

Discovering parasite biodiversity in the Tropics: A framework based on multi-host-species ecological niche models

Diego Santiago-Alarcon ^{1*} | Octavio Rojas-Soto ²

¹Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C. Xalapa, C.P. 91070. México.

²Red de Biología Evolutiva, Instituto de Ecología, A.C. Xalapa, C.P. 91070. México.

Corresponding address

Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C. Xalapa, C.P. 91070. México.
Email: diego.santiago@inecol.mx

Funding

This research was supported by the Consejo Nacional de Ciencia y Tecnología (CONACYT; México): Problemas Nacionales program (2015-01-1628).

Academic Editor:

Luis A. Sánchez González

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ABSTRACT

The current threats to biodiversity imposed by human activities highlights the need to focus efforts not only in conserving what we already know, but also in the discovery of new species, particularly of poorly known but ecologically important groups such as parasites and underground fauna. Focusing on parasites, we must consider that their hosts represent their entire habitat, that most host species are infected by more than one parasite species, and that many studies have shown that some host traits (e.g., host body size, geographic range) and host diversity in general are positively correlated with parasite diversity. Thus, host diversity can be a surrogate for parasite diversity, where we would always expect higher parasite species richness than host species richness. Here, we propose a framework using multi-host-species ecological niche models – i.e., stacked species distribution models – or alternatively, the use of host joint species distribution models to guide parasite biodiversity discovery studies. We suggest then to focusing biodiversity surveys on areas with high host species richness and endemism, which will help making use of limited economic resources because it will concentrate field surveys in areas with a higher likelihood of parasite discovery (e.g., host diversity hotspots that provide larger habitat heterogeneity for parasites).

KEYWORDS

Biotic interactions, ecological niche, host communities, parasite assemblages, vector-borne diseases, parasite biodiversity.

Why bother with parasite studies? First, parasitism is important due to its adverse impacts on hosts' health, such as avian malaria (Ilgūnas *et al.*, 2019). Second, parasites represent a large proportion of the planet's biomass, thus they are vital for ecosystem functioning due to their impacts on host population dynamics, and their direct and indirect influence on community interactions (Marcogliese, 2005; Lafferty *et al.*, 2008; Hatcher & Dunn, 2011). Third, parasitism has evolved

How to cite this article: Santiago-Alarcón D & Rojas Soto OR 2021. Discovering parasite biodiversity in the Tropics: A framework based on multi-host-species ecological niche models. *Ecotropicos*. 33: e0016

independently many times (e.g., ca. 100 convergence events in eukaryotes) across the tree of life (Poulin, 2011; Poulin *et al.*, 2011), making it the most successful lifestyle on Earth, with approximately 50% of known organisms being parasitic –but the actual figure depends on the definition of parasitism (Poulin, 2014). Thus, parasites rather than simply being a concern for eradication, are a group we must strive to study in their own right, starting by analyzing their biodiversity (Clark *et al.*, 2014) and understanding their coevolutionary history with their hosts (McQuaid & Britton, 2013).

There is a long history of research trying to determine the factors that affect the geographical distribution of biodiversity (see below), and only during the last decade has parasite biodiversity started to receive due attention (Carlson *et al.*, 2020a,b). Given that for parasites the host represents both its habitat and resources, it was suggested that host body size must be a strong predictor of parasite species richness (Poulin *et al.*, 2011). However, for helminth parasites there is a weak association between host body size and parasite richness; yet, there seems to be phylogenetic influence indicating that certain host families, independent of body size, are more likely to harbor higher parasite species richness –i.e. hot-host species (Poulin *et al.*, 2011; Krasnov *et al.*, 2019). Other studies have demonstrated that parasite species richness is strongly predicted by host species richness (Hechinger & Lafferty, 2005; Poulin, 2014; Krasnov *et al.*, 2019), but the magnitude of the association depends on both the biological (i.e., host individual, population or community) and spatial scales of analysis (i.e., local to landscape level or metacommunity) (Johnson *et al.*, 2016; Clark, 2018; Krasnov *et al.*, 2019). For instance, amphibian species richness contributed more to beta helminth parasite richness (i.e., among-host species) than to alpha parasite species richness; furthermore, as the spatial scale increased, parasite species richness increased, whereas host species richness reached a plateau (Johnson *et al.*, 2016). Because parasite diversity is always higher than host diversity (Poulin, 2014), we expect such a pattern to emerge across spatial scales (Fig. 1).

