

Drivers of parasite sharing among Neotropical freshwater fishes

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Summary

1. Because host–parasite interactions are so ubiquitous, it is of primary interest for ecologists to understand the factors that generate, maintain and constrain these associations. Phylogenetic comparative studies have found abundant evidence for host-switching to relatively unrelated hosts, sometimes related to diversification events, in a variety of host–parasite systems. For Monogenoidea (Platyhelminthes) parasites, it has been suggested that the co-speciation model alone cannot explain host occurrences, hence host-switching and/or non-vicariant modes of speciation should be associated with the origins and diversification of several monogenoid taxa.

2. The factors that shape broad patterns of parasite sharing were investigated using path analysis as a way to generate hypotheses about the origins of host–parasite interactions between monogenoid gill parasites and Neotropical freshwater fishes.

3. Parasite sharing was assessed from an interaction matrix, and explanatory variables included phylogenetic relationships, environmental preferences, biological traits and geographic distribution for each host species.

4. Although geographic distribution of hosts and host ecology are important factors to understand host–parasite interactions, especially within host lineages that share a relatively recent evolutionary history, phylogeny had the strongest overall direct effect on parasite sharing.

5. Phylogenetic contiguity of host communities may allow a ‘stepping-stone’ mode of host-switching, which increases parasite sharing. Our results reinforce the importance of including evolutionary history in the study of ecological associations, including emerging infectious diseases risk assessment.

Key-words: antagonistic interactions, ecological fitting, ecological networks, host-switching, Monogenoidea, partial least squares path modelling, stepping-stones

Introduction

Parasitism may be the most common mode of life in nature (Price 1980). Organisms that spend most of their lifetime feeding in or on a single individual of another species can be found in diverse groups of organisms. Monogenoidea, for instance, is a class of strictly parasitic Platyhelminthes, mostly composed of ectoparasites of the gills or body surface of freshwater and marine fishes (Boeger, Vianna & Thatcher 2006). Several species, however, are endoparasitic and/or found in a variety of host groups, such as crustaceans, molluscs and even one species of mammal. In the Neotropics, the diversity of the

Monogenoidea of fishes is still largely unknown, with more than 300 species described in approximately 70 genera, from 144 species of hosts (Boeger, Vianna & Thatcher 2006). Dactylogyridae is the most abundant family in continental waters of South America and many species of Gyrodactylidae (*sensu* Boeger & Kritsky 1997; Boeger, Kritsky & Pie 2003) are being systematically described. On the other hand, Diplectanidae, Monocotylidae and Hexabothriidae appear to be poorly represented in the freshwater Neotropical fauna (Boeger, Vianna & Thatcher 2006).

Because host–parasite interactions are so ubiquitous, it is of primary interest for ecologists to understand the factors that generate, maintain and constrain these associations (Agosta, Janz & Brooks 2010), with implications for studies on emerging infectious diseases (Brooks & Ferrao

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2005; Brooks & Hoberg 2007), biological control, biological invasions and biotic responses to climate change (Brooks & McLennan 2002). The growing incidence of emerging infectious diseases (EID) increases the need for a proactive capacity to explore pathogen diversity and the factors that determine the structure and distribution of host–parasite systems (Brooks & Hoberg 2013).

One of the remarkable features of parasitism is the conservatism in the range of hosts used, both on ecological and evolutionary time-scales (Brooks & McLennan 1993, 2002; Thompson 1994, 2005; Futuyma & Mitter 1996). For this reason, the prevailing perspective of the evolution of host–parasite associations was, until recently, centred on host specificity. However, phylogenetic comparative studies have found abundant evidence for host-switching to related and unrelated hosts, sometimes associated with diversification events, in a variety of host–parasite systems (Boeger & Kritsky 1997; Agosta 2006; Janz, Nylin & Wahlberg 2006; Hoberg & Brooks 2008; Nyman 2010). Agosta, Janz & Brooks (2010) called the conflict between resource specialization and the ability to host-switch as the ‘parasite paradox’ and suggested ecological fitting (Janzen 1985) as a major process underlying host-switching. Indeed, there is much evidence for ecologically fit associations among hosts and parasites (Hoberg & Brooks 2008, 2010), which encouraged the formulation of a new paradigm for host–parasite diversification.

The Stockholm Paradigm (Agosta, Janz & Brooks 2010; Hoberg & Brooks in press) resolves the ‘parasite paradox’ integrating four key concepts: the oscillation hypothesis (Janz & Nylin 2008), ecological fitting (Janzen 1985), the geographic mosaic theory of co-evolution (Thompson 2005), and the Taxon Pulse Hypothesis (Erwin 1985). The oscillation hypothesis postulates that host expansions by specialists set the stage for the evolution of generalists, which then become fragmented into new specialists. Ecological fitting allows specialists to colonize new hosts without prior evolution of novel host-use capabilities, expanding host range. The geographic mosaic explains the emergence of new specialists from ancestral generalists through the microevolutionary co-adaptive dynamics among the new host–parasite combinations. The taxon pulse dynamics gives the opportunities for host-switches to occur, altering geographic and trophic ecological contexts. The transition from specialist to generalist (host-switches) is maximized during phases of biotic expansion, and phases of geographic isolation promote the emergence of new specialists.

