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## ECOLOGICAL FITTING AS A DETERMINANT OF THE COMMUNITY STRUCTURE OF PLATYHELMINTH PARASITES OF ANURANS

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**Abstract.** Host–parasite associations are assumed to be ecologically specialized, tightly coevolved systems driven by mutual modification in which host switching is a rare phenomenon. Ecological fitting, however, increases the probability of host switching, creating incongruences between host and parasite phylogenies, when (1) specialization on a particular host resource is a shared characteristic of distantly related parasites, and (2) the resource being tracked by the parasite is widespread among many host species. We investigated the effect of ecological fitting on structuring the platyhelminth communities of anurans from a temperate forest and grassland in the United States and tropical dry and wet forests in Mexico and Costa Rica. The six communities all exhibit similar structure in terms of the genera and families inhabiting the frogs. Parasite species richness is highly correlated with the amount of time a host spends in association with aquatic habitats, a conservative aspect of both parasite and host natural history, and determined in a proximal sense by host mobility and diet breadth. The pattern of parasite genera and families within host genera across the regions examined is consistent with the prediction that ecological fitting by phylogenetically conservative species, coupled with historical accidents of speciation and dispersal, should be evidenced as a nested-subset structure; the shared requirement for aquatic habitats of tadpoles provides a baseline assemblage to which other parasite taxa are added as a function of adult host association with aquatic habitats. We conclude that parasite communities are structured by both ecological fitting and coevolution (mutual modification), the relative influences of which are expected to vary among different communities and associations.

**Key words:** anurans; coevolution; community structure; Costa Rica; ecological fitting; frogs; Mexico; nested subset; parasitic platyhelminths; phylogenetic conservatism; toads; United States of America.

### INTRODUCTION

There are two approaches to studying the evolution of host–parasite associations. The first and newer research program, maximum co-speciation, assumes that hosts and their parasites share such a specialized and exclusive evolutionary association (Page 2003, Clayton et al. 2004, Johnson and Clayton 2004) that speciation in one lineage causes speciation in the other (synchronous co-speciation; Hafner and Nadler 1988, 1990). Host–parasite phylogenies are thus expected to be completely congruent, with departures from congruence explained by invoking extinction in one lineage or the other. The second and original research program (Brooks 1979) is also based upon comparing host–parasite phylogenies and identifying points of congruence as instances of co-speciation (the term coined by Brooks in [1979]). There are, however, no assumptions about underlying pro-

cesses, nor is there an expectation of complete congruence. Brooks proposed that the incongruent portions of host–parasite phylogenies falsified the hypothesis of co-speciation at those nodes and thus required investigations into the influence of other factors (e.g., dispersal and host switching) on the evolution of the association. For example, parasites might diverge more rapidly than their hosts via sympatric speciation, producing sister species inhabiting the same host (Brooks and McLennan 1993; or “lineage duplication” sensu Page [2003]), or ecological or immunological evolution in the host lineage could cause parasite extinction (lineage sorting or “missing the boat” sensu Page [2003]).

Although the maximum co-speciation program has been moving closer to Brooks’ propositions about the way incongruences should be treated, there is still one area of dispute between the two perspectives, the importance of host switching during the evolution of host–parasite associations. This debate is a logical extension of the assumption that hosts and parasites share a specialized exclusive evolutionary association, making it extremely unlikely that a parasite could

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PLATE 1. Major habitat types in Area de Conservacion Guanacaste, Costa Rica (clockwise from upper left); Pitilla approach, tropical cloud forest habitat at entrance to Pitilla Field Station; Cuajiniquil approach, Santa Elena Peninsula, seen from road to Cuajiniquil, tropical dry forest habitat; Rio Pizote, permanent swamp near Rio Pizote, between Dos Rios and Brasilia, tropical rain forest habitat. Pitilla Forest, tropical cloud forest habitat near Pitilla Field Station. All photos were taken in June 2005. Photo credits: D. R. Brooks

change host species. This assumption, however, arises from believing that it is the host *species*, not a biological characteristic or combination of characteristics of the host, that is important to the parasite (Brooks and McLennan 1993). Once researchers began thinking in terms of traits rather than taxonomy, it became evident that parasites might be able to switch hosts if the trait they were tracking was shared among two or more hosts. The fact that present-day associations might be shaped in part by the distribution of phylogenetically conservative traits is called ecological fitting (Janzen 1985).

There are many macroevolutionary manifestations of ecological fitting. For example, any given parasite species might be a resource specialist, but also might share that specialist trait with one or more close relatives. That is, specialization on a particular resource can be plesiomorphic within a group (for an extensive discussion and examples see Brooks and McLennan [2002]). On the other hand, the resource itself might be at once very specific and taxonomically and geographically widespread if it is a persistent plesiomorphic trait in the hosts. The evolutionary basis for ecological fitting is thus deceptively simple, yet powerful. If specific cues/resources are widespread, or if traits can have multiple

functions (or both), then the stage is set for the appearance of ecological specialization and close (co)-evolutionary tracking as well as host switching. Ecological fitting thus explains how a parasite can be ecologically specialized and still switch hosts: if the resource is widespread across many host species, then the parasite can take advantage of an opportunity to establish a “new” specialized association *without the cost of evolving novel abilities* (Brooks and McLennan 2002).

