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

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A B S T R A C T

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

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.

2.4. Phylogenetic signal in parasitism and in local assemblage composition

We tested whether host assemblages exploited by each parasite were composed of species that are phylogenetically closer than expected by chance. The Jaccard index (1912) was used to measure composition dissimilarity in the group of parasites infecting each avian species and tested for a correlation with a matrix of host phylogenetic distance with a Mantel test. Similarly, we tested for phylogenetic signal in local host assemblages, using the Jaccard index as a measure of dissimilarity in local occurrences. Mantel statistics were based on Spearman's rank correlation rho and for each test 1000 permutations were performed.

2.5. Network analysis

The data were organised as a binary adjacency matrix (presence/absence) for the network analysis (Supplementary Table S2). According to Krasnov et al. (2012), the properties of parasitic interactions make binary data more appropriate than weighted data for this kind of analysis.

To test for the existence of modules in the host–parasite network we used an optimisation method based on simulated annealing (Guimerà and Nunes Amaral, 2005) and calculated an index of modularity (M) based on the Newman algorithm (Newman and Girvan, 2004). To estimate the significance of M we used a Monte Carlo procedure (1000 randomizations) based on the 'null model 2' of Bascompte et al. (2003), in which the probability of an interaction in a given cell of the matrix is proportional to the marginal sums of its columns and rows. To perform the M analysis we used the software Modular (Marquitti et al., 2014). We tested for phylogenetic and geographic signals in host module composition using Mantel tests with a matrix of pairwise values of dissimilarities in module identity (based on the Jaccard index) and matrices of phylogenetic distance and dissimilarity in local occurrences, respectively.

3. Results

To build the host phylogenetic tree we obtained 423 bp of COI, 999 bp of CytB and 1025 bp of ND2, which provided a total of 2447 bp of concatenated sequences. For all mtDNA genes, the GTR + G + I was the best-fit substitution model chosen. The Bayesian trees obtained from the Bayesian analyses differ from each other in topology and degree of resolution for each isolated gene. Thus, we used the partitioned tree with all genes in our analysis (Supplementary Fig. S1).

Basic host specificity of malaria lineages varied from one to 11 host species. Among the analysed lineages, only COSQU01 did not have its prevalence indices calculated, since its host species sampling was below 10 individuals. Specific prevalence varied from 0.04 (TARUF01) to 0.39 (VIOLI01), and maximum prevalence reached 0.6 (VIOLI01). All indices for malaria lineages calculated in our analysis are presented in Supplementary Table S3. There was no correlation between any measure of prevalence and basic or phylogenetic specificity (Table 1).

The host–parasite network contained 92 vertices (28 malaria lineages and 64 avian host species) and only 105 realised connections out of 1792 potential connections (connectance = 0.06). There is a high degree of modularity in our network (M = 0.7, Average M of randomised matrices = 0.62, P = 0.014) and twelve modules were detected (Fig. 1).

The phylogenetic distance among host species was correlated with the composition of hosts within the modules and of the assemblages exploited by each parasite lineage. Nevertheless,

Table 1
Results of generalised linear models testing the relationships between prevalence and specificity indices. Each response variable in the table represents a model. For the significant variables, the values shown are those of the minimum model and for the non-significant variable, values are those of the maximum model. All generalised linear models were best fitted to a quasibinomial distribution of errors.

Response variable	Explanatory variables	D. F.	Dev.	R. D.F.	R. Dev.	F	P value
Maximum prevalence	Basic specificity	1	0.11	25	73.82	0.033	0.86
	S*TD	1	0.00	24	73.82	0.000	0.98
Specific prevalence	Basic specificity	1	9.29	25	94.99	2.203	0.15
	S*TD	1	0.49	24	94.50	0.117	0.74