Agosta & Klemens (2008) explored the role of ecological fitting on the formation of new interactions. According to the authors, parasites are able to ecologically fit with new hosts in at least two ways. First, parasites may shift to a new host species that provides the same or highly similar resources as the old host, that is ecological fitting via resource tracking. Secondly, parasites may achieve realized fitness in hosts representing a new resource, that is ecological fitting via sloppy fitness space.

These two ways are not mutually exclusive and may represent the extremes of a continuum (Agosta & Klemens 2008).

For monogenoid parasites, it has been suggested that host occurrences cannot be explained solely by the co-speciation model, hence host-switching and/or non-vicariant modes of speciation should be associated with the origins of several monogenoid taxa (Boeger & Kritsky 1997). This is especially apparent for the evolution of the speciose Gyrodactylidae (Zietara & Lumme 2002; Bakke, Cable & Harris 2007; Blazek, Bagge & Valtonen 2008; Bueno-Silva, Boeger & Pie 2011). Boeger, Kritsky & Pie (2003) suggested that the Gyrodactylidae originated after a host-switch from a marine to a demersal South American freshwater catfish host and that the association between plesiomorphic traits – ability for transmission as adults – and apomorphic traits – hyperviviparity, among others – represents the key innovation for the diversification of the viviparous Gyrodactylidae (Boeger & Kritsky 2003; Boeger *et al.* 2005), enhancing the ability of the group to speciate by host-switching.

For most monogenoids, however, transmission is limited to the free-swimming larval stage. Despite that, the distribution of *Lamellodiscus* Johnston and Tieggs, 1922 (Diplectanidae, Monogenoidea) species on Sparidae (Teleostei) hosts in the Mediterranean Sea cannot be explained by co-speciation alone (Desdevises *et al.* 2002). Instead, species of *Lamellodiscus* were shared among hosts that displayed social behaviour and ecological similarities, suggesting that intense host-switching events influenced the studied system.

The present study comprises only gill parasites, which form the best-known group of monogenoids in continental waters of the Neotropical region. Furthermore, these species have similar processes of transmission and dispersion, which reduces the inclusion of new sources of variation in the analysis. Because few parasite species occur in more than one host species in our data base (most likely due to sampling biases) (Braga, Araújo & Boeger 2014), we opted to analyse how parasite genera are shared by hosts, based on two implied assumptions. First, parasite genera likely represent monophyletic groups, composed by species that descend from a single common ancestor, and secondly, resource requirements are most likely phylogenetically conserved. Members of the same genus should theoretically share a number of ecological, morphological and behavioural characters solely because they are descended from a relatively recent common ancestor (Brooks & McLennan 2002; Burns & Strauss 2011).

In this study, the factors that influence broad patterns of parasite sharing were investigated, using comparative analysis to generate hypotheses about the evolution of host–parasite interactions between Monogenoidea and Neotropical freshwater fishes. These hypotheses can then be tested in specific systems in subsequent studies as phylogenies for parasite clades become available.

Materials and methods

Parasite sharing was assessed from an interaction matrix between 105 fish species of seven fish orders and 53 genera of gill parasites of five families (see Braga, Araújo & Boeger 2014 for more details). Parasites were classified in two groups by host range: parasites with hosts from the same family (specialists, 42 genera), and parasites that occur in more than one host family (generalists, 11 genera). Information on environmental variables, biological traits and geographic distribution was gathered for each host species, mainly from FishBase (Froese & Pauly 2012) but also from Reis, Kullander & Ferraris (2003). Variables that were available for most host species were used as putative predictors of parasite sharing. Environmental variables included (i) salinity – fish tolerance to brackish water, (ii) climate – tropical or subtropical, (iii) habitat – pelagic, benthopelagic or demersal and (iv) lakes – whether the species occurs in lakes. Biological traits were (i) maximum male length, (ii) trophic level and (iii) vulnerability to fishing. Based on the geographic distribution of host species, 23 Neotropical watersheds were selected, where fish species could be present or absent.

The backbone for the phylogenetic tree for all host species was based on Betancur *et al.* (2013). Within this cladogram (Fig. 1), the relationship among characiform species was based on Oliveira *et al.* (2011) and, for best resolution within Serrasalminidae, on Hubert & Renno (2006) and Ortí *et al.* (2008); the relationship among siluriform species was based on Sullivan, Lundberg &

Hardman (2006) and on Lundberg, Sullivan & Hardman (2011) for resolution within Pimelodidae; Betancur *et al.* (2013) was used to determine the relationship within Percomorphaceae and Lopez-Fernandez, Winemiller & Honeycutt (2010) for resolution within Cichlidae. The cladogram was assembled in Mesquite 2.75 (Maddison & Maddison 2011), adding all species whose position was known and excluding polytomies. In cases in which polytomies could not be solved, the pair of species in the clade with the greatest available information on geographic distribution, ecology and biology were chosen.

Multiple relationships between blocks of variables were assessed using partial least squares path modelling using the PLS-PM package (Sanchez & Trinchera 2012) of R 2.15.1 (R Core Team 2012). There are various comparative methods to detect a phylogenetic signal, to control for phylogenetic influence and to estimate the relative effects of phylogeny and other factors on a given response variable (Poulin *et al.* 2011; Cooper *et al.* 2012; Faria *et al.* 2013). The greatest advantage of PLS path modelling is that it measures both direct and indirect effects of explanatory variables on the response variable by accounting for the relationships between explanatory variables. Although this method was previously used in the study of ecological networks (Thébaud & Fontaine 2010), to our knowledge, this is the first time it is applied to the study of host–parasite associations.