Just because a resource is widespread does mean that it is automatically available. The geographic distribution of the parasite might not coincide with the geographic distribution of all hosts having the resource (Pellmyr 1992a, b), or some other aspect of host biology might make the resource inaccessible to the parasite. For example, if host species A bearing resource  $x$  is highly abundant in a community, then less-abundant host species B and C, which also bear  $x$  might not be “apparent” to a parasite specializing on that resource (Feeny 1976, Wiklund 1984, Courtney 1985). Such density-dependent factors provide the appearance of close ecological tracking between the parasite and species A at time  $T_0$ . If some environmental stressor later decreases the abundance of species A, and C

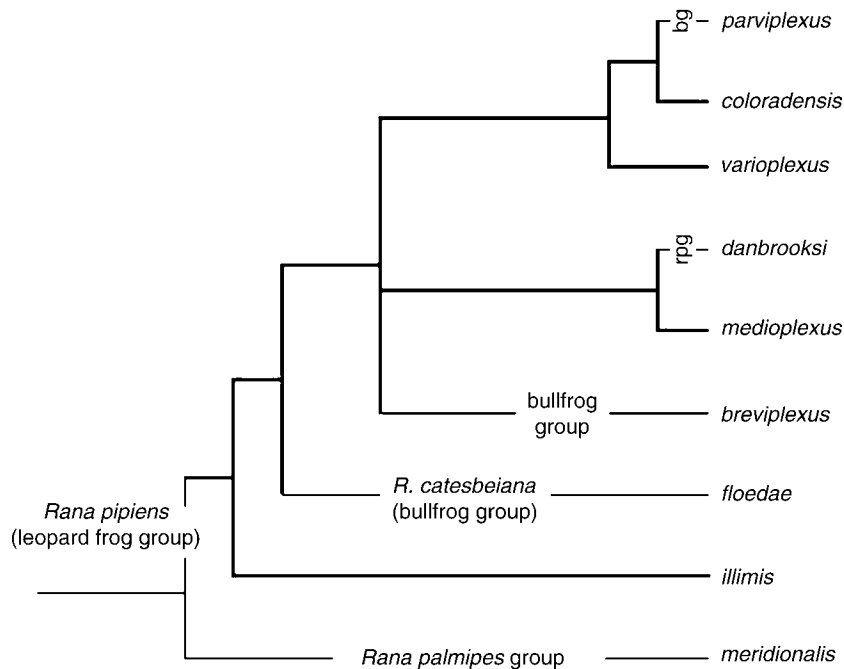


FIG. 1. Ecological fitting in frog lung flukes. A clade of lung flukes (*Haematoloechus* spp.) arose in conjunction with the evolution of leopard frogs (rpg; *Rana pipiens* group). *Haematoloechus floedae* arose through speciation by host switching to bullfrogs (bg; *Rana catesbeiana*). *Haematoloechus floedae* was introduced into Costa Rica with bullfrogs, where it expanded its host range to include local species of leopard frogs, members of the ancestral host group. Bullfrogs subsequently died out in Costa Rica, but *H. floedae* survives today due to ecological fitting (from Brooks et al., *in press*). Thick lines indicate episodes of cospeciation; thin lines indicate episodes of speciation by host switching.

becomes relatively more apparent, then the parasite will become associated with C at time  $T_1$ . This manifestation of ecological fitting could explain seemingly rapid and virtually unconstrained evolution of novel specialized host associations. Finally, a parasite might have a hierarchy of host preferences, even though it is tracking the same resource (host rank order; Singer et al. 1971; Janz and Nylin 1998 and references therein). The hierarchy arises because the costs of accessing the resource might not be identical across all host species or even across individuals in the same species (Singer et al. 1992). Such costs will depend on many different factors, including concentration of the resource, host density, and difficulty in extracting the resource. Overall, parasites accessing a plesiomorphically (or, less often, homoplasiously) distributed resource are “faux generalists” (Brooks and McLennan 2002): specialists whose host range appears large, but who are in reality using the same resource.

