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Abstract of the Dissertation

The origins of diversity in frog communities: phylogeny, morphology, performance, and dispersal

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In this dissertation, I combine phylogenetics, comparative methods, and studies of morphology and ecological performance to understand the evolutionary and biogeographical factors that lead to the community structure we see today in frogs. In Chapter 1, I first summarize the conceptual background of the entire dissertation. In Chapter 2, I address the historical processes influencing body-size evolution in treefrogs by studying body-size diversification within Caribbean treefrogs (Hylidae: *Osteopilus*). In this chapter I combine analyses of resource use, community assembly, phylogenetics, and rates of body-size evolution within *Osteopilus* to examine support for the influence of past competition on body-size evolution within the genus. In Chapter 3, I develop an approach to quantify the relative importance of in situ evolution (ISE) within a region and ecologically conservative dispersal (ECD) from outside that region to better understand the evolutionary and biogeographical processes that influence community

structure in Middle American hylid treefrogs. I also test whether colonization of the region (Middle America) is related to climatic similarity of invaded areas to ancestral areas of colonizers, and whether temporal staggering of colonization is related to subsequent evolution within the region. Last, I determine whether species that are ecologically similar can co-occur in communities and whether ecological differences are necessary for a species or lineage to colonize the region. Finally, in Chapter 4 I examine the evolution of microhabitat use, morphology, and performance in three assemblages of frogs to ask whether these processes (ISE and ECD) are important on a worldwide scale across a large clade. I examine the consequence for morphological and performance evolution of both cross-continental, ecologically conservative dispersal of lineages, as well as microhabitat diversification within a single clade in a single geographic location. Overall, these studies suggest that the ecological, morphological, and performance diversity we see in a given location is a mixture of both ISE and ECD, even at the global scale.

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I hereby state that permission has been granted by myself and Dr. John J. Wiens (dissertation advisor) to reproduce the article "Phylogenetic evidence for competitively-driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*)." This paper was published in the journal Evolution, which is published by the Society for the Study of Evolution and Blackwell Publishing. The full reference for this publication is as follows:

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Chapter 1: Introduction

Background

An important issue in community ecology is understanding what factors influence the structure of a given community (e.g., number of species, ecological diversity). Traditional approaches have largely focused on local factors, such as abiotic aspects of the environment and biotic factors such as predation and competition (Morin 1999). For example, if two potential species could each individually persist within a single community but strongly compete with each other, the principle of competitive exclusion would predict that only one of the species could exist within the community (Hardin 1960, MacArthur and Levins 1972, Morin 1999), at least in the absence of evolution. More generally, much of the ecological diversity of a community may largely be dictated by the local environment (e.g. resource availability, climate). A tropical rainforest, for example, is expected to have many more species and ecological diversity than the Antarctic simply because the latter presents climatic conditions much too inhospitable for the survival of most organisms on the planet.

However, ecologists have also long recognized the importance of larger-scale processes, such as biogeographic dispersal and evolutionary diversification (e.g. MacArthur 1972). Despite this recognition, this aspect of community ecology did not advance much until the early 1990s, when robust phylogenies of many organisms and statistical tools to use those phylogenies became more widely available (Brooks and McLennan 1991, Losos 1996). Much work since then has focused on one of these processes, namely evolutionary diversification (e.g. Schluter and McPhail 1993, Losos et al. 1998, Kornfield and Smith 2000). However, studies of biogeographic dispersal (coupled with phylogenetic conservatism) have lagged behind (Ackerly 2003, Stephens

and Wiens 2004). Yet both are fundamental – in any given community, the observed phenotypes (ecological, morphological, performance) evolved in some place, and that place may have been within the community of interest or outside of it. In other words, the ultimate source of phenotypic diversity in a given community necessitates an understanding of both in situ evolution and ecologically conservative dispersal (Losos 1996). As such, I focus here on the evolution of phenotypic diversity both within and outside of a region of interest, and how the biogeographical context of that evolution can say much about the origins of current community structure.