The generality of these patterns is difficult to gauge, however, given the strong bias toward a few parasite groups (i.e., helminths and ectoparasites); some limiting factors include the lack of expert taxonomists across many parasite groups and the lack of appropriate geographical approaches –but see Pappalardo *et al.* (2020)– to focus limited economic resources into parasite study and discovery. A detailed explanation for the

proposal of a Global Parasite Project is available in Carlson *et al.* (2020a,b). Given the strong association between host and parasite diversity (Poulin, 2014) and considering that birds are the best-known vertebrate group with the highest diversity in the Neotropical region (Cheviron *et al.*, 2005; Lovette & Fitzpatrick, 2011), in this paper, we used Neotropical bird diversity in order to propose a framework for parasite biodiversity discovery.

The proposal framework.- We use avian haemosporidians, a Diptera-borne parasite group, as our parasite model (Santiago-Alarcon & Marzal, 2020). Generalist avian haemosporidians commonly infect closely related hosts and not necessarily hosts with similar niches; thus, host phylogenetic beta diversity likely predicts parasite beta diversity (Clark & Clegg, 2017). Consequently, avian *Plasmodium* and *Haemoproteus* phylogenetic diversity differs between geographical areas where avian hosts are also distinct –e.g., endemism areas of the Amazon basin (Fecchio *et al.*, 2018), whereas it is more similar in communities with higher connectivity (Clark & Clegg, 2017) or located closer geographically (Scordato & Kardish, 2014). In haemosporidians, the latitudinal diversity pattern is either absent on haemosporidian phylogenetic diversity (Clark, 2018) or inverse, as in the genus *Leucocytozoon* (Fecchio *et al.*, 2020).

In terms of climatic variables, there is higher parasite specialization and unique assemblages in areas with more seasonality in both rainfall and temperature (Fecchio *et al.*, 2019). Also, there is a negative correlation between *Plasmodium* phylo-beta diversity and maximum temperature, whereas the association is positive for *Haemoproteus* phylo-beta diversity (Clark & Clegg, 2017). Another important issue is host specificity, with many parasite taxa strongly host specific and probably candidates for co-distribution and co-extinctions (due to human activities) with their hosts (Proctor & Owens, 2000; Carlson *et al.*, 2017). However, in avian haemosporidians there is variation in host specificity patterns, which may be attributed to host switching among ecologically similar birds, or to the persistence of a parasite on phylogenetically related avian species (i.e., the same parasite is present on multiple host species that may or may not be geographically isolated) (Hoebeg *et al.*, 1997; Santiago-Alarcon *et al.*, 2014; Clark & Clegg, 2017). Species richness, the most commonly used measure of biodiversity, is a function of individual abundance and