PLS Path Modelling calculates latent variables (parasite composition, phylogeny, geographic distribution, environment and biology) as linear combinations of their indicators (variables). To

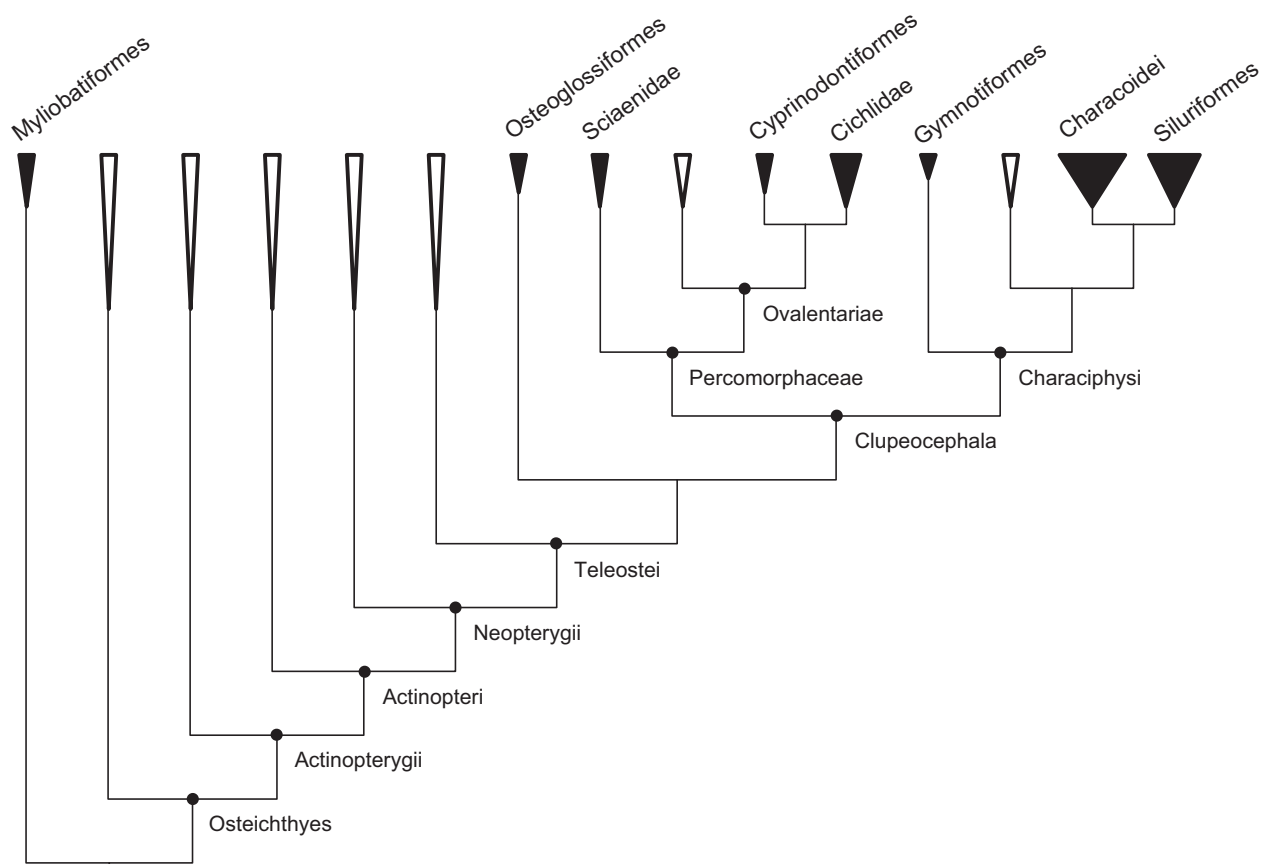


Fig. 1. Phylogenetic relationship of major fish groups. Open triangles indicate taxa not included in this study. Size of filled triangles is proportional to the number of species in the study. Modified from Betancur *et al.* (2013).

use all available information, pairwise distances between host species were used as descriptors (as in Rezende *et al.* 2007; Cooper *et al.* 2012). Phylogenetic distances were calculated using the *phydist* function of the *PICANTE* package of R (Kembel *et al.* 2010). Distances in parasite composition (based on the interaction matrix), geographical, environmental and biological distances were calculated using Gower's method in *daisy* function of the *CLUSTER* package (Maechler *et al.* 2012). Significance of path coefficients was assessed by bootstrap validation with 1000 resamples. In each analysis, the model was evaluated and uninformative indicators were removed when necessary. Correlations between latent variables and indicators (cross-loadings) were assessed to test if geographic distribution, environmental preferences and/or biological traits of host species differentially affect the distribution of generalist and specialist parasites.

As each order of fish interacts with its own subset of parasites (Braga, Araújo & Boeger 2014), the analysis was also carried out using submatrices of the three main fish orders – that is 'Perciformes', Siluriformes and Characiformes – to evaluate possible differences in parasite sharing between fish orders. Additionally, fish orders were compared at the structural level by permutation resampling using the *plspm.groups* function of the *PLSPM* package (Sanchez & Trinchera 2012).

