usually higher for
100 *Haemoproteus* than for *Plasmodium* (Ricklefs and Fallon, 2002;
101 Beadell et al., 2009; Hellgren et al., 2009).

102 Host specialisation has proven important in determining inva-
103 sion success through host switches undergone by introduced
104 blood-borne parasites (Ewen et al., 2012). Generalist blood-borne
105 parasites of the genera *Plasmodium* and *Haemoproteus* are a threat
106 to birds worldwide, occasionally causing significant mortalities in
107 native bird species (Atkinson et al., 2009). For example, the intro-
108 duction of *Plasmodium relictum* and its main vector *Culex quinque-*
109 *fasciatus* to the Hawaii archipelago triggered a dramatic decline
110 and extinction of native species of honeycreepers (van Riper
111 et al., 1986). Similarly, generalist *Haemoproteus* parasites have
112 caused mortality in various species of captive parrots throughout
113 Germany (Olias et al., 2011). It has been shown that generalist
114 *Plasmodium* and *Haemoproteus* parasites are better colonisers of
115 island avifauna (Ewen et al., 2012; Pérez-Rodríguez et al., 2013)
116 compared with specialist parasites and that they can reach the
117 highest prevalence in a single host species, making them the most
118 common in the host community (Hellgren et al., 2009). Generalist
119 blood-borne parasites are good candidates to develop into emerg-
120 ing disease risks when moved outside their native areas. Therefore,
121 it is important to determine which geographic areas of the world
122 house the greatest diversity of these potential sources of EIDs.

123 Here we analyzed the host specificity of avian *Haemoproteus*
124 and *Plasmodium* blood-borne parasites in a megadiverse bird
125 community of Wisui, located in a lowland tropical forest in
126 southeastern Ecuador, and compared it with other areas through-
127 out tropical and temperate areas. Ecuador forms part of the tropical
128 Andes biodiversity hotspot (Myers et al., 2000) and its 1628
129 described avian species make it one of the most bird diverse coun-
130 tries in the world (Ridgely and Greenfield, 2006) and hence a good
131 candidate to explore if high bird diversity promotes the evolution
132 of generalist parasites. First, we analyzed whether *Haemoproteus*
133 parasites have evolved a host generalist strategy in the diverse host
134 community of Wisui as natural selection could favor this strategy
135 through the benefits of the amplification effect. As *Haemoproteus*
136 parasites are normally more host-specific, they are a good model
137 to explore this hypothesis. Under these circumstances, *Plasmodium*
138 parasites are expected to be generalists as well, as they are usually
139 global. Secondly, if the parasite communities of Wisui are general-
140 ist, we explored whether these parasites have diverse phylogenetic
141 origins and are related to specialist parasites, which would support
142 the hypothesis that they evolved towards generalism upon colonisa-
143 tion. There are two possible evolutionary trajectories leading to
144 the evolution of a generalist community of blood-borne parasites.
145 The parasite community could represent a local radiation of general-
146 alist parasites formed by the descendants of a generalist ancestor.
147 Alternatively, the parasites could be distantly related to one
148 another, sustaining the hypothesis of multiple origins of the local
149 parasite fauna. Finally, we compared the host specificity of this

150 parasite fauna with similar *Plasmodium* and *Haemoproteus* commu-
151 nities throughout tropical and temperate areas to test if Ecuadorian
152 parasite communities are more generalist than elsewhere. This
153 study will contribute to our knowledge of how generalist parasites
154 evolve and help us identify reservoirs of potential EIDs caused by
155 avian blood-borne parasites.

2. Materials and methods 156

2.1. Study area and field methods 157

158 The study was conducted in the Wisui reserve on the western
159 slopes of the Cutucú Mountain range in southeastern Ecuador
160 (Taisha canton, Morona-Santiago Province). The range is classified
161 as an Important Bird Area with more than 480 registered bird
162 species (Santander et al., 2009), classifying it as a megadiverse
163 biodiversity hotspot (Myers et al., 2000). Our sampling area (the
164 Wisui forest: 02°07'S, 77°44'W, 650 m altitude) is located within
165 a 3000 ha primary forest. The climatic conditions are tropical and
166 very humid, with an annual average temperature between 23 °C
167 and 25.5 °C and an average precipitation of 3000 mm. During the
168 sampling period (April 2010), the weather was cloudy with
169 frequent heavy rainfalls.

170 We set up 14 mist nets (12 m long × 2.5 m high, 25 mm mesh -
171 size) for 30 days at four different sites in the rainforest, which were
172 similar in vegetation structure and separated by less than 500 m.
173 We determined species of all captured birds by consulting several
174 references (Hilty and Brown, 1986; Ridgely and Greenfield, 2006;
175 Schulenberg et al., 2007) and according to the latest checklist of
176 the South American Classification Committee ([http://www.mu-
177 seum.lsu.edu/~Remsen/SACCBaseline.htm](http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm)). We took standard
178 body measurements of all captured birds (wing, tail and tarsus
179 length, and body mass), and photographed individuals to confirm
180 difficult species identifications. We collected blood samples
181 (5–80 µl, depending on body size) by puncture of the brachial vein.
182 Some of the blood was used to make two blood smears which were
183 air dried and fixed in absolute ethanol. The remaining blood was
184 kept in absolute ethanol to preserve DNA, at ambient temperature
185 in the field and then at –20 °C until molecular analysis. Once
186 processed, birds were marked using an individual feather clip
187 code to avoid repetition, and released unharmed at the site of cap-
188 ture. Bird sampling was performed in compliance with Ecuadorian
189 and Spanish environmental regulations and with the authorisa-
190 tions issued by the Ecuadorian Ministry of Environment of the
191 Morona-Santiago province under research permit number
192 007-2010-B-DPMS/MAE.

2.2. Laboratory methods 193

194 Blood smears were stained with GIEMSA solution (pH 7.2) for
195 75 min. Each blood smear was observed with a light microscope
196 (LEICA DM2500). We first scanned smears at relatively low
197 magnification (400×) to cover the whole smear in the search for
198 parasites. Then we screened those at 1000× magnification, focus-
199 ing on intra-erythrocytic parasites, until approximately 100,000
200 erythrocytes were inspected.

201 Total DNA was extracted from blood samples with a standard
202 ammonium acetate protocol (Green et al., 2012). We amplified
203 the MalAvi barcode for avian haemosporidians (479 bp of the
204 cytochrome *b* gene (*cyt b*); (Bensch et al., 2009)), which has been
205 sequenced for the majority of the known diversity of these
206 parasites and consequently facilitates the analysis of their evolu-
207 tionary relationships. It was ensured that all samples were of good
208 quality for PCR by amplifying bird sexing markers (Fridolfsson and
209 Ellegren, 1999). Parasite infections were screened for by using the

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