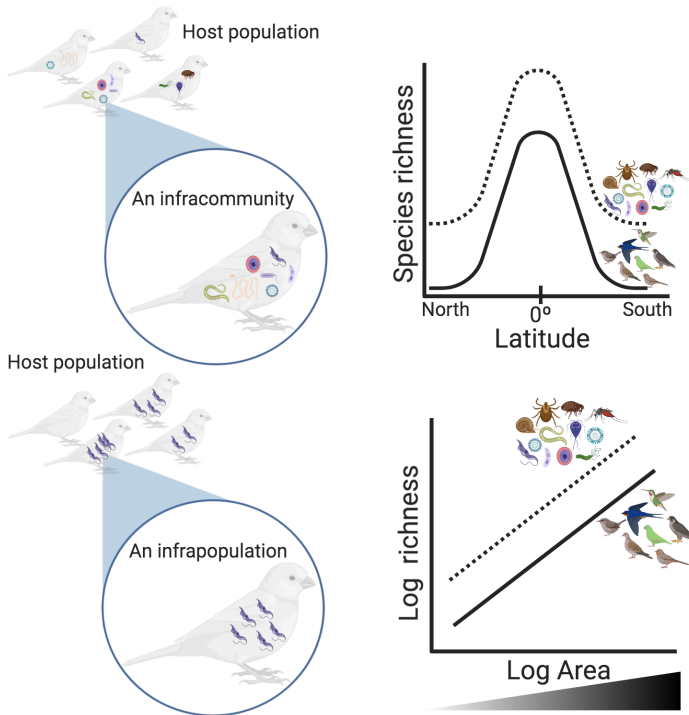


FIGURE 1 Cartoons representing a parasite infra-population (some host individuals are either not infected or have a lower parasite load) and a parasite infra-community. For a detailed explanation about important parasitological concepts see Bush *et al.* (1997). The diagrams on the right-hand side represent the expected latitudinal and area species richness patterns for both parasite and host species. Parasite richness (dotted lines) is expected to be higher than host richness (solid lines).

species heterogeneity, and a high richness of hosts should contribute to a high richness of parasites as discussed above. Thus, the ranges of both hosts and parasites are historically constrained by genealogical and ecological associations (Brooks, 1985).

Three general hypotheses have been used to explain the diversity patterns of species distribution. One ecological hypothesis is related to the species carrying capacity, a second evolutionary hypothesis is focused on the rates of diversification, and a third named historical hypothesis focuses on the duration and extent of tropical environments in Earth's history (Mittelbach *et al.*, 2007). The Neotropics possess the highest diversity of birds (Lovette & Fitzpatrick, 2011), which respond to the three hypotheses mentioned above, as follows:

i) Ecological factors along latitudinal and altitudinal gradients are defined by climate, energy, aspect, among others (Roth, 1976; Rohde, 1992; Wright, 1993; Poulsen & Krabbe,

1997; Rahbek & Graves, 2001); in addition, a complex topography favors the most exceptional ecosystem richness in the world (Rahbek & Graves, 2001; Hawkins *et al.*, 2003a,b);

ii) Diversification rates are faster due to higher rates of speciation (caused by increased opportunities for isolation, molecular evolution, and the increased importance of biotic interactions) and lower extinction rates (Currie *et al.*, 2004; Mittelbach *et al.*, 2007);

iii) Tropical climates have been historically more stable and encompass a larger area, allowing more opportunities for diversification; also, temperate taxa are often younger than tropical taxa (Hawkins *et al.*, 2006; Mittelbach *et al.*, 2007; Jetz *et al.*, 2012) and basal clades are more diverse in lowland areas, whereas derived ones are more diverse at high elevations (Hawkins *et al.*, 2007).

Aligned with these ideas, it may be expected parasites to be more diverse in the tropics due to higher habitat or niche

heterogeneity –i.e., habitat heterogeneity hypothesis (Johnson *et al.*, 2016; Stephens *et al.*, 2016). Yet, some studies on birds (Prieto-Torres *et al.*, 2019b) and parasites (Bordes *et al.*, 2010; Fecchio *et al.*, 2020) have shown an inverse latitudinal gradient. In the case of birds, restriction to only one type of ecosystem (e.g., seasonal dry forests) may be invoked as a probable explanation, therefore suggesting that historical factors may have affected diversification and extinction rates differently depending on both local and regional conditions (Ricklefs, 2004). In contrast, for parasites, it may be first explained by lower sampling efforts in tropical than temperate regions in the case of avian haemsporidians (Santiago-Alarcon & Marzal, 2020), and second, life history traits of parasites –i.e., biological and physiological constraints– may dissociate parasite diversity from host diversity (Krasnov *et al.*, 2019). Keeping in mind that for parasites a host represents their entire habitat, and each host is home to a diverse array of parasites, many of which are phylogenetically unrelated (Hatcher & Dunn, 2011), all individuals of a parasite species within a host represent an infrapopulation, and all individuals of different parasite species infecting a host represent an assemblage known as an infracommunity (Bush *et al.*, 1997) (see Fig. 1). Hence, our attention in terms of parasite biodiversity must be directed toward two pressing issues: a more extensive spatial sampling in tropical areas and the need for more expert parasite taxonomists.

During the last two decades, Ecological Niche Modeling (ENM) and Species Distribution Modeling (SDM) have arisen as useful tools to anticipate species' distribution potential in novel regions at broad ecological and biogeographical scales (Barve *et al.*, 2011; Owens *et al.*, 2013). Thus, the correlation of known occurrences of species and modeling approaches allows the improvement of potential presence hypotheses based on the ecological niches of the species being modeled. These methods possess the advantage that estimating a species' environmental preferences allows the model's transference toward similar conditions on different spaces and times (Owens *et al.*, 2013). These capabilities could explain the massive usage of these methodologies in recent years (Lobo *et al.*, 2010; Peterson *et al.*, 2011), including assessing questions of parasites, vectors, or host species in avian parasites (Prieto-Torres *et al.*, 2020). Among avian hosts, the narrow distributions of many parasites (host specificity) have traditionally been accepted as a reflection of well established, historically maintained co-evolutionary relationships (Brooks *et al.*, 1991;

Hoberg *et al.*, 1997). Therefore, it is expected that this inseparable relationship between host and parasites produce similar distributions that then can be tackled at macro-ecological scales via stacked species ENM/SDM, or alternatively by joint species distribution models (Ovaskainen & Abrego, 2020).

The selection of particular areas for future study of avian parasite diversity in the Neotropics should be driven by specific and essential features along this region, identified in bird diversity studies; for example, areas of high species turnover along elevation gradients (Terborgh, 1971; Rahbek, 1995, 1997; Kattan & Franco, 2004) or high diversity areas such as the Amazon basin, the Chocó, or the Atlantic forest. Other important areas are those identified as “islands” of vegetation such as high mountain-humid forest or the most isolated paramos in the Andes which house a large number of endemic areas. These isolated tropical areas have a good fit to the expectations of island biogeography for host species and their parasites. For instance, the species-area curve offers a reasonable prediction of species numbers, and the numbers of endemics can best be predicted by some measure of interisland distance (Vuilleumier, 1970). For a detailed example of amphibian parasites see Johnson *et al.* (2016). Furthermore, processes such as competitive exclusion and ecotones among significant biogeographical barriers account for several distributional limits of diverse avifaunas –e.g., basins that allow higher values of replacements of species (Terborgh & Weske, 1975; Terborgh, 1985). Another critical feature to be considered for selecting future avian parasite analyses is represented by those areas concentrating high levels of migrant species, which can exploit diverse habitats and are exposed to a more diverse parasite fauna (Ishtiaq & Renner, 2020), assuming of course that there is a community of parasites shared between migrant and resident species.

The shape of parasite diversity within host populations is affected by both distribution patterns and habitat use of resident and migratory birds (Leung & Koprivnikar, 2016; Gutiérrez *et al.*, 2017). Therefore, from an avifaunistic perspective, ecological and biogeographical biodiversity hotspots within the Neotropical region should represent a significant focus for future parasite research. For example, the higher elevation-continental islands (i.e., paramos, cloud forests, humid-mountain forest), homogenous valleys with marked vegetation discontinuities (i.e., seasonal tropical forest, inter-Andean valleys), ecotones (particularly those that represent critical biogeographical barriers such as isthmus and depressions

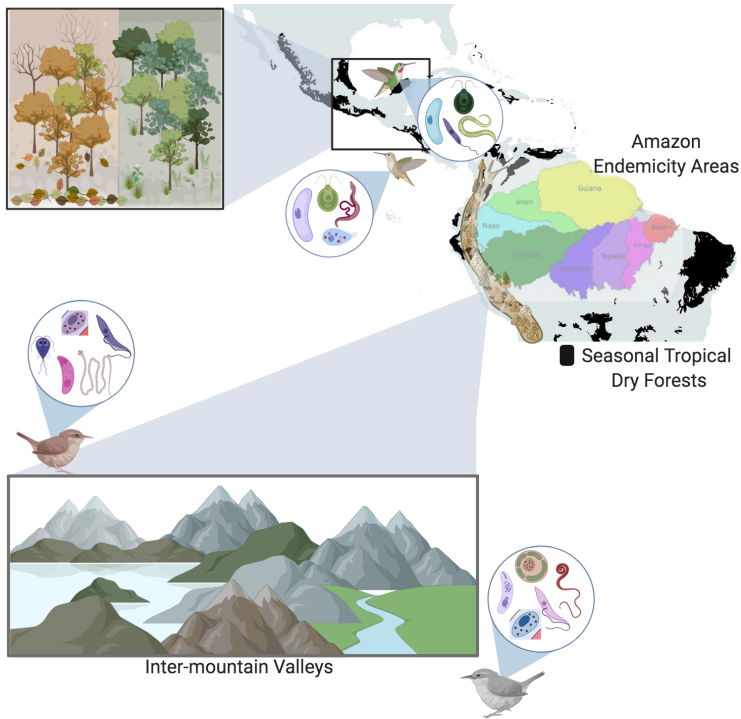


FIGURE 2 An illustration showing tropical dry forests (black areas) across some portions of the Neotropical region, Amazon endemicity areas (in colors: Guiana [yellow], Imeri [light green], Napo [light blue], Inambari [dark green], Rondônia [deep blue], Tapajós [purple], Xingu [pink], Belém [red]), and also depicting valleys along mountain ranges. Geographic discontinuities by mountain ranges, rivers, and ecotones isolate populations of animals, facilitating diversification and eventually divergence in community composition (Prieto-Torres *et al.*, 2019a,b). Such geographical isolation creates opportunities for allopatric speciation of both hosts and parasites (see bird silhouettes depicting sister bird species [same bird but different color] along with their parasite communities; some parasites have co-diverged with their hosts [same parasite shape but different color] and other parasites are unique to each geographic location). Given that a single host usually carries more than one parasite species (see Fig. 1), it is expected that vertebrate diversity hotspots are also hotspots of parasite diversity.

ons), and the lowlands throughout the region. There, we foresee the discovery of many new parasite taxa and complex interactions that will recreate similar patterns to those observed in the avian hosts (Fig. 2). These predictions are particularly relevant for parasite groups that contain many generalist species such as avian haemosporidians, which are known to readily switch host species (Santiago-Alarcon *et al.*, 2014; Fecchio *et al.*, 2019; Pacheco & Escalante, 2020). Thus, the discovery of avian haemosporidian diversity would be expected to be largest in bird biodiversity hotspots that have some degree of isolation and/or discontinuities, such as the Amazon avian endemicity areas (Fecchio *et al.*, 2018) and the seasonal dry

forests (Prieto-Torres *et al.*, 2019a,b) (see Fig. 2). The above-proposed framework will help to focus biodiversity surveys on areas with high host species richness and endemicity (Pappalardo *et al.*, 2020). This approach will help make use of limited economic resources because it will concentrate field surveys in areas with a higher likelihood of parasite discovery, i.e., host diversity hotspots that have been historically stable providing larger habitat–host–heterogeneity within and across geographical areas.

Most parasites have an obligate life stage on top (ectoparasites; e.g., ticks) or within (endoparasites; e.g., worms) a host; they directly depend on their hosts to complete their life cy-

cle. This dependency suggests that factors producing population declines and extinctions of host species will also affect the survival of parasites infecting those host species, which will directly lead to host-parasite co-declines and co-extinctions (Strona, 2015; Carlson *et al.*, 2017). Among the most detrimental factors for nature are those associated with human activities – e.g., urbanizations and agriculture – that directly destroy and modify ecosystems, increasing extinction risk and population declines (Maxwell *et al.*, 2016). Therefore, if we consider that parasite diversity is higher than host diversity, such impacts will more strongly affect parasites as for one host species that goes extinct more than one parasite species is likely to disappear (some parasite species [e.g., an infra-community] may disappear even before their host goes extinct due to an abundance threshold, which does not allow parasites to complete their life cycle, akin to an Allee effect). Although parasites are some of the most diverse and ecologically essential organisms on Earth, most conservationists still work within priority systems for funding and effort that exclude or ignore them, even treating parasites as an obstacle to overcome (Carlson *et al.*, 2020b; Kwak *et al.*, 2020). There has been a warning about the threat of parasite co-extinctions for decades, even suggesting that co-extinction might be the most common form of biodiversity loss; if each host species has several host-specific parasites, this could result in a more significant loss of parasite diversity than of free-living species (Dunn *et al.*, 2009; Wood *et al.*, 2020). Thus, parasites must be considered relevant targets in conservation programs (Gómez & Nichols, 2013).

ACKNOWLEDGMENTS

We thank two anonymous reviewers whose suggestions greatly improved the presentation of the paper, as well as to Editor in Chief for invitation to write this work. DS-A and ORR-S were supported by CONACYT via a competitive grant from the Problemas Nacionales program (2015-01-1628).

CONFLICTS OF INTEREST

The authors confirm that co-author Diego Santiago-Alarcon is an Ecotropicos Editorial Board member and that this does not alter the authors' adherence to the journal's Editorial policies and criteria. Figures were created in BioRender.com.

RESUMEN

Descubriendo la biodiversidad de parásitos en los Trópicos: Un marco de referencia basado en modelos de nicho ecológico de múltiples especies hospedadoras.

Los actuales grados de amenaza hacia la biodiversidad impuestos por las actividades humanas resaltan la necesidad de concentrar esfuerzos no solo en conservar lo que ya conocemos, sino también en el descubrimiento de nuevas especies, particularmente de grupos poco estudiados pero ecológicamente importantes, como lo son los parásitos y la fauna subterránea. Para el caso de los parásitos, debemos considerar que sus hospedadores representan todo su hábitat, que la mayoría de las especies hospedadoras están infectadas por más de una especie de parásito y que muchos estudios demuestran que algunos rasgos del hospedador (p.ej. el tamaño del cuerpo, el rango de distribución) y la diversidad de hospedadores se correlacionan positivamente con la diversidad de parásitos. Por lo tanto, la diversidad de hospedadores puede ser un sustituto de la diversidad de parásitos, donde siempre esperaríamos una mayor riqueza de parásitos que de especies hospedantes. Por ello, proponemos un marco de referencia utilizando modelos de nicho ecológico de múltiples especies hospedadoras (es decir, uso de modelos de distribución de especies conjuntas de hospedadores) para guiar los futuros estudios de la diversidad de parásitos. Sugerimos enfocar estos estudios en áreas con alta riqueza y endemismo de especies hospedadoras, para así optimizar el uso de los limitados recursos económicos en áreas con una mayor probabilidad de descubrimiento de parásitos (p.ej. puntos críticos de diversidad de hospedantes que proporcionan mayor heterogeneidad del hábitat para los parásitos).

Palabras clave: Biodiversidad de parásitos, comunidades hospedadoras, conjuntos de parásitos, enfermedades transmitidas por vectores, interacciones bióticas, nicho ecológico.

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