Results

Most parasite genera are restricted to one species or to closely related hosts, which produces the diagonal shape of the interaction chart (Fig. 2). Some genera are more dispersed (vertically) within and among fish orders. *Anacanthorus* Mizelle and Price, 1965 and *Notozothecium* Boeger and Kritsky, 1988 have a wide host range among Characiformes; *Demidospermus* Suriano, 1983 is widely spread among Siluriformes; and *Sciadicleithrum* Kritsky, Thatcher & Boeger 1986; among Perciformes (strict to Cichlidae). The only genus with representatives in more than one order is *Urocleidoides sensu strictu* Mizelle and Price, 1964 (as defined by Kritsky, Thatcher & Boeger 1986), which parasitizes species of Characiformes, Gymnotiformes, and Cyprinodontiformes.

According to the path analysis, all latent variables (i.e. interactions, phylogeny, geographic distribution, environment and biology) are related to 2–4 other variables. All response variables are related to parasite sharing when all fish orders are analysed together (Fig. 3a). Phylogenetic relatedness of fish hosts has the strongest direct effect on parasite sharing, followed by geographic distribution, ecological preferences and biological traits. In this model, 21% of the variance in parasite sharing is explained by its independent latent variables ($R^2 = 0.21$). Moreover, correlations between parasite sharing indicators and latent variables show that geographic distribution, environmental preferences and biological traits do not affect the distribution of specialist and generalist parasites differently.

For Perciformes (20 host species with six specialist parasite genera), phylogenetic relatedness of hosts has a stronger effect than geographic distribution (Fig. 3b). However, the influence of host phylogeny is restricted to the distribution of parasites among host families

(Cichlidae and Sciaenidae). Within Cichlidae, parasites are dispersed across host phylogeny (Fig. 1). Among Siluriformes (31 host species with 10 specialist and three generalist parasite genera), environmental preferences (habitat and lakes) have the strongest effect on parasite sharing (Fig. 3c). Phylogeny has a smaller effect on parasite sharing compared to the distribution of parasites on the Characiformes. For parasite sharing among Characiformes (46 host species with 21 specialist and eight generalist parasite genera), phylogenetic relatedness between hosts is the most important factor influencing parasite sharing, followed by geographic distribution (Fig. 3d).

Differences in path models of host orders were confirmed by comparing path coefficients using permutation resampling, which shows that the influence of phylogenetic relatedness on parasite sharing is significantly higher among Characiformes hosts ($P < 0.05$) and that the influence of environmental preferences is higher among Siluriformes hosts.

Discussion

Our results suggest that interactions between monogenoid gill parasites and their fish hosts are best predicted by the phylogenetic relationship of the hosts, followed by the geographic distribution of their hosts. Environmental and biological attributes presented a lower explanation power. A similar pattern was recently found using parasite co-occurrence modelling for the distribution of helminth parasites on fish hosts (Strona & Lafferty 2013). Phylogenetic relatedness could also predict, for species in the same trophic level, the identity of the species with which they interact in a number of mutualistic networks (Rezende *et al.* 2007). These findings reinforce the importance of including evolutionary history in mechanistic models of network formation and maintenance (Cattin *et al.* 2004) for both mutualistic and antagonistic interactions. Additionally, as a broad assessment of patterns of host–parasite interactions in the light of the Stockholm Paradigm (Hoberg & Brooks in press), this study provides a critical test of which host-related variables are more important for host-switching, increasing our capacity to assess EID risk.

Although most parasite genera are restricted to one fish order, this cannot be considered evidence for co-speciation, even if phylogenetic relationships among parasite genera were known (Althoff, Segraves & Johnson 2014). There is no macroevolutionary pattern that, on its own, can distinguish between co-speciation, evolutionary arms races and colonization (host-switch) scenarios (Brooks & McLennan 2002). For Monogeneoidea, most parasite lineages seem to be restricted to higher taxonomic levels, that is family or above, most likely due to broad historical constraints acting at large scale (Boeger & Kritsky 1997; Desdevises *et al.* 2002). In addition to the difference in composition of parasite communities, each fish order has a particular pattern of parasite sharing apparently related to historical factors.