If a parasite species evolves the ability to utilize a novel resource, a second and more complicated type of host preference hierarchy can arise if the parasite also retains sufficient information to use the plesiomorphic resource (Wiklund 1981, Courtney et al. 1989). For example, *Haematoloechus floedae* is a fluke native to the southeastern United States where it lives in the lungs of the bullfrog, *Rana catesbeiana*. When bullfrogs were introduced to the southwestern United States, the

Yucatán, and Costa Rica, the parasite went with them, and is now found in bullfrogs in those areas, as well as in leopard frogs in the Yucatán and Costa Rica. Leopard frogs (*Rana pipiens* clade) are the plesiomorphic hosts for *Haematoloechus* (Fig. 1). Although the ancestor of *H. floedae* switched to bullfrogs, the presence of the fluke in leopard frogs indicates that the parasite has retained its clade’s plesiomorphic ability to infect leopard frogs (Brooks et al., *in press*). Interestingly, bullfrogs have disappeared from Costa Rica, but the parasite persists, having survived the “extinction” of its preferred host. This is the first demonstration that parasites, like phytophagous insects (Janz et al. 2001 and references therein) might display ancestral host preferences under certain circumstances.

Ecological fitting is generally investigated in insect–plant systems, because researchers can reconstruct phylogenetic patterns of association between the two clades, then examine the processes underlying those patterns by (1) identifying the resource being tracked by the insect, (2) determining the distribution of that resource among host plants, and (3) delineating the host preference hierarchy of the insects (Brooks and McLennan 2002). Currently, we do not have this degree of detailed information for any host–parasite system. It is possible, however, to take advantage of “natural experiments” (e.g., the case of *H. floedae*), or even to make inferences based on contemporary patterns of

host–parasite association, if hosts vary in their use of a habitat to which parasite species are constrained. The associations between anurans and their platyhelminth parasites provide a model system for such an investigation, because the majority of helminths require water for the development and transmission of infective stages, while most, but not all, major groups of anurans have a sexual and developmental tie to aquatic habitats. Brandt (1936) suggested that species richness in anuran parasite communities was directly related to the amount of time the host spent in or near water, an observation confirmed by subsequent studies (Prokopic and Krivanec 1975, Brooks 1976). A shared plesiomorphic requirement for an aquatic habitat, coupled with a gradient of adult anuran preferences ranging from aquatic to arboreal, suggests that ecological fitting as a determinant of the parasites associated with a given anuran taxon should be evidenced as a nested-subset structure (Patterson and Atmar 1986) of host–parasite associations across anuran taxa (Zelmer et al. 2004).

At one extreme, if all the host–parasite associations are the result of ecological fitting, then all host taxa are interchangeable from the point of suitability for the parasites, and associations will be determined solely by the habitats the host utilizes and its feeding preferences. The shared requirement of tadpoles for aquatic habitats should thus provide a baseline assemblage of parasites that infect the tadpole stage, while the parasites of adult anurans should accumulate in anuran host species as a function of the time they spend in aquatic habitats as adults. If specialized coevolutionary processes dominate, sympatry between anurans and the infective parasitic stages will result in parasitism of only appropriate hosts, producing idiosyncratic (i.e., “unexpected”) presences and absences in the matrix of host–parasite associations.

#### MATERIALS AND METHODS

Compound parasite communities are defined as the array of parasite species inhabiting an array of host species in a given area (Holmes and Price 1986). We have data for six compound communities of platyhelminths that parasitize frogs as definitive hosts in North and Central America: the temperate hardwood forests of North Carolina (Brandt 1936), the temperate grasslands of Nebraska (Brooks 1976), and the tropical wet and dry forests of Costa Rica (see Plate 1) and Mexico, derived from biodiversity inventories currently being coordinated by D. R. Brooks (Costa Rica) and V. León-Règagnon (Mexico) (see the Appendix).

We sampled 75 anuran species in the six areas; 59 were sampled in one area, 14 species were sampled in two areas, and two species were sampled in three areas (see the Appendix, Table A1). Of the 57 platyhelminth species collected, 38 were found in one area, 13 species were found in two areas, four species were found in three areas, and two species (*Langeronia macrocirra* and *Haematoleechus complexus*) were found in four areas (see the Appendix, Table A2). The parasites inhabit 34

of the 75 sampled anurans, only six of which (*Rana catesbeiana*, *Rana vaillanti*, *Smilisca baudinii*, *Smilisca phaeota*, *Leptodactylus melanonotus*, and *Bufo marinus*) have been sampled in two areas, and one of which (*Bufo marinus*) was sampled in three areas. From this we conclude that comparisons of compound community structure among the six sites will not be confounded by multiple samples of the same anuran community, and therefore the same anuran parasite (i.e., pseudo-replication). Moreover, given the geographical and taxonomic breadth of the surveys, it is assumed that the resultant presence/absence matrices of host–parasite associations, at the taxonomic levels examined (i.e., host genera and parasite genera and families) are representative of the possible associations, and not strongly biased by ecological factors, such as host and parasite ranges and relative abundances.

Anuran species were ranked based on their association with aquatic habitats as follows: 7, riparian, prolonged breeding (several months); 6, semiaquatic, prolonged breeding; 5, terrestrial, prolonged breeding; 4, terrestrial, explosive breeding (1–2 wk); 3, arboreal, prolonged breeding; 2, arboreal, explosive breeding; 1, fossorial. The relationship between the ranked association and trematode species richness was evaluated using Spearman's rank correlation analysis.