Study system

Anuran amphibians (frogs) represent an excellent system in which to examine questions about the role evolutionary diversification and biogeographic dispersal on the ecological and phenotypic diversity we see in modern-day communities. Most tropical lowland sites around the world have many frog species co-occurring locally (e.g., Lloyd et al. 1968; Duellman 2005), and it has long been recognized that a certain number of common “ecomorphs” (species of similar morphology that utilize similar microhabitats; Williams 1972) occur at these sites (Bossuyt and Milinkovitch 2000; Pough et al. 2002; Bossuyt et al. 2006). The taxonomic composition of these assemblages often reflects evolutionary diversification of major clades within a given region, suggesting that shared selection may have led to evolutionary convergence. For example, ranoid frogs dominate in Africa and Asia, whereas hyloid frogs dominate in North, Middle, and South America (Roelants et al. 2007; Wiens 2007; Amphibiaweb 2008), and each group has species in many microhabitat categories (Duellman and Trueb 1986). On the other

hand, some clades are globally widespread (e.g. Bufonidae, Microhylidae; Duellman and Trueb 1986), suggesting that biogeographic dispersal of lineages (and whether phenotypic diversification has happened before or after dispersal) may also influence community structure. On a finer scale, even within regions and ecomorphs there are diverse circumstances related to within-region evolutionary diversification and ecologically conservative biogeographical dispersal. For example, within Middle America (Mexico to Panama), hylid treefrog communities contain a mixture of species, both from a clade that has diversified within the region and species from other lineages that have colonized the region more recently from North and South America (Duellman 2001). The composition of these communities (i.e., from which lineages the species are derived) varies based on both elevation and geography (e.g. relative distance from South America). Taken together, these diverse biogeographical and evolutionary circumstances (both around the world and within regions, across microhabitat use specialists and within one type) allow one to ask about the relative roles of in situ evolution and ecologically conservative dispersal.

Overview

Throughout this dissertation I combine phylogenetics, phenotypic data, and comparative methods to address these general questions in evolutionary ecology and macroevolution. In Chapter 2, I examine body-size diversification within Caribbean treefrogs (Hylidae: *Osteopilus*) to address the historical ecological factors that may have affected body-size diversification in arboreal frogs around the world. I measure morphology in *Osteopilus* to show that body size is major axis of variation with the

genus, examine patterns of resource use across species, develop models of community assembly, estimate phylogeny, and examine rates of body-size evolution within *Osteopilus* and all other hylid treefrogs. All analyses suggest that past competition has played a large role in body-size diversification in *Osteopilus* and other arboreal frogs. In Chapter 3 I address the importance of various evolutionary and biogeographic processes on the phenotypic and ecological diversity of 39 communities of hylid treefrogs in Middle America. I first address the importance of phenotypic evolution within a region (in situ evolution; ISE) and colonization of the region without character evolution (ecologically conservative dispersal; ECD) on the structure of these communities. Next, I ask whether lineages colonize areas in Middle America that are similar in climate to the areas from which they came. I then estimate the timing of colonization of the region by all of its lineages and estimate rates of evolution to ask whether earlier colonizing lineages have diversified more, perhaps due to increased ecological opportunity. Finally, I ask whether co-occurring species are necessarily phenotypically different, and whether such differences are a prerequisite for colonization of the region. Together, these results shed light on potentially general principles of community assembly that operate on much larger temporal and biogeographic scales than are generally considered by ecologists studying local community structure. In Chapter 4 I extend these questions of ecologically conservative dispersal and in situ evolution to the many types of microhabitat use in frogs, asking whether they are important on a global scale and in both morphology and performance. For this study I conducted fieldwork in Australia, China, and Colombia to collect data on morphology and performance in ecologically relevant behaviors in frogs, such as swimming speed,

maximum jump distance, and clinging ability. I first ask whether these three assemblages have converged in morphological and performance diversity. I next address the relationships among microhabitat use, morphology, and performance in these three assemblages. Finally, I ask (1) what is the consequence for the evolution of morphology and performance when clades show biogeographic change with no ecological change (i.e., ECD), and (2) how has diversification in morphology and performance proceeded during ecological diversification within a single geographic location? This is the first study to show that ECD from another continent can contribute to the phenotypic diversity in an assemblage. Additionally, it is the first to examine convergence in both morphology and performance across frog species that use the same microhabitat but in different parts of the world. Overall, this dissertation shows how both evolutionary diversification within a region on the one hand, and phylogenetic conservatism coupled with biogeographic dispersal from another region on the other, can both be important drivers of the phenotypic and ecological diversity that we see in communities today.