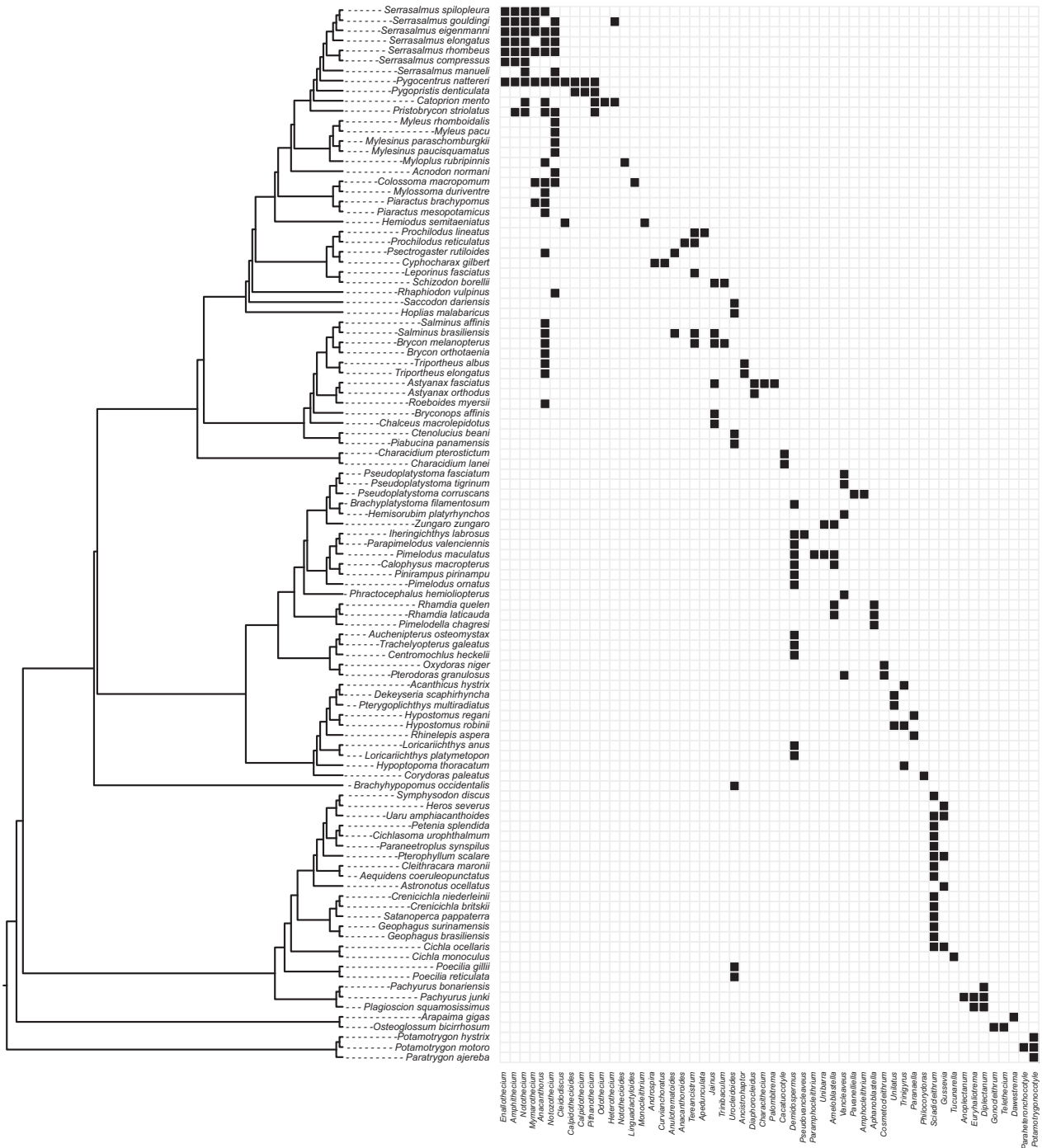


Fig. 2. Phylogenetic distribution of parasite genera. Host phylogeny is on the left; host species are on lines and parasite genera are in columns. Interactions are indicated by black squares.

Each fish order has a unique past history in the Neotropics (Fig. 4). Although Cichlidae and Sciaenidae were traditionally allocated within Perciformes, recent advances in molecular phylogenetics of fishes revealed an older split between these lineages (Betancur *et al.* 2013). Both families are within subdivision Percormorphaceae but in different Series – Cichlidae (Carangimorpharia, Ovalentariae, Cichliformes) and Sciaenidae (Percormorpharia, *incertae sedis*) – with time of divergence approximately 110 Mya

(Betancur *et al.* 2013). In the Neotropics, each family is derived from a particular freshwater invasion event (Fig. 4a). Neotropical Cichlidae (Cichlinae) is a monophyletic sister-clade to an African cichlid clade (Sparks & Smith 2004; Friedman *et al.* 2014). Sciaenidae mainly includes primarily marine fishes. Freshwater sciaenids in South America are marine derivatives that secondarily colonized continental waters (Sasaki 1989; Casatti 2000). For example, phylogenetic hypotheses suggest that the