Without data from experimental infections, ecological fitting and co-speciation cannot be distinguished as explanations for extant, and apparently specific, host–parasite associations. Thus, parasite species and host species were grouped by genera for the purpose of nested-subset analysis, increasing the likelihood that the host and parasite clades had at one time been sympatric. Given the degree of local adaptation for both the host and parasite species, pooling hosts by genera and parasites by genera and families should not increase the likelihood of a nested-subset pattern occurring, given a mechanism of co-speciation. Thus it is necessary to view such a pattern as having been produced by ecological fitting. Examination of the nested-subset structure of parasite genera within the pooled anuran genera across all six localities was conducted using the nestedness temperature calculator (Atmar and Patterson 1995), which calculates the temperature of the matrix (a measure of order, with lower temperatures indicating a higher degree of order) and idiosyncratic host and parasite temperatures, which indicate host species and parasite species contributing disproportionately to the lack of order in the matrix (Atmar and Patterson 1993).

Nested-subset patterns can arise as artifacts of random draws of individual items from categories that vary in their representation (Connor and McCoy 1979). In a proximal sense, within a given locality, this would involve host individuals acquiring parasites from a species pool where the probabilities of infection varied among the parasite species because of an uneven distribution of infective stages within the environment. Considering the patterns of association between host

and parasite taxa, assuming that the various host taxa are sympatric in a regional sense, nestedness could be expected to arise by a similar passive mechanism if the parasite taxa vary in the degree of sympatry between their respective geographic ranges and those of the hosts. For tests of passive sampling involving community data, the relative abundances of the species sampled is not known for the source pool, requiring estimation of these relative abundances from the available data. Models that test for passive sampling typically base this estimate on the occurrence of species in the sample (RANDOM1; Patterson and Atmar 1986, Fischer and Lindenmayer 2002), which will result in overestimation of the colonization probabilities of rare species unless none of the populations present in the sample were further supplemented by dispersal from the source pool following the initial colonization (Andrén 1994).

Constructing an appropriate null model for passive sampling would require knowledge of the contribution of immigration from the source pool to the observed relative abundances. In the absence of such information, a null model (RELABUND) defining the opposite extreme, i.e., each individual present in a population is assumed to be an immigrant from the source pool, can be used in concert with RANDOM1, with the appropriate, but unavailable, null model falling between these extremes (Zelmer et al. 2004). Given that the distributions of temperatures of matrices produced by these models represent extremes in terms of the effect of immigration on the observed population sizes within a community, overlap with the tails of these distributions cannot be evaluated with a simple decision rule and must be interpreted in light of ecological evidence for the expected effects of immigration.

By analogy, the evaluation of passive mechanisms that produce nested-subset patterns of associations between host taxa and parasite taxa would require an understanding of the contribution of host capture to the observed associations. Species-level host and parasite phylogenies do not yet exist for the taxa in question (an exception is *Haematoloechus*; León-Régagnon and Brooks 2003), so the number of times a particular host genus acquired any particular parasite genus or family cannot be directly inferred, and must be estimated from the available presence/absence data. Analogous models to RANDOM1 and RELABUND were employed, using the occurrence of parasite taxa within host taxa to parameterize the Monte Carlo simulations for RANDOM1, and using the number of independent host-parasite associations to parameterize RELABUND. (For example, there are two species of *Langeronia*, one infecting four host species, the other infecting one. Thus, for the RELABUND model considering parasite genera, five “individuals” of *Langeronia* are distributed randomly among the host taxa. Within the Lecithodendriid family, in addition to the associations mentioned for *Langeronia*, there are two other parasite species, one infecting two host species, and one infecting a single

species. For the RELABUND model considering parasite families, eight “individual” lecithodendriids are distributed randomly among the host taxa.) As with the interpretation of these models for nestedness in communities, some of the associations observed will be the result of host capture, and some by inheritance, placing the appropriate, but unknown, null model between the extremes. Both the RANDOM1 and RELABUND null models were applied to presence/absence matrices of platyhelminth genera within anuran genera, trematode genera within anuran genera, and matrices where parasite genera not represented in all three regions were pooled by family and evaluated within host genera and host ecotype ranking.

To evaluate whether the patterns of presence and absence revealed across regions by the nested-subset analysis were reflected at smaller scales, we employed Spearman's rank correlation analysis to assess covariance between the total number of host genera occupied by a parasite genus or family (pooled across all six localities), and the number of host species, genera, and families occupied by each species within that taxon within each of the six localities. We also used Pearson's analysis to determine covariance between the total number of host genera occupied by a parasite genus or family (pooled across all six localities) and the number of host species, genera, and families occupied by those taxa within each region (United States, Mexico, and Costa Rica).

## RESULTS

The ranked association with aquatic habitats of the anuran species with nine or more individuals necropsied per locality positively covaried ( $r = 0.785$ ;  $P < 0.0001$ ) with the trematode richness of the frog host species (Fig. 2), with no clear differences in the pattern of increase among the six localities.

The temperature (the measure of matrix order derived by Atmar and Patterson [1993]) of the presence/absence matrix of platyhelminth genera within anuran genera (Fig. 3) was significantly more ordered than the matrices produced by the RANDOM1 ( $P = 0.00063$ ) or RELABUND ( $P = 0.00002$ ) null models. Nested-subset analysis designated four of the 21 parasite taxa as idiosyncratic; two monogenean genera and two cestode genera. Such idiosyncrasies are an indication of different colonization histories for these genera (Atmar and Patterson 1993) relative to the other parasites considered, suggesting the importance of phylogenetic congruence as a determinant of the anuran associations with monogenean and cestode species. Consequently, the remaining analyses focused on the trematodes.

The nested-subset structure of the trematode genera within the pooled anuran genera (Fig. 4) also was significantly colder than the matrices generated from both null models (RANDOM1,  $P = 0.000001$ ; RELABUND,  $P = 0.0000004$ ), and also revealed idiosyncratic parasite genera. These idiosyncrasies all occurred in

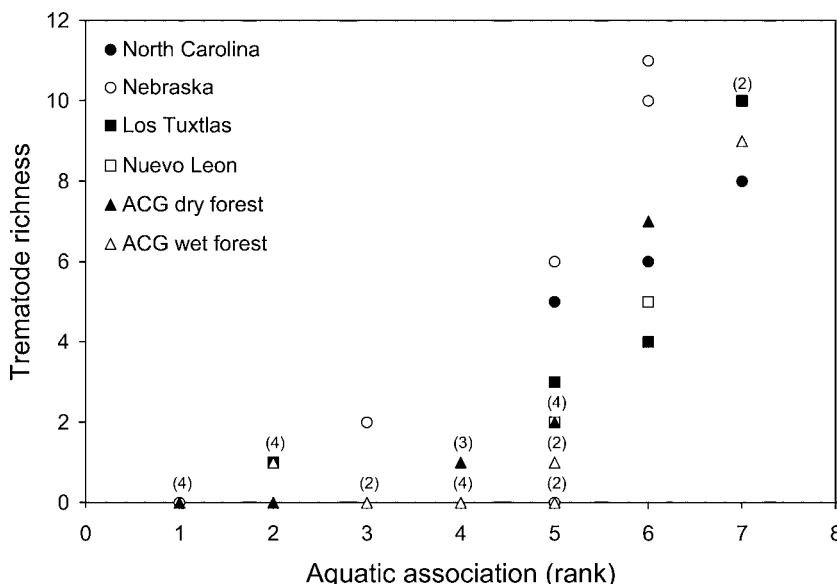


FIG. 2. Increasing trematode species richness in anuran host species from each of six localities, with increased anuran association (ranked) with aquatic habitats. Multiple observations at a single coordinate are indicated parenthetically above the coordinate. ACG denotes Area de Conservación Guanacaste.

genera that were missing from at least one of the three regions sampled (North America, Mexico, or Costa Rica). Thus, in order to evaluate the potential for the interaction of the anuran host genera with specific landscapes to produce nested subset patterns, we arbitrarily pooled parasite genera not represented in all three areas into their respective families, thereby ensuring that all anuran genera included in the analysis have the potential to draw from the same parasite pool. The resulting matrix is depicted in Fig. 5.

The temperature of the presence/absence matrices of trematode genera/families in pooled anuran genera overlaps the cold tail of the distribution produced by the RANDOM1 model ( $P = 0.0025$ ) and the cold tail of the distribution produced by the RELABUND model ( $P = 0.0885$ ). Thus, the observed nested-subset pattern could only be attributed to passive mechanisms by adhering to the RELABUND model's assumption that all host-parasite associations occur independently. Given that extreme assumption, however, interpretations of the observed matrix as nonsignificant with regards to passive sampling must be made with caution.

Examination of the presence/absence matrix of trematode genera and families within ranked anuran ecotypes (Fig. 6) supports the contention that the semiaquatic anuran habitat creates overlap with infective stages of a greater number of trematodes than a purely aquatic habitat. The temperature of this matrix falls within the cold tail of the distribution of the temperatures produced by both models (RANDOM1,  $P = 0.0018$ ; RELABUND,  $P = 0.165$ ). As with the parasite associations with anuran genera, one must conclude that passive mechanisms could produce this pattern only under the independent-association assumption of the RELABUND model, again with

the caveat that the distribution of the appropriate null model presumably has a warmer central tendency than that produced by the RELABUND model.

The total number of host genera occupied by a parasite genus or family (pooled across all six localities) positively covaried with the number of host species ( $r = 0.321$ ;  $P = 0.0104$ ), genera ( $r = 0.425$ ;  $P = 0.0005$ ), and families ( $r = 0.426$ ;  $P = 0.0005$ ) occupied by each species within that taxon within each of the six localities. The total number of host genera occupied by a parasite genus or family also positively covaried with the number of host species ( $r = 0.492$ ;  $P = 0.0147$ ), genera ( $r = 0.668$ ;  $P = 0.0004$ ), and families ( $r = 0.645$ ;  $P = 0.0007$ ) occupied by each species within that taxon within each of the three regions (United States, Mexico, and Costa Rica).

## DISCUSSION

### *Parasite habitat preference and transmission patterns*

Fifty-four of the 57 parasite species (see the Appendix, Table A3) exhibit the plesiomorphic pattern of requiring water for transmission, either by utilizing aquatic intermediate hosts (digeneans and cestodes), or by swimming from one host to another (monogeneans). In other words, transmission patterns are phylogenetically conservative in this phylum (Brooks and McLennan 1993, Adamson and Caira 1994). This explains why 45 of the 57 platyhelminth species were found only in aquatic and semiaquatic frogs. Of the remaining 12 species, 10 occur in terrestrial, arboreal, and fossorial frogs, but infect the tadpole stage of their hosts. Digeneans in the genus *Glyptelminis* and the family Paramphistomidae cluster with the brachycoelids (*Brachycoelium* and *Mesocoelium*) in the maximally

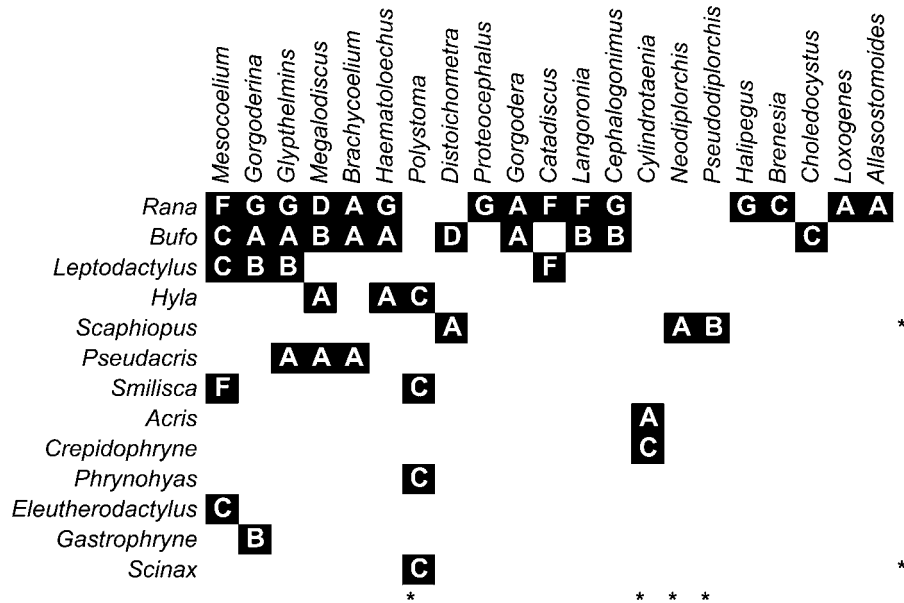


FIG. 3. Maximally packed presence/absence matrix for pooled parasite genera (columns) within pooled host genera (rows) from all six localities. Stars indicate idiosyncratic hosts and parasite species. Letters within the matrix denote geographic region where associations were observed: A, United States only; B, Mexico only; C, Costa Rica only; D, United States and Mexico; E, United States and Costa Rica; F, Mexico and Costa Rica; G, United States, Mexico, and Costa Rica.

packed matrix (Fig. 5) as parasite taxa common to a number of anuran genera within localities and regions, as well as across regions. All that is required for infection is that the frog species comes to water to breed in a population density high enough to ensure infection. This behavior is plesiomorphic for, and phylogenetically conservative among, frogs. The last two species, members of the sister groups *Brachycoelium* and *Mesocoelium*, have terrestrial life cycles, which explains why they occur so frequently in terrestrial anurans and in frogs that occasionally forage away from water.

*Choledocystus intermedius* (one of the idiosyncratic taxa in the presence/absence matrix depicted in Fig. 4) inhabits only *Bufo marinus*, and it is the only adult platyhelminth restricted to that host. Razo-Mendivil et al. (*in press*) recently have shown *C. intermedius* to be closely related to members of the families Ochetosomatidae and Telorchidae. Life cycles for members of those families involve aquatic molluscs as first intermediate hosts, and tadpoles as second intermediate hosts, which are ingested by the final host. The absence of *C. intermedius* from other anuran hosts that ingest tadpoles might indicate that the

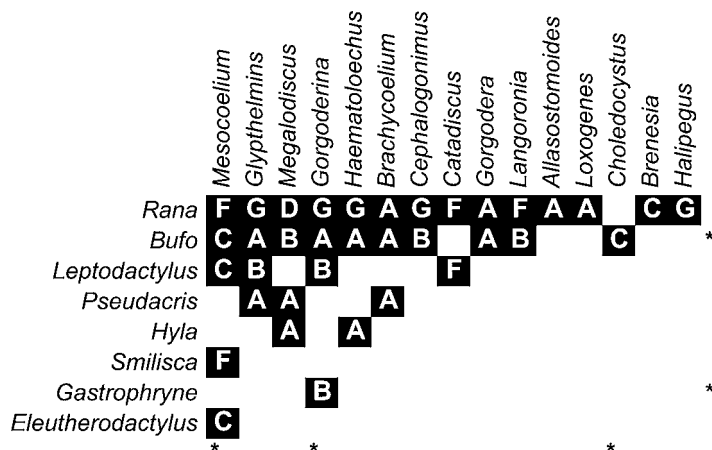


FIG. 4. Maximally packed presence/absence matrix for pooled trematode genera (columns) within pooled host genera (rows) from all six localities. Stars indicate idiosyncratic host and parasite species. Letters within the matrix are as in Fig. 3.



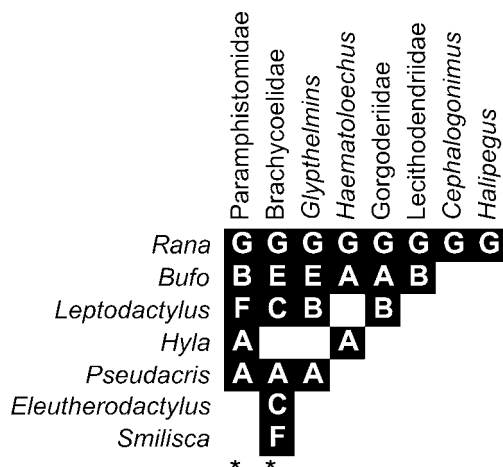


FIG. 5. Maximally packed presence/absence matrix for trematodes (columns) pooled by genera, or by family for those genera that did not occur in all three regions (United States, Mexico, and Costa Rica), within pooled host genera (rows) from all six localities. Stars indicate idiosyncratic host and parasite species. Letters within the matrix are as in Fig. 3.

association between *C. intermedius* and *Bufo marinus* involves more specialization than ecological fitting.

The remaining parasite taxa, whose associations with their hosts cannot easily be interpreted as manifestations of ecological fitting (based on the idiosyncratic patterns revealed in the nested subset analysis), also infect tadpoles at some stage in their lives. The monogeneans *Polystoma naevius*, and the probable sister species *Neodiplorchis scaphiopi* and *Pseudiplorchis americanus*, infect tadpoles and develop into adults when the tadpoles metamorphose. Anecdotal reports exist of tadpoles eating proglottids of nematotaeniid cestodes, suggesting that four additional species (*Cylindrotaenia americana* and *C. sp.*, *Distoichometra bufonis* and *D. kozloffii*) gain infection in a manner similar to the first three species. Perhaps infection of a tadpole requires greater specificity on the part of the parasite than infections of adult anurans, making parasites with such life cycle patterns less amenable to ecological fitting.

#### Habitat use by hosts

Forty-two of the 58 species of adult platyhelminths (72%) occur in ranids. Of those 42 species, 27 are found only in ranids, indicating that some character or suite of characters associated with being a ranid is the resource being tracked by the parasites. Of the remaining 15 species, 11 always occur in higher prevalences in ranids (one measure of the host preference hierarchy), two occur at lower prevalences, and two are equivocal (possibly an artifact of small sample size). The low-prevalence occurrences in nonranid hosts might be an additional example of ecological fitting if the nonranids are suitable hosts, but their lack of exposure to aquatic habitats renders them "not apparent" to the parasites. *Brachycoelium hospitale*, for example, is generally found

in plethodontid salamanders and has a terrestrial life cycle. Not surprisingly it is more common in a terrestrial nonranid (*Pseudacris brimleyi*) than in a ranid host.

It is clear that a role for coevolutionary processes exists for variations in associations of parasite genera within families, and species within those genera in terms of their specific host association. However, no explanatory power is gained from considering anurans by their genera, as opposed to their ecotype, in terms of associations with the genera and families of the trematodes infecting them. This equivalence occurs, in part, because ecotype preference for anuran hosts (e.g., all aquatic and semiaquatic host species in all six sites are members of the same genus, *Rana*), and transmission dynamics for the parasites (e.g., all species of *Haematoleochus* utilize odonate naiads as second intermediate hosts) are phylogenetically conservative (Snyder and Janovy 1994, Wetzel and Esch 1996).

#### The host landscape

As evidence for phylogenetic conservatism in host and parasite biology, 80% of the parasite species discovered in these six communities inhabit only 13% of the frog species sampled. How do these species coexist? Part of the answer lies in perhaps the most fundamental element of ecological fitting: allopatry. Only 38% of the 48 parasite species inhabiting aquatic and semiaquatic anurans occur in more than one community.

Another aspect of the process of co-occurrence lies in parasite microhabitat diversification, or, as commonly

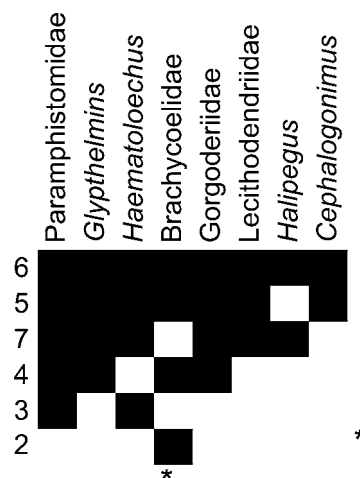


FIG. 6. Maximally packed presence/absence matrix for trematodes (columns) pooled by genera, or by family for those genera that did not occur in all three regions (United States, Mexico, and Costa Rica), within host species from all six localities, pooled by ecotype (ranked association with aquatic habitats). Stars indicate idiosyncratic host and parasite species. Variation in rank within genera was (no. species at rank) as follows: ranids, two at rank 7, six at rank 6, and two at rank 5; bufonids, two at rank 4, three at rank 5; leptodactylids, two at rank 4, one at rank 5; hylids, two at rank 3; see *Materials and methods* for rank designations. No trematodes were found to infect the fossorial species.

phrased, diversity in preferred site of infection within the host (Brooks and McLennan 1993, 2002, Adamson and Caira 1994, Radtke et al. 2002). Platyhelminth species occur in the buccal cavity, lungs, gall bladder and hepatic ducts, small intestine, rectum, and urinary bladder of anuran hosts, such that multiple species from different clades can infect the same host and form complicated communities without interacting physically, i.e., they are microallopatric. Many species having similar transmission modes occur in the same hosts, but live in different parts of that host. On the other hand, because the diversification of infection site is phylogenetically conservative, multiple, distantly related parasite species living within a given geographic area can exhibit the same kind of site specificity, which should amplify competition. In some cases, the parasite species occur in different host species; for example, polystome monogeneans and gorgoderid digeneans live in the urinary bladder, but do not infect the same species of frogs. In other cases, the parasites have markedly different biological requirements. Cestodes living in the host gut absorb nutrients from the host intestinal contents, whereas digeneans living in the host gut forage for host epithelial cells, cell and tissue exudates, and blood.

#### CONCLUSIONS

These six communities of frog parasites are both complex and similar to each other. Their complexity rules out simple phylogenetic replication, namely, that these communities are products of a simple history of vicariance and/or co-speciation. The taxonomic similarity of the communities, coupled with their occurrence in such markedly different environments, rules out the possibility that they are the result of convergent adaptation. Brooks (1980, 1985), Futuyma and Slatkin (1983), and Janzen (1985) suggested that relatively weak phenomena (in this case, phylogenetic conservatism in host and parasite natural history) have the potential to produce marked ecological structure. That a great deal of the stable and predictable structure of contemporaneous anuran parasite communities appears to be a result of phylogenetic conservatism in the evolution of both parasite and host biology, coupled with the historical biogeographic contingencies of speciation and dispersal, is consistent with those views.

These observations, of course, do not rule out the possibility of ongoing strong evolutionary interactions between any of these parasites and their hosts or each other, particularly at the small spatial and short temporal scales associated with Thompson's (1994) *coevolutionary mosaic*. Nor do the observations imply that ecological fitting explains everything; only that assumptions about the low probability of host switching must be viewed with far more caution in the future. Tracking a plesiomorphic resource in parasites is the equivalent of free-living organisms dispersing into new habitat, but retaining their ecological niche; both are aspects of ecological fitting. Given this, we expect that

parasite communities will be *macroevolutionary mosaics* of ecological fitting and co-speciation, just as are communities of free-living organisms (e.g., colubrid snakes; Cadle and Greene 1993). Additionally, because communities and associations are subject to evolutionary forces that will vary across space and time, we also expect that the importance of ecological fitting and co-speciation will vary among communities and among associations.

Finally, our analysis implies that many parasites currently restricted to particular hosts in particular localities could survive in other hosts and other localities if they could get there. Episodes of major climate change, for example, result in range contractions and expansions bringing together species that have been allopatric during their previous evolutionary histories. In such cases, we would expect an increase in host switching, not as a result of evolution of novel host utilization capabilities, but as a manifestation of ecological fitting. As discussed above (see the *Introduction*), some parasites might well survive extinction of their original hosts. Discovering the importance of ecological fitting as a determinant of the structure of anuran parasite communities thus underscores the need for more comprehensive ecological and evolutionary understanding of host specificity in assessing the risk of parasite transmission into native hosts resulting from the introduction of exotic host species along with their parasites.

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## APPENDIX

Geographic distributions of anuran hosts and their platyhelminth parasites in six areas in North and Central America (*Ecological Archives* E087-112-A1).