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Chapter 2: Phylogenetic evidence for Competitively-driven divergence: Body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*)

INTRODUCTION

Competition is considered to be an important force driving evolutionary diversification (Schluter 2000a,b) and has been shown to be prevalent in present-day communities (Connell 1983; Schoener 1983; Gurevitch et al. 1992). However, identifying the role of past competition can present a methodological conundrum: how does one test if competition is responsible for creating present patterns of phenotypic diversity if taxa have diverged such that they are no longer competing today (Connell 1980)? Many studies have shown experimental evidence for current competition among taxa (e.g., Gurevitch et al. 1992; Schluter 2000b; Pfennig et al. 2007). However, evidence of current competition does not necessarily indicate that competition was important in the past, nor does a lack of competition today prove that it was unimportant in the past. Thus, explaining present-day patterns of phenotypic diversity in communities and clades also requires comparative approaches that address past diversification among species. Although experimental studies within modern species are critical for understanding ecological and evolutionary processes, many assumptions are required to extrapolate their results to explain patterns that arose millions of years ago, and they are only one of many types of evidence that should be considered. Here, we study the repeated evolution of similar extremes of body sizes among species in different communities as a potential signature of competitively-driven divergence. To do this, we develop a general comparative methodology for inferring past competition that combines analyses of resource use, community assembly models, phylogeny, and rates of body-size evolution.

Body size determines patterns of resource use in many organisms (e.g., Fisher and Dickman 1993; Woodward and Hildrew 2002; Duellman 2005). Given this, many studies in community ecology have examined body-size similarity or dissimilarity as a metric of current or past competition, respectively (reviewed in Strong et al. 1984; Dayan and Simberloff 2005). Basing their expectations on the idea that species that are most similar in body size will compete the most strongly (MacArthur and Levins 1967; May and MacArthur 1972), these studies sought evidence of past and present competition by examining patterns of body sizes among species within communities. Such studies looked for even spacing between the body sizes of co-occurring species, a lack of overlap in intraspecific body-size distributions, and/or similar ratios of body sizes among pairs of sequentially larger coexisting species (reviewed in Dayan and Simberloff 2005).

There are a number of thoroughly-studied examples of even spacing between body sizes among species within communities (reviewed in Schoener 1974; Dayan and Simberloff 2005). However, there are also many assemblages lack these patterns (e.g., Duellman and Mendelson 1995; Duellman 2005; Lim and Engstrom 2005; Ridgely et al. 2005; Rodrigues et al. 2005; Vernes et al. 2006). In these latter communities, either there are many species that have very similar body sizes, or else there is uneven spacing between the mean body sizes of different species. Does this really mean that competition had no role in generating the body-size diversity seen in those communities today?

Focusing on body-size extremes across communities may reveal a signature of competively-driven divergence that is less likely to be "erased" by subsequent processes within a community. For example, adaptive diversification in body size may be important upon initial colonization of a region, while at later stages processes such as allopatric speciation, extinction, and dispersal may be more influential in determining local species composition and body-size distributions (Cornell and Lawton 1992). Alternatively, divergence in different aspects of the niche might allow similar-sized species to coexist after the initial body-size diversification. In both situations, despite the important role of competitive diversification early in the history of the clade in the region, even-spacing between the mean body sizes of species may no longer occur in the community today. In contrast, the body-size extremes should continue to persist.