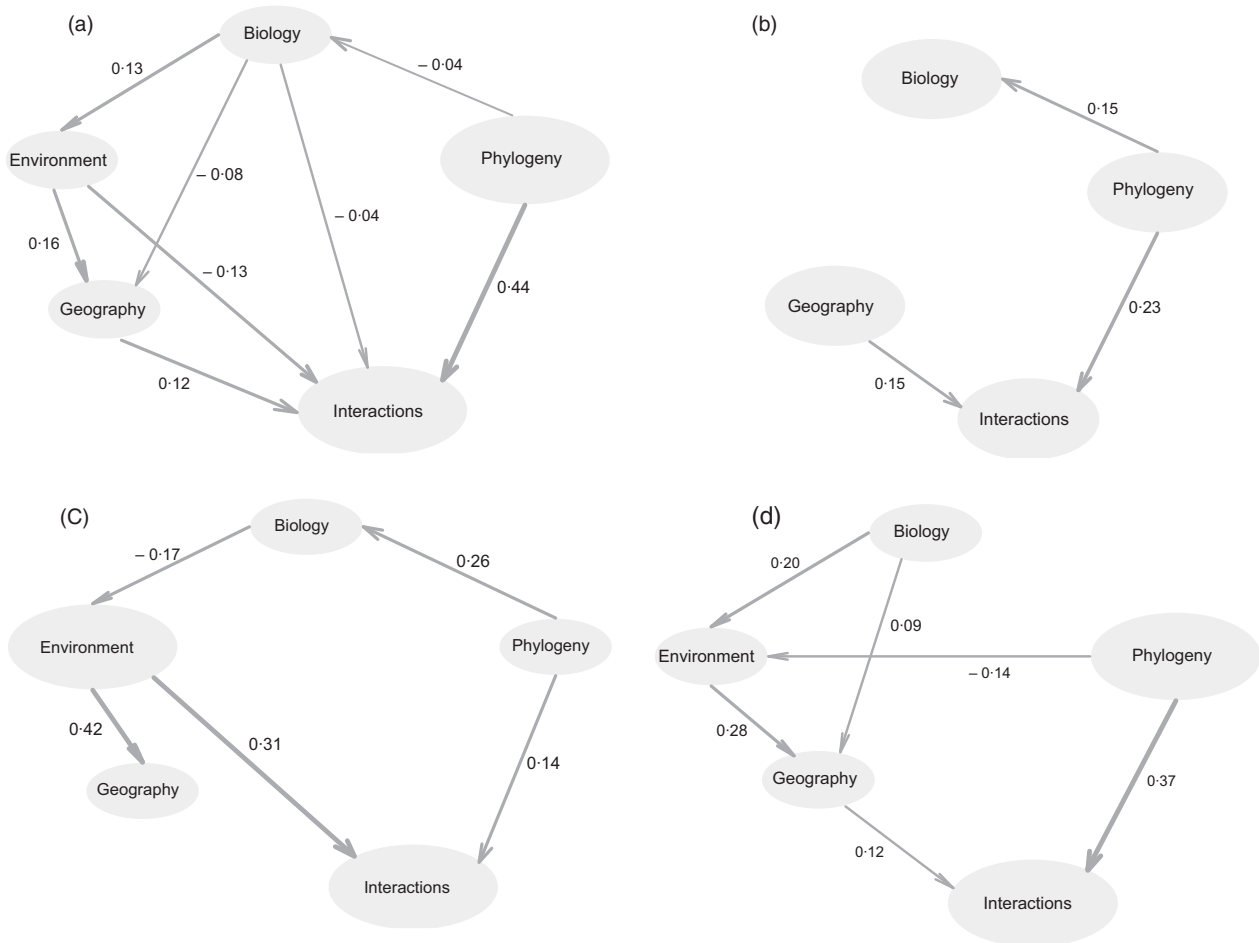


Fig. 3. Summary diagrams of the effects of all factors on parasite sharing including all hosts (a), only Perciformes (b), only Siluriformes (c) and only Characiformes (d). Arrows represent paths from an effect variable to a response variable. Only statistically significant effects ($P < 0.05$) are presented.

origin of *Plagioscion* spp. and their parasites occurred after freshwater colonization approximately 20 Mya, via marine transgressions (Boeger & Kritsky 2003).

Thus, it is reasonable to postulate that cichlid and sciaenid fishes do not represent a similar resource for their parasites, hampering host-switching between lineages. However, most cichlids (14 of 17 species) are parasitized by species of *Sciadicleithrum*, and *Gussevia* Kohn and Paperna, 1964 is recorded from 5 cichlid species spread across distantly related species within the family. Therefore, phylogeny explains only the difference between cichlid and sciaenid parasites. Parasite sharing among cichlids (17 out of 20 of 'perciform' species in this study) is best explained by host co-occurrences in river basins (Fig. 3b), strongly suggesting that host-switching shaped the present parasite distribution within Cichlidae.

Siluriformes, the second most diverse order in the data base (31 out of 105 species), is a diverse clade with a world-wide, mostly freshwater distribution. Neotropical Siluriformes does not compose a monophyletic group but includes four monophyletic clades (Sullivan, Lundberg & Hardman 2006; Fig. 4b). Three of them are represented in

our analysis (Loricariidae + Callichthyidae, Auchenipteridae + Doradidae, and Pimelodidae + Heptapteridae). Although the complete phylogenetic relationship between Neotropical Siluriformes is still uncertain, there is sufficient support to the separation between the basal Loricarioidei and the remaining taxa (Sullivan, Lundberg & Hardman 2006; Nakatani *et al.* 2011; Chen, Lavoué & Mayden 2013). Divergence time estimates vary from approximately 97 Mya (Chen, Lavoué & Mayden 2013) to approximately 180 Mya (Nakatani *et al.* 2011), suggesting a long divergence of Loricarioidei from the other two lineages of hosts considered herein (Silurioidei).

Parasite sharing within Siluriformes appears to reflect this deep divergence. There is a small overlap between Loricarioidei and Silurioidei parasite communities (Figs 2 and 4b). Only species of *Demidospermus*, the genus of Monogenoidea with the largest host range within Siluriformes, occurs in both clades. In addition to *Demidospermus*, species of *Vancleaveus* Kritsky, Thatcher & Boeger 1986 also occur in both host lineages within Silurioidei (specifically in Doradidae and Pimelodidae). Within

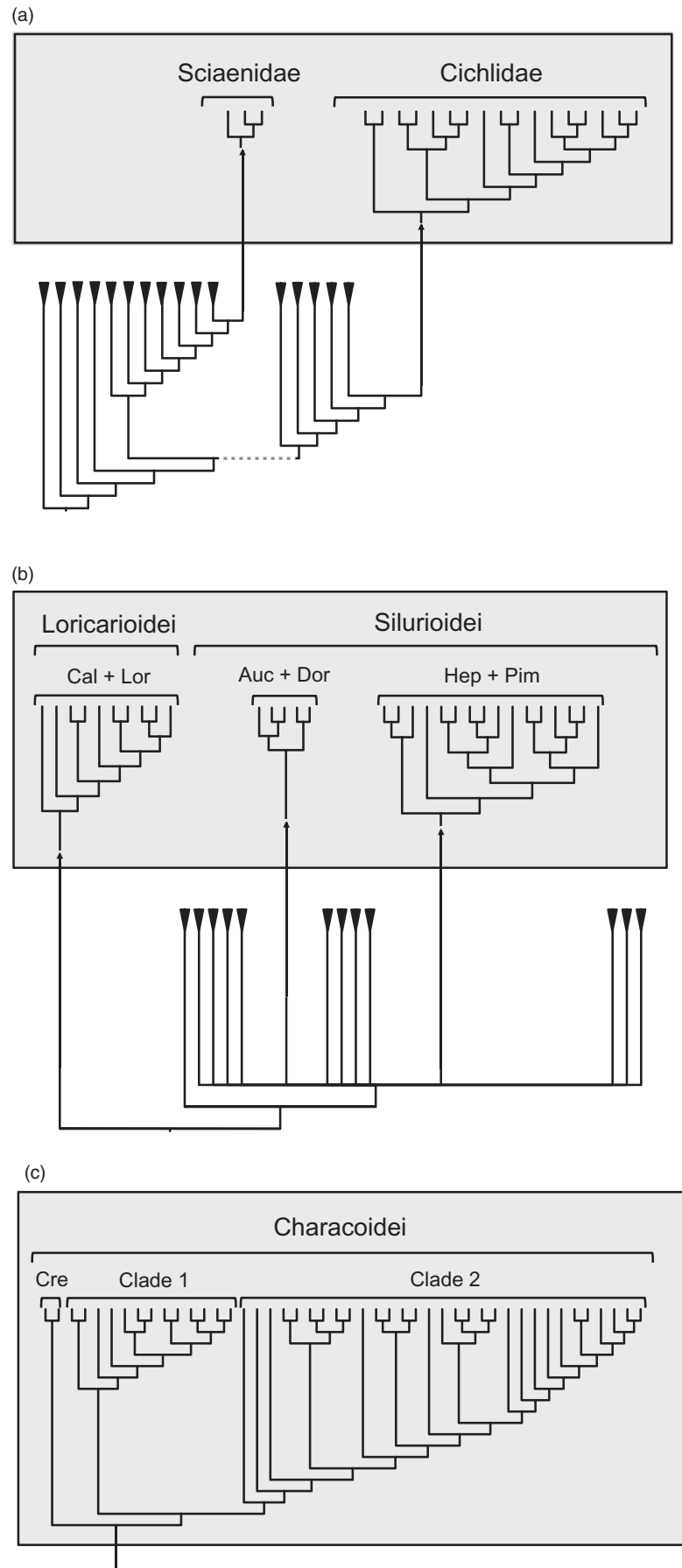


Fig. 4. Phylogenetic relationship within Percomorphaceae (a), Siluriformes (b) and Characoidei (c). Boxes highlight diversification within Neotropical freshwaters.

monophyletic clades, parasite sharing is higher, especially within families. Similarly to Cichlidae and Sciaenidae, Loricarioidei and Silurioidei diverged a long time ago and that is a putative reason for them to share only one genus of Monogenoidea. Accordingly, lineages that have a longer common evolutionary history share an increasing number of parasite genera, suggesting that switches between phylogenetically close hosts are more likely than switches between non-related hosts.

The Characiformes are one of the largest components of the freshwater fish fauna world-wide and are distributed across the New World and Africa (Nelson 2006). Neotropical Characiformes form a monophyletic clade and are grouped in 14 families (Oliveira *et al.* 2011; Fig. 4c). Similarly to Siluriformes, early divergence events within Characiformes (Characoidei) date from approximately 93 Mya (Chen, Lavoué & Mayden 2013) to approximately 192 Mya (Nakatani *et al.* 2011). The most likely basal group of the order is Crenuchidae, and different studies support an early separation between two clades composed by (i) Characidae, Ctenoluciidae and Lebiasinidae, and (ii) Serrasalminae, Hemiodontidae, Curimatidae, Prochilodontidae, Anostomidae, Cynodontidae, Parodontidae and Erythrinidae (Nakatani *et al.* 2011; Oliveira *et al.* 2011).

Parasites of Characiformes display a variety of distribution patterns in host phylogeny, for example host species specificity, restriction to phylogenetically closely related hosts and wide distribution across host phylogeny. Parasite sharing among distant lineages is more intense among Characiformes hosts than among other groups. Six genera occur in families from both clades cited above. We suggest that parasites within Characiformes have a higher chance to reach distant hosts because diversification of this monophyletic group of fishes occurred solely within the continental Neotropical realm. Instead, Neotropical Perciformes (Percomorphaceae) and Neotropical Siluriformes are not individually monophyletic and represent discontinuous assemblages of lineages of hosts that diversified initially in the marine environment (or elsewhere) and secondarily invaded the continental environs. Neotropical Characiformes, thus, represents a contiguous set of hosts with no 'phylogenetic gap' between lineages (Fig. 4c). Experimental infections with species of *Gyrodactylus* (Monogenoidea) showed that infection and establishment success decreases with phylogenetic distance between host species (King & Cable 2007; King, van Oosterhout & Cable 2009). Hence, the phylogenetic contiguity observed within Characiformes likely allowed parasites to reach distant hosts by subsequently colonizing similar, phylogenetically neighbouring hosts, increasingly farther from the original ancestral host and closer to the new host. We call this process the 'stepping-stone' mode of host-switching, analogous to the same process observed in the geographic expansion of free-living organisms (Taylor *et al.* 1993). Further support for the existence of this pattern of host-switching in defining the host-parasites

associations observed within Characiformes is the nested structure of interaction networks of this fish group and their Monogenoidea gill parasites, as reported by Braga, Araújo & Boeger (2014).

Apart from the phylogenetic relationships of host species, geographic distribution is also an important factor shaping parasite sharing. Despite the observed host-order specificity of parasite genera, *Urocleidoides sensu stricto* spp. occur in at least seven species of six families and three orders (one Cyprinodontiformes, one Gymnotiformes and four Characiformes families) of the Supercohort Clupeocephala (as defined by Betancur *et al.* 2013). There are overlaps in the geographic distribution of these fish species; for instance, all of them co-occur in the region between Central America and the Orinoco River basin. Although there is not enough information to reconstruct the history of *Urocleidoides* species and their hosts, this can be seen as evidence that lineages of monogenoid gill parasites can use a diverse range of hosts. Once hosts coexist in Panama rivers, host-shifts either by resource tracking or sloppy fitness space may have occurred. The same likely occurred elsewhere, but our knowledge on the distribution of *Urocleidoides* spp. and their hosts is limited.

Although there is a lack of information on parasite phylogenetic relationships, and on the diversity and geographical distribution of host-parasite interactions, our results match those found for different types of associations using various methods. Phylogenetic relatedness between hosts is the most important predictor of parasite sharing (Cooper *et al.* 2012; Faria *et al.* 2013; Strona & Lafferty 2013), restricting parasites to higher host taxa, for example orders and families (Boeger & Kritsky 1997; Desdevises *et al.* 2002), to lineages within families, for example Dactylogyridea on Cichlidae hosts (Pouyaud *et al.* 2006) or to closely related hosts (Schoelink, Cruaud & Justine 2012). Additionally, phylogenetic contiguity in host communities may facilitate the stepping-stone mode of host-switching, increasing the risk of EID.

Within host lineages that share a relatively recent evolutionary history, ecological and geographical aspects may play an important role, providing more opportunity for a host-switch. This has also been reported for monogenoid parasites that are able to exploit ecologically similar hosts (Desdevises *et al.* 2002), for viral cross-species transmission between hosts whose distributions overlap geographically (Faria *et al.* 2013) and for a diverse group of primate parasites including viruses, helminths, protozoa, bacteria and fungi, whose distribution is influenced by ecology and geographical distribution of hosts (Cooper *et al.* 2012). Finally, biological traits – trophic level, size and those considered in the definition of 'vulnerability' (as defined by Cheung, Pitcher & Pauly 2005) – accounted only for a small part of the variation in parasite sharing. While the reasons for this modest influence of host biology on parasite sharing is not immediately evident, it agrees with previous findings for both mutualistic

(Donatti *et al.* 2011) and antagonistic networks (Faria *et al.* 2013; Strona & Lafferty 2013).

In the present study, distribution patterns of host–parasite interactions were analysed. These patterns can then be used as basis for future studies searching for the specific mechanisms underlying parasite sharing and host-switching within each subset of host–parasite interactions, as information on parasite phylogenetic relationships becomes available. Although host geographic distribution and ecology emerged as key factors increasing the chance of colonization of phylogenetically unrelated hosts, our results reinforce the importance of including evolutionary history in the study of ecological associations, including EID risk assessment. As suggested by Brooks & Ferrao (2005), emerging diseases by host-switching are ‘evolutionary accidents waiting to happen’. Information about the phylogenetic relationships of host species can be a proxy for the probability of a host-switch. For instance, far more human infectious diseases originated in the Old World than in the New World likely because humans are phylogenetically closer to Old World monkeys (especially apes) than to New World monkeys (Wolfe, Dunavan & Diamond 2007). Another important aspect is that EIDs can reach unrelated hosts by the stepping-stone mode of host-switching. While phylogenetic gaps may represent barriers, phylogenetic contiguity of host communities may act as bridges to pathogen transmission between distantly related species. However, it is generally accepted today that parasites and pathogens are active resource trackers rather than simply passive followers of their host evolutionary history (Hoberg & Brooks 2008). Thus, direct host-switches among distantly related species, although unexpected, can occur if the hosts possess similar resources. An important issue to address in future studies is to understand what are the resources that parasites need and track, and to what extent they are phylogenetically determined.

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Data accessibility

All data used in this manuscript are present in the manuscript and online supporting information file Data S1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1 Interaction matrix between host species and parasite genera.