D.F., Degrees of Freedom; Dev., Deviance; R. D.F., Residual Degrees of Freedom; R. Dev., Residual Deviance.
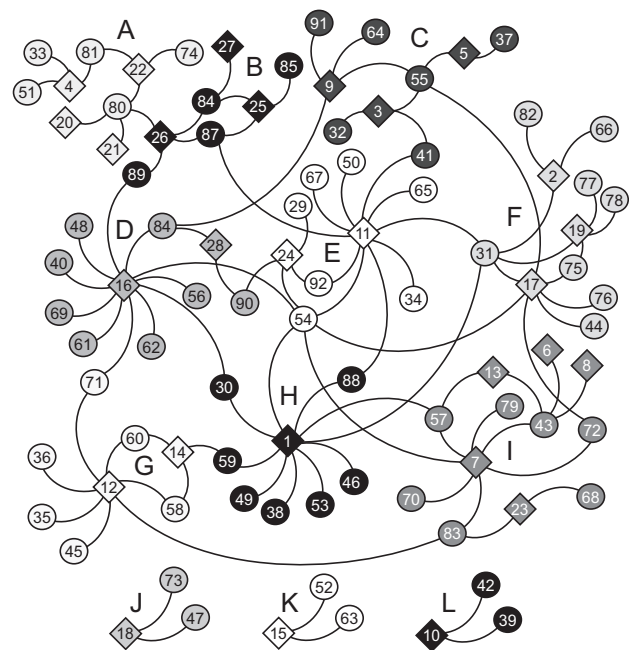

Fig. 1. The host–parasite network with bird species (circles) and malaria lineages (diamonds). Modules of the network are represented in grey tones and identified by letters (A–L). Vertices (i.e., parasites lineages and host species) in the graph are disposed to visually emphasise modules, and line length has no meaning (the edges are not weighted). Names of bird species (according to the Brazilian Ornithological Records Committee (http://www.cbro.org.br)) and malaria lineages are presented in Supplementary Table S2).

there was no phylogenetic signal in local host assemblages or a geographic signal in the composition of host within the modules (Table 2).

Table 2
Results of Mantel tests for signal analyses. The Mantel statistic is based on Spearman's rank correlation rho. Each test was performed for 1000 permutations.

Hypothesis tested	Mantel statistic r	P.95%	P value
Phylogenetic signal in host assemblage exploited by each lineage	**0.1331**	**0.049**	**0.0009**
Phylogenetic signal in local assemblages	0.0091	0.060	0.3826
Phylogenetic signal in modules	**0.1051**	**0.038**	**0.0019**
Geographic signal in module	−0.0140	0.046	0.7222

P.95%, 95th percentile of permutations (null model). Statistically significant values in bold.

4. Discussion

Our results point to no relationship between prevalence and basic or phylogenetic specificity, which contradicts predictions from both the trade-off (Poulin, 1998) and the resource breadth hypotheses (Krasnov et al., 2004). One implicit assumption of the trade-off hypothesis is that eventually new adaptations that increase performance in one host will represent maladaptation to other hosts in the community. On the other hand, the implicit assumption of the resource breadth hypothesis is that those new adaptations increase performance in all hosts. We did not see empirical or theoretical support to assume one or the other hypothesis as a universal explanation for all cases. Krasnov et al. (2004) suggested that the hypothesis that best explains a particular case depends on the phylogenetic structure of the studied community of hosts. In addition, the relationship between specialisation and performance will be better explained by one or the other hypothesis in different systems. We think that this explanation, despite being logically valid, can only be applied if the phylogenetic distance between hosts varies gradually, which is not the case in our system.

The host assemblage studied here has high phylogenetic and ecological diversity but is composed of subgroups of closely related species. While on the one hand we have host species of different bird orders (i.e., Collumbiformes, Galbuliformes, Passeriformes and Piciformes), on the other hand we have four species of the same genus (i.e., *Turdus*). In a scenario such as this, in which the host assemblage is composed of clusters of closely related hosts separated from each other by discontinuous phylogenetic differences, we expect the effects of evolutionary changes in a given parasite to differ between hosts of different clusters, which confounds the relationship between performance and host specificity in the system. Instead of processes in which an increase in the performance in one host species leads to an increase (resource breadth hypothesis) or decrease (trade-off hypothesis) in the performance of all others, most likely there is a predominance of processes in which an increase in the performance in one host species leads to an increase in the performance in hosts of the same cluster but to a decrease in the performance in hosts of other clusters (Fig. 2). The observed phylogenetic signal in parasitism (Table 2) is good evidence to assume that host phylogeny is important to specialization. Nevertheless, it is important to note that the dendrograms presented in Fig. 2A are not phylogenetic trees, but representations of host species distances, considering every character that can affect the performance of parasites (e.g., habitat preferences, behavioural and immunological defences, and chemical composition of blood) (Thompson, 1994). The biological dendrogram will be very similar to the phylogenetic tree of the group if there is strong phylogenetic conservatism in the evolution of the biological traits considered although, in several cases, convergence can unite phylogenetically distant species and separate phylogenetically close species.

We found that the modules of our network were not composed of geographically close species, but of phylogenetically close host species. Therefore, in our study system, phylogenetic clusters of hosts are reflected in the modular network structure. Several authors have argued that modularity usually emerges from a combination of shared phylogenetic history and trait convergence (Olesen et al., 2007; Krasnov et al., 2012; Schleuning et al., 2014). If this is true, modules should be composed of species that are closer to each other than to species of other modules, considering not only phylogenetic distance but also all biological characters (either homologies and convergences) that affect the interaction, which is exactly the same as the host clusters presented in Fig. 2A. Considering that the network was built based on connections that are
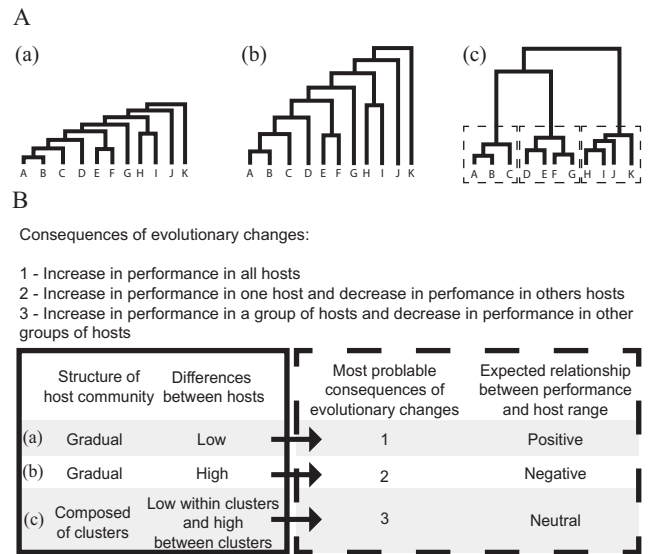
A

(a)   (b)   (c)

B

Consequences of evolutionary changes:

1 - Increase in performance in all hosts
2 - Increase in performance in one host and decrease in perfomance in others hosts
3 - Increase in performance in a group of hosts and decrease in performance in other groups of hosts

	Structure of host community	Differences between hosts	Most probable consequences of evolutionary changes	Expected relationship between performance and host range
(a)	Gradual	Low	1	Positive
(b)	Gradual	High	2	Negative
(c)	Composed of clusters	Low within clusters and high between clusters	3	Neutral

Fig. 2. A new explanation for the conflicting results observed in the relationship between performance and host range of parasites. (A) Dendrograms of hypothetical host communities with: (a) low differences among hosts that change gradually in the community; (b) high differences among hosts that change gradually in the community; (c) a clustered structure in which the differences among hosts are low within each cluster and high between clusters. Dashed rectangles delimit clusters of close species. (B) Expected effects of host community structure and the difference among hosts in the relationship between performance and host range. The cases (a), (b) and (c) correspond to dendrograms in Fig. 2A.

effectively made in the system, we conclude that the network structure is the final outcome of the process of parasite specialisation and that modularity results from trade-offs and breadth resource processes that occur simultaneously at different scales in the host community. This conclusion is, in a few words, what we are calling here "The Integrative Hypothesis of Parasite Specialization".

The Integrative Hypothesis of Parasite Specialization is based on three assumptions: (i) the specialisation of parasites always involves trade-offs between performance in different hosts, and the trade-offs will be stronger with greater dissimilarity between hosts; (ii) resource breadth processes always play a role in parasite specialization, but they are weaker with greater the dissimilarity between hosts; (iii) in most host communities, host dissimilarity is not gradually structured. Natural communities are commonly composed of clusters of similar organisms separated from other clusters by discontinuous differences.

Once these assumptions are accepted we can conclude that the specialisation of parasites is driven by a balance between the costs of trade-offs and the benefits of resource breadth processes. As new adaptations that increase a parasite's performance in a host species generally increase its performance in similar host species and decrease its performance in dissimilar host species, there is no point in considering trade-off and resource breadth hypotheses as mutually exclusive. In fact, both are two sides of the same coin and exert greater influences at different scales of the host community. As the dissimilarity among host species is much larger between than within clusters of host community, there is a discontinuity in the balance between trade-off and resource breadth processes. Instead of a gradual increase in the effect of trade-off and a gradual decline in resource breadth processes with the broadening of host range, there will probably be an abrupt change when the limits of clusters are exceeded. Within clusters, resource breadth processes predominate and between clusters, trade-off is expected to be stronger.
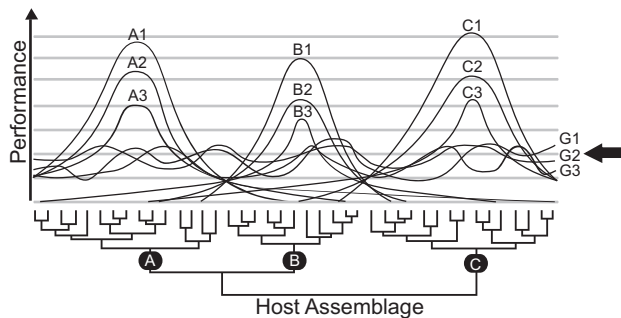
Fig. 3. Patterns of performance predicted by the Integrative Hypothesis of Parasite Specialization, in which resource breadth processes are stronger within each cluster of biologically close hosts and trade-offs are stronger between clusters. Curves represent the performance of each parasite lineage or species. A1, A2 and A3 are the parasites specialised in cluster A; similarly for clusters B and C. G1, G2 and G3 are generalist parasites. Specialised parasites with high performance in a host species have also a high performance in all other hosts of the same cluster. However, this high performance in all host species of a cluster is related to a very low performance in hosts of other clusters. The most generalist parasites are able to infect hosts of all clusters, but have a low performance in each host. Clusters of similar hosts, from the perspective of parasites, are the main unit of specialization, and host specificity is better measured in terms of how many clusters each parasite infects, rather than how many host species it infects. The arrow is a possible detection limit for those parasites. Parasites above this limit have a significant chance of being detected in the host population. Obviously, this limit is variable for each system and is influenced by sampling method and effort. Moreover, the randomness of sampling can result in parasites with low performance being detected in a given host species, while other parasites with better performance are not.

A relationship between performance and cluster specialisation (Fig. 3) will emerge with the clusters as the main unit of specialization. Consequently, a parasite is considered specialised if it infects hosts of a single or a few clusters, while generalised parasites infect hosts of several clusters.

Based on this new theoretical perspective, we make novel predictions aimed at explaining the conflicting results reported in the literature. First of all, it is important to notice that the predictions shown in Fig. 2 and the hypothesis of Krasnov et al. (2004) are not rejected here. On the one hand, when the entire host assemblage is composed of closely related species (Fig. 2Aa) the assemblage itself is the cluster of specialization, resource breadth processes will predominate, and a positive relationship between performance and host range is expected. On the other hand, when dissimilarities between host species are high from the perspective of the parasite (Fig. 2Ab), each species may be the cluster of specialization, trade-offs gain importance, and a negative relationship is expected.

When the host community is composed of clusters, the relationship between performance and specificity will be strongly influenced by sampling scale and contrasting results are expected. We may expect three different results when comparing a study that samples a single group of closely related hosts, a second that samples few hosts of several clusters, and a third that samples several hosts of several clusters (Fig. 4). We are not referring to the real host diversity, but to the subset of host species sampled. Once generalist parasites have poorer performance than specialists, they have a lower chance of being detected in all of their real hosts, either due to a sampling error in the least sampled species or random fluctuations in local prevalence. This underestimation of host range leads to parasites with low prevalence being considered more specialised than they actually are, which masks the trade-offs involved in generalisation. When a study samples a single cluster, this bias creates an artificial relationship between performance and host range (Fig. 4A). On the other hand, when a few hosts in each cluster are sampled, the host ranges of parasites that infect all hosts of a single cluster may be even more underestimated,

because only a few of their hosts were sampled. In this case what is being masked is the effect of resource breadth processes acting within these clusters, and an artificial negative relationship between performance and host range may be observed (Fig. 4B). When all host species are sampled, neither trade-off nor resource breadth processes are masked, and no correlation between performance and host range is observed (Fig. 4C). In this last scenario, the integrative hypothesis of parasite specialisation predicts a positive relationship between host range inside each cluster and performance of parasites, but a negative relationship between the number of clusters infected by a parasite and its performance.

A good example of the predictions of the new hypothesis can be provided by comparing our results with two previous studies that tested the trade-off and resource breadth hypotheses in avian malaria (Hellgren et al., 2009; Szöllosi et al., 2011). In contrast to our findings, Hellgren et al. (2009) found a positive relationship between performance and host range in avian malaria. However, the host assemblage analysed in their study was composed only of species of the suborder Passeri, whereas in the present study Passeri was a phylogenetic subgroup of the whole host assemblage and represented only 43.75% of the host species (28 in 64). The presence of diversified clades in our analyses that are absent in Hellgren et al. (2009) (i.e., suborder Tyranni and the orders Columbiformes, Galbuliformes and Piciformes) explains the difference between our results, with our dataset comprising some of the most marked phylogenetic and ecological discontinuities in birds (Sick, 1997). Furthermore, our samples were taken from one of the most biodiverse regions in the world and have a strong environmental discontinuity (i.e., they include birds that occur in three different vegetation types) (Lacorte et al., 2013), which probably results in an even higher diversity and a more clustered structure in our host assemblage than expected by phylogeny alone. Szöllosi et al. (2011) presented a more extreme example of micro scale analysis by sampling host populations of a single species and, as expected, they also found a positive relationship between host range (number of host populations in which each lineage was found) and prevalence.

It is important to understand the effect of the processes explained by the Integrative Hypothesis of Parasite Specialization in the shaping of interaction networks. As we observed, the clustered structure of host community can be reflected in a modular network structure. This occurs due to the intensity of trade-offs in performance in hosts of different clusters, or in other words, modularity is a consequence of strong trade-offs between host clusters. Moreover, we think that resource breadth processes can also affect network structure by generating another common pattern described in the ecological network literature - nestedness. Modularity and nestedness have traditionally been seen as mutually exclusive (Bascompte et al., 2003), but recently they have been recognised as patterns that can interact with one another (Fortuna et al., 2010). Similarly to trade-off and resource breadth processes in our hypothesis, these patterns can also occur at different scales in a network structure. Future studies should focus on understanding the relationship between specialisation and network structure based on real world field data and not only on mathematical simulation.

In the present study we: (i) performed a network analysis for avian malaria together with the commonly used specificity indices, (ii) tested for a phylogenetic signal in parasitism, (iii) built a molecular phylogenetic tree of hosts to calculate phylogenetic specificity while previous studies used only taxonomic distance, and (iv) tested the predictions of the trade-off and resource breadth hypotheses in a species-rich environment. Despite those hypotheses leading to opposite predictions, after performing our study we reached the conclusion that they are not mutually exclusive. Therefore, (v) we propose a new hypothesis about parasite performance and host specialisation that integrates the trade-off and
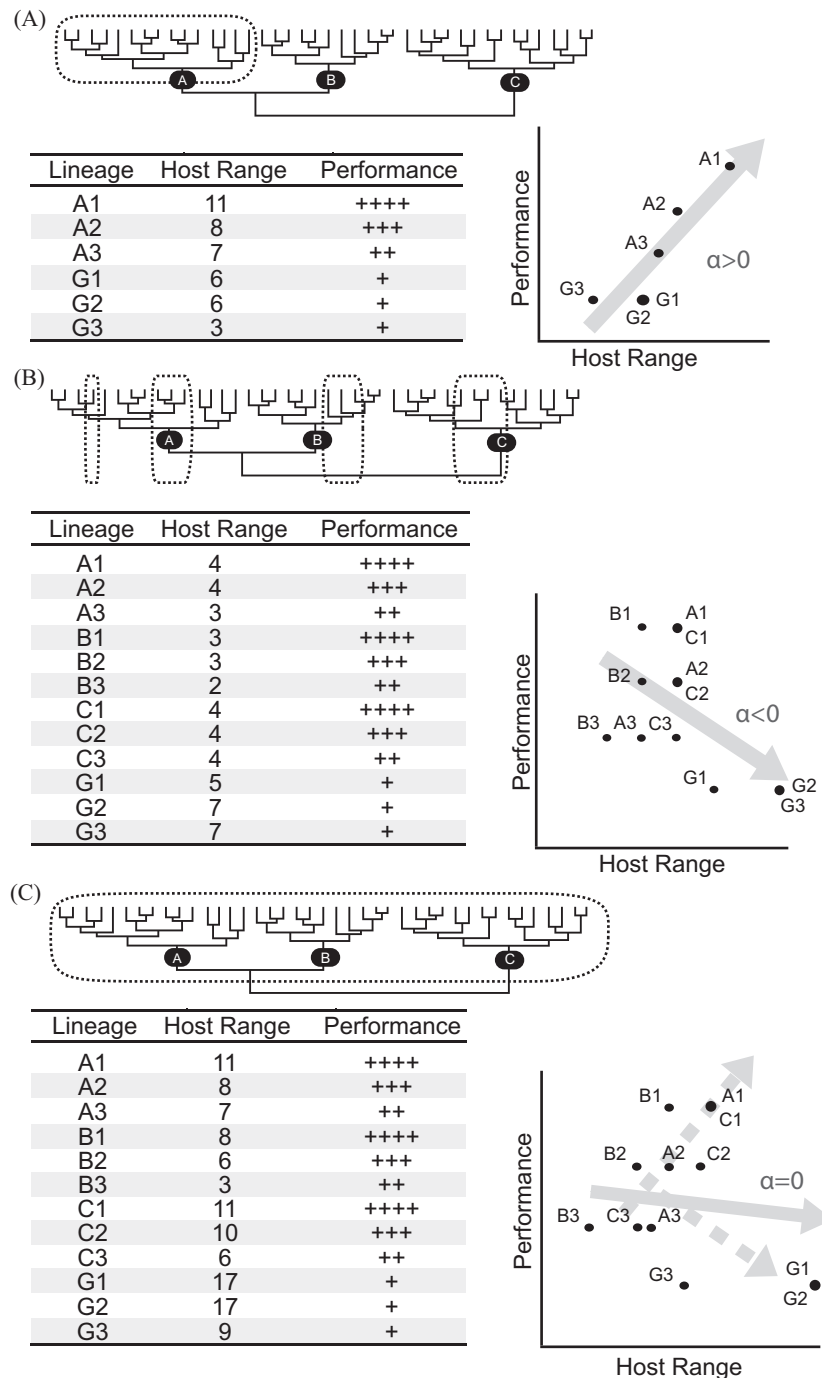
Fig. 4. Effect of sampling on the detection of different relationships between performance and host range in a host–parasite system. Dendrograms correspond to the host communities in Fig. 3, and dashed rectangles represent the host species sampled. Host ranges were defined according to the detection limit (arrow), and performance was categorised in four groups based on the curves presented in Fig. 3. Here, we illustrate the expected relationship between performance and host range when the sample is composed of (A) a cluster of related hosts, (B) a few hosts from several clusters, and (C) the whole host community.

breadth resource hypotheses within a single, more general, framework by taking into account the biological structure of the entire host community and the sample. The Integrative Hypothesis of Parasite Specialization can explain the contrasting results found in previous studies that tested the relationship between performance of parasites and host specificity, and it helps to advance the debate further. Moreover, our hypothesis generates several testable predictions and we kindly invite the scientific community to put those to the test.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ijpara.2015.10.002.

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