No studies to date have focused specifically on the evolution of the minimum and maximum body sizes among species within a clade or guild in a community context (we use "guild" sensu Root 1967). Because competition is potentially a diversifying force (Slatkin 1980; Taper and Case 1985; Doebeli 1996; Schluter 2000b), competitive interactions may result in the evolution of similar body-size extremes across communities. Under this model, an ancestral species that initially colonizes a region may rapidly diversify to create a set of species with a broad range of body sizes. These species can then collectively utilize the full range of resources in the environment (for that clade), given selection to reduce competition (e.g., ecological character displacement, sensu Schluter 2000a). Alternately, competition might create a similar pattern but without evolutionary diversification, if size-mediated establishment success

only allows species larger or smaller than those within a community to successfully colonize, thus increasing the body-size extremes seen within the community (i.e., size assortment; Losos 1990). Another possibility is that competition is not important at all, and that both body size evolution and community assembly are random or determined by other processes.

Given these considerations, we make four general predictions regarding competively driven divergence in body sizes across communities. First, there should be evidence that body-size divergence facilitates resource partitioning within the group. Second, in evolutionarily young communities within a group (e.g., those with very few species but due to limited time for speciation, and not extinction), there should be non-random patterns of even body-size spacing, suggesting competitively driven evolution to reach the extreme body sizes, even if this body-size spacing is absent in older communities. Third, phylogenetic analysis should show that similar body size extremes have evolved repeatedly in different geographic locations, indicating that deterministic processes (e.g., competition) drive this pattern and that size assortment is not responsible. Fourth, phylogenetic analyses of rates of body size evolution should show exceptionally rapid evolution of body size in the clades making up these young communities, relative to clades in older communities in which there are multiple similarly sized species. We test these predictions in Caribbean treefrogs (genus *Osteopilus*). This set of analyses can be viewed as a general comparative approach for testing the possible role of past competition in explaining present day patterns of phenotypic diversity. Our approach follows those of Losos (1990) and Gillespie (2004) in

combining phylogenetic analyses and traditional community assembly models, but adds analyses of resource use and rates of character evolution between clades making up different communities.

Treefrogs represent a guild of animals in which body-size extremes among species within communities may be shaped by competition. Treefrogs are anuran amphibians that are specialized for arboreal habitat use (e.g., modified toe pads; Pough et al. 2002), and which belong to several different clades (e.g., Hylidae, Mantellidae, Rhacophoridae; Duellman and Trueb 1986). Here, we show that throughout the world's tropics, the treefrog species within a given region show similar body-size extremes to those seen in other regions (Fig. 2.1, Table 2.1, see MATERIALS AND METHODS and RESULTS for details). This pattern is replicated despite differences in the geographic location and species richness of these assemblages. Additionally, our examination of the phylogenetic composition of these assemblages (see MATERIALS AND METHODS) indicates that these body-size extremes have independently evolved multiple times throughout the world. The regional body-size extremes occur in many local communities within each region (Table 2.1), suggesting the possible importance of local-scale interactions between species. Finally, treefrogs in general appear to be dietary generalists (on arthropods) in which prey size is strongly associated with body size (e.g., Duellman 2005; RESULTS). Thus, differences in body size should allow species to reduce competition for food. Although these patterns are suggestive, a deeper investigation of the evolution of body-size extremes is necessary to test

competition's role in producing the body-size extremes seen across tropical treefrog assemblages.

Caribbean treefrogs (genus *Osteopilus* and *Hypsiboas heilprini*; 9 species total) represent a relatively simple system in which to examine the evolution of body-size extremes. One species (*Osteopilus septentrionalis*) occurs on Cuba, the Bahamas, and the Cayman Islands. Jamaica and Hispaniola each have a different set of four endemic species (Jamaica: *O. brunneus, O. crucialis, O. marianae, O. pulchrilineatus*; Hispaniola: *H. heilprini, O. dominicensis, O. pulchrilineatus, O. vastus*). On Jamiaca and Hispaniola, these sets of species are each sympatric across most of the islands (Schwartz and Henderson 1991; IUCN et al. 2006), span nearly the entire range of treefrog body sizes observed globally (Table 2.1), and have similar body-size distributions (i.e., each island shows an approximately even number of species across non-overlapping body-size categories). This indirect evidence supports the idea that these communities may be structured by competition, with resource partitioning based on body size. Additionally, the graph of time-of-colonization versus regional species richness in Wiens et al. (2006b) indicates that assemblages in the Caribbean are relatively young (as opposed to the low diversity being explained primarily by extinction). This observation suggests that these Caribbean assemblages represent an early stage in the process of community evolution in tropical treefrogs. In studying *Osteopilus*, we may be able to understand how the evolutionary radiation of body sizes began in older, more complex assemblages.

In the current study, we review the evidence for convergence in body-size extremes in treefrog communities across the world, and then analyze the patterns within the Caribbean treefrogs in depth. We first analyze morphological variation within *Osteopilus*, showing that overall body-size is the major axis of phenotypic diversity within this genus. We then examine patterns of dietary resource use, showing that *Osteopilus* are generalists in which prey size is strongly influenced by body size. Next, we characterize the apparent non-randomness of the body-size distributions of species on Hispaniola and Jamaica, establishing a link between body-size extremes within a community and even representation of species across body-size classes (a more traditional indicator of past competition; reviewed in Dayan and Simberloff 2005). To do this, we compare the fit of a statistical distribution that assumes no constraint on multiple species co-occurring within a given size category (i.e., no competition) versus one which does. We then estimate the phylogeny of Caribbean treefrogs to address the question of whether the similar body-size distributions on Jamaica and Hispaniola evolved in replicate or if species of similar body size on different islands are closely related; the former pattern would provide the strongest evidence for the deterministic evolution of body-size extremes. Subsequently, we estimate the rate of body-size evolution within Caribbean treefrogs and compare it to the South American hylids from which Caribbean treefrogs are derived. We predict that the absence of other hylid clades in the Caribbean might lead to an accelerated rate of body-size evolution among *Osteopilus* species, driving them to reduce competition by evolving to the extremes seen in mainland tropical South America (and in other communities around the world).

Alternatively, the absence of such an increased rate in *Osteopilus* might suggest that the extremes of body size on Hispaniola and Jamaica evolved (or were otherwise assembled) randomly rather than deterministically. Finally, we discuss alternate explanations that might explain patterns of treefrog body sizes apart from competition, and find little evidence to support them.

Materials and Methods

BODY-SIZE EXTREMES IN TREEFROG ASSEMBLAGES

To assess the similarity of body-size extremes found across treefrog assemblages, we compiled previously-published body-size data and species lists for regional assemblages throughout the world and for local sites within regions. We use the term "treefrog" in a general sense, indicating the treefrog ecomorph rather than a specific clade of frogs (i.e., arboreal frogs with enlarged toe pads; Pough et al. 2002). It should be noted that we excluded some lineages that might be considered "treefrogs" by some criteria; we detail these exceptions and our justification for their exclusion in Appendix 2.

We divided the world into eight regions. Each region was considered to be largely independent because nearly all of its treefrog fauna arose from either (1) a single hylid treefrog colonization within the region (Holarctic, Middle America, Australasia, the Caribbean; Wiens et al. 2006b), or (2) an independent evolutionary origin of the treefrog ecomorph (Africa, Madagascar, Southeast Asia, South America; Bossuyt et al. 2006; Roelants et al. 2007; Wiens 2007). We also present two examples of well-sampled local sites within each region to document that local assemblages may

also exhibit the size extremes typical of the regional fauna. A more detailed explanation of our literature search methods is available in Appendix 2.

We used snout-to-vent length (SVL) as a metric of body size (see next section). Because most sources of local species composition did not list the SVL data for local populations, we used maximum reported SVL for all species to maintain consistency. Note that this means that our "mimimum body size" for a clade or region is the maximum size of the smallest species (i.e., a minimum maximum size). Maximum SVL data were gathered primarily from field guides or surveys that covered broad regions, as follows: Africa (Schiøtz 1999; Channing 2001), Madagascar (Glaw and Vences 1994), Holarctic (Conant and Collins 1998; Fei et al. 1999; Arnold 2003; Stebbins 2003; Goris and Maeda 2004; Lannoo 2005), Southeast Asia and India (Berry 1975; Manthey and Grossman 1997; Daniel 2002), Australasia (Barker et al. 1995; Menzies 2006), Middle America (Duellman 2001), South America (many sources; see Table A2.3 of Appendix 2), and the Caribbean (Trueb and Tyler 1974; Schwartz and Henderson 1991).

MORPHOMETRICS

To ascertain whether body size is an important axis of morphological differentiation between Caribbean treefrog species (compared to a trait like gape width, for example), we measured specimens at the U.S. National Museum of Natural History (see Appendix 1 for specimen numbers). With one exception, between four and ten individuals of each sex of each species were measured, depending on specimen availability. Morphometric data consisted of 12 linear measurements typically used to quantify body shape and

size in treefrogs (e.g., Duellman 2001): (1) snout-to-vent length (SVL; tip of snout to anterior margin of cloaca), (2) tibia length (tip of knee to tip of heel), (3) foot length (proximal edge of inner metatarsal tubercle to tip of fourth toe), (4) head length (posterior corner of jaw to tip of snout), (5) head width (distance between posterior corners of jaw), (6) interorbital distance (width of bone between two orbits), (7) internarial distance, (8) eye-to-nostril distance (posterior tip of nostril to anterior corner of eye), (9) eye diameter (distance between anterior and posterior corners of eye), (10) hand length (proximal edge of outer palmar tubercle to tip of third finger), (11) thumb length (insertion point of thumb into hand to tip of thumb), and (12) radioulnar length (elbow to distal edge of outer palmar tubercle). All measurements were ln-transformed before analysis.

Because these measurements are potentially correlated with one another, we partitioned them into orthogonal axes of variation by performing principal components analysis (PCA; Manly 1994) on the correlation matrix. We examined the proportion of variation explained by each component and examined the loadings for each variable to interpret each component in terms of the original variables. The PCA was conducted in JMP IN (Version 4.0.4, SAS Institute, Inc., Cary, NC, 2001). Based on these analyses (see RESULTS) we use snout-vent length (SVL) as a standard measure of body size throughout the paper.

RESOURCE USE DIVERGENCE

Within an island, different species of *Osteopilus* seem to utilize similar habitats and microhabitats (USNM specimen records document multiple different species collected at the same site on the same date, results not shown; Schwartz and Henderson 1991). Thus, diet appears to be the most obvious resource axis on which adults might potentially compete. To assess the influence of body size on resource use in *Osteopilus*, we examined the diet of *Osteopilus* species and tested for (1) general overlap in the types of items consumed by each species, and (2) a correlation between body size of individuals and the size of the prey they consumed. If different *Osteopilus* species overlap in prey type and show a strong relationship between body size and prey size, then this would lend support to the idea that differences in body size between species may facilitate resource partitioning (i.e., all species potentially eat the same prey but reduce overlap in diet by consuming prey of different size).

To evaluate these two questions, we gathered data on the type and size of prey items for each species by examining the gut contents of wet-preserved (in ethanol) museum specimens. Sample sizes for each species varied based on both specimen availability and presence/absence of contents within each specimen's gut. We report sample sizes as the number of specimens we examined that contained food items within their stomachs. Sample sizes varied from N = 4–34, with a mean of 13.14. In total, we examined 227 individuals (89 with prey items) across seven species of *Osteopilus* (very few specimens of *O. crucialis* exist in museum collections, and none we examined contained prey).

For each specimen, we first measured its snout-to-vent length (SVL). We then excised its stomach and emptied the contents (intestinal contents were too digested to diagnose prey items). We identified each prey item to its taxonomic order (for Insecta and Arachnida) or class (Mammalia and Myriopoda), using Borror and White (1970) and Grimaldi and Engel (2005). If possible, we then measured the minimum size of each prey item by measuring its largest intact body part, though in many cases we were able to measure the entire organism. We used the largest body part as an index of prey size because this is the minimum size of prey that passed into the frog's digestive system without breaking (i.e., it would not have been consumed in multiple bites).

If *Osteopilus* are dietary generalists, we would expect that the diversity of prey taxa found in the diet of a given species would be related to the number of prey items sampled for that species. That is, we expected a correlation between the number of prey items for a species and the number of different types of prey (a sampling effect; reviewed in Hill et al. 1994; Rosenzweig 1995; Lyman and Ames 2007). For this analysis, we simply counted the number of prey items for each species and examined whether it was correlated with the number of orders/classes of prey items in the diet of that species. Because we found prey diversity to be linearly related to the log of sampling effort [see also, for example, the simulations of Hill et al. (1994)], we first ln-transformed the number of prey items for each species. We then estimated a Pearson product-moment correlation on these data to best estimate the effect of sampling on prey diversity (using JMP IN; see above). We also estimated a Spearman's rank correlation to test the robustness of these data to parametric assumptions. Note that

the explanatory variable we use here indicates the number of prey items found for each species. However, it is conceivable that this might violate assumptions of independence, as an individual with multiple prey items might have specialized on certain prey types (Bolnick et al. 2003) or may have consumed all its prey in a single location in which that type of prey was abundant. Thus, we also conducted analyses using the number of frog individuals in each species that had at least one prey item, rather than the total number of prey items in a species (see definition of "sample size" above). Results were qualitatively identical, so we only present results from the former analyses.

Second, we examined the diet overlap of each species, expecting that most species would be relatively similar in the proportions of each type of prey in their diet (across individuals). We used an index of proportional resource overlap

$$C_{xy} = 1 - \frac{1}{2}\sum_i \left| p_{x,i} - p_{y,i} \right|$$

to quantify the overlap of each pair of species, where $p_{x,i}$ and $p_{y,i}$ denote the proportion of the diets of species *x* and *y*, respectively, that is in category *i* (Schoener 1970; Colwell and Futuyma 1971). *C* takes values between 0 (no overlap) and 1 (complete overlap). Note, however, that we use this as a rough estimate of prey-type overlap, as this index is quite sensitive to sample size (as is any model of random sampling in which raw data are converted to proportions; F. J. Rohlf, pers. comm.), which was low for a few species. We also note that the abundance of each prey type may change

along different areas of the prey-size spectrum, and this may strongly influence our results. For example, the diet of the smallest species, *Osteopilus wilderi*, showed a preponderance of leafhoppers (Hemiptera: Cicadellidae), insects which are all generally very small (Borror and White 1970). We did not conduct statistical analyses of these data because the null distribution to which we would compare our observed overlap values is not clear.

Finally, we examined the potential correlation between body size (SVL) and prey size. If body size in *Osteopilus* is related to dietary resource use, we expect body size to be positively correlated with prey size across and within species. Thus, we conducted a correlation analysis on ln-transformed body-size and prey-size data, using the same procedure as outlined above for the sampling effect on prey diversity. Because the influence of body size on prey size should be both an intraspecific and interspecific phenomenon, we conducted two types of correlation analyses. First, we conducted correlation analyses on minimum prey size, mean prey size, and maximum prey size for each individual across all species. Note, however, that since many individuals had only one prey item, these three measures are not independent. We simply assessed all three to demonstrate the influence of body size on all aspects of the diets of individuals. Second, since individuals within a species and species within a clade may not be independent due to evolutionary history (Felsenstein 1985), we also conducted correlation analyses on the mean prey size and body size of species. For this analysis, we conducted both standard correlation analyses (i.e., using only body and prey size data) and phylogenetic generalized least squares (PGLS; Martins and

Hansen 1997) correlation analyses. These latter analyses were conducted in COMPARE (Martins 2004), which allowed us to incorporate data on intraspecific variation by using it to specify the variances in the error matrix of the PGLS model (Martins and Hansen 1997). We used the topology from our combined Bayesian analysis of *Osteopilus* and the branch lengths from the *r8s* analysis using the younger root date (see below).

COMMUNITY ANALYSES

To investigate whether body sizes of the treefrog faunas on Jamaica and Hispaniola are each structured non-randomly, we compared two models of community assembly (i.e., the process by which species are added to a local assemblage). These analyