



# Trade-offs and resource breadth processes as drivers of performance and specificity in a host–parasite system: a new integrative hypothesis <sup>☆</sup>



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## ABSTRACT

One of the unresolved issues in the ecology of parasites is the relationship between host specificity and performance. Previous studies tested this relationship in different systems and obtained all possible outcomes. This led to the proposal of two hypotheses to explain conflicting results: the trade-off and resource breadth hypotheses, which are treated as mutually exclusive in the literature and were corroborated by different studies. In the present study, we used an extensive database on avian malaria from Brazil and combined analyses based on specificity indices and network theory, in order to test which of those hypotheses might best explain our model system. Contrary to our expectations, there was no correlation between specificity and prevalence, which contradicts both hypotheses. In addition, we detected a strong modular structure in our host–parasite network and found that its modules were not composed of geographically close, but of phylogenetically close, host species. Based on our results, we reached the conclusion that trade-off and resource breadth hypotheses are not really mutually exclusive. As a conceptual solution we propose “The Integrative Hypothesis of Parasite Specialization”, a novel theoretical model that explains the contradictory results found in our study and reported to date in the literature.

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## 1. Introduction

Ecological specialisation can be defined, in a broad sense, as a restriction in the niche of a species (Futuyma and Moreno, 1988; Devictor et al., 2010). Parasitism is an interesting model for studying specialization, as the hosts represent both habitat and food for the parasites. Therefore, the simplest way to measure the niche breadth of a parasite is through host specificity (Poulin et al., 2011).

One of the unresolved issues in the ecology of parasites is the relationship between host specificity and performance (Thompson, 1994). Previous studies tested the relationship between host range and measures of parasite performance (usually

abundance or prevalence) in different systems and obtained all possible outcomes: negative (Poulin, 1998), positive (Barger and Esch, 2002; Krasnov et al., 2004; Hellgren et al., 2009), and neutral (Morand and Guegan, 2000). As a consequence of those conflicting results, two main hypotheses with opposite predictions have been formulated: the trade-off hypothesis (Poulin, 1998) and the resource breadth hypothesis (Krasnov et al., 2004).

On one hand, the trade-off hypothesis assumes that adaptations for a more effective exploitation of particular hosts evolve at the cost of the capacity to exploit a wide range of host species, and vice versa. In other words, there is a trade-off between performance and host range in parasites (Futuyma and Moreno, 1988). This hypothesis is commonly illustrated in the scientific literature by the figure of speech “Jack of all trades, master of none” and predicts a negative relationship between host range and performance. On the other hand, the resource breadth hypothesis is an extension of the classical hypothesis proposed by Brown (1984), which predicts that species with broader niches tend to have both high local abundance and broader distribution. The basic assumption of this hypothesis is that the same attributes that enable a species to live in diverse environments allow it to more efficiently exploit each

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one of those. By applying the resource breadth hypothesis to parasitism and considering that hosts are the environments where parasites live, we can predict that parasites with broader niches will perform better in each host species and have a wider host range (Krasnov et al., 2004). According to this hypothesis, there is no trade-off between host range and performance; both are results of the same biological attributes of parasites and, therefore, will be positively related. In this paper we define resource breadth processes as all evolutionary and ecological processes that may lead to this positive relationship, including the “amplification effect” (i.e., in diverse parasite-host-vector communities, parasites with a broader host range may have an increased host encounter rate) (Keesing et al., 2006).

Krasnov et al. (2004) suggested that the taxonomic composition of the host assemblage may be key in understanding this variety of outcomes. From this perspective, predictions derived from the resource breadth hypothesis tend to be confirmed when the host assemblage is composed of phylogenetically close species, but those tend to be rejected when the hosts are phylogenetically distant from each other. The basic idea leading to this generalisation is that closely related hosts have similar defence mechanisms, thus ecological and evolutionary processes that cause an increase in performance in one host species will probably have the same effect on all other species. In a phylogenetically diverse host assemblage, however, an increase in performance in one host species generally occurs at the expense of performance in others.

The simplest measure of host specificity is the number of host species exploited by a parasite (basic host specificity), but other aspects of the interaction can also be quantified, such as the phylogenetic distinctiveness of host species (phylogenetic host specificity) (Poulin and Mouillot, 2003; Poulin et al., 2011). Recently, network theory has acquired great importance in ecology as an integrative approach to study ecological interactions in multi-species systems by focusing on the interactions rather than on the species (Proulx et al., 2005; Bascompte, 2009) and it can be applied to studies on specialization (Blüthgen et al., 2007; Poulin, 2010). One of the most important network proxies for specialisation is modularity, which can be defined as the presence of cohesive subgroups of densely connected species in a network (i.e., modules) (Olesen et al., 2007; Mello et al., 2011). Generally, the modules are composed of phylogenetically close species or species that converge in traits that affect the interaction (Schleuning et al., 2014). Network analysis has also been successfully used to study parasitism and a highly modular structure is commonly found in parasitic networks (Fortuna et al., 2010; Bellay et al., 2011; Krasnov et al., 2012), which is probably related to the high intimacy of host–parasite interactions.

Avian malaria, a vector-borne disease caused by protozoan parasites of the paraphyletic genera *Plasmodium* and *Haemoproteus* (Outlaw and Ricklefs, 2011), is found in birds of all continents except for Antarctica and represents an excellent model for studies on the evolutionary ecology of parasitism (Lapointe et al., 2012). Recent molecular studies on bird communities, which screened the blood of birds for *Plasmodium* and *Haemoproteus*, revealed a diversity of lineages that can be as high as that of the hosts (Pérez-Tris et al., 2007; Lacorte et al., 2013) and lead to the construction of large databases used in ecological and evolutionary studies (Fallon et al., 2005; Pérez-Tris et al., 2007; Hellgren et al., 2009). Recently, Svensson-Coelho et al. (2014) published the first known study that applies network theory to an avian malaria system. However, their study focused on comparing host specificity of malaria lineages between a tropical and a temperate assemblage, and the network analysis was restricted to the calculation of two network specialisation indices.

In the present study we performed a thorough assessment of one tropical avian malaria system using network theory, specificity

indices and phylogenetic analysis. We aimed to understand the relationship between host specificity and performance of parasites, and worked with two alternative scenarios based on the classic trade-off and resource breadth hypotheses. First, we expected a modular network in which the modules have strong phylogenetic signals (i.e., host species of each module are phylogenetically closer than expected by chance). Second, if the trade-off hypothesis is the best explanation for the patterns found in our study system, we expected avian malaria lineages that infect several host species to have lower performance. Third, if the resource breadth hypothesis is the best explanation in this case, we expected widespread malaria lineages to have better performance than lineages that infect a single or few hosts.

## 2. Materials and methods

### 2.1. Data collection and phylogenetic analysis

The same parasite lineages and avian host species previously described by Lacorte et al. (2013), which were collected in 10 sites in southeastern Brazil, were used in our study. However, in order to quantify specificity with more accuracy, we only used lineages reported five times or more (28 out of 110). This procedure is important, since lineages observed only a few times appear in only a few host species, whether or not those are intrinsically specialised, which could produce a spurious correlation between low prevalence and specialization.

After removing lineages with a small number of occurrences, our host community was composed of 64 bird species of four orders. A phylogenetic tree of hosts was built to calculate phylogenetic specificity, phylogenetic signal in parasitism, phylogenetic signal in local host assemblages, and phylogenetic signal in module composition. To build host phylogenetic trees, we included data from three mitochondrial (mt) DNA gene regions: cytochrome oxidase subunit 1 (COI), cytochrome B (CytB) and NADH dehydrogenase subunit 2 (ND2). Phylogenetic analyses using Bayesian inference were run in the programme MrBayes v3.2.1 (Ronquist et al., 2012). For details on laboratory procedures and phylogenetic reconstructions see [Supplementary Data S1 and Table S1](#).

### 2.2. Specificity indices

The basic specificity of each parasite lineage was calculated as the number of host species in which it was found. To calculate phylogenetic host specificity we used a modified version of the  $S_{TD}$  index (Hellgren et al., 2009) in a phylogenetic context. Formulae and details of specificity indices are described in [Supplementary Data S2](#).

### 2.3. Prevalence versus specificity

We measured two types of prevalence for each malaria lineage: specific prevalence and maximum prevalence. Specific and maximum prevalences are commonly calculated in specificity analyses and represent, respectively, the prevalence of a parasite lineage in all avian species infected by it and the maximum prevalence in any single host species infected by that parasite.

To test for associations between indices of prevalence and indices of specificity we used generalised linear models (GLMs). The GLMs were checked with residual analyses to find the suitable error distribution and we accepted the minimally significant model. We only calculated prevalence when the number of sampled individuals of host species was at least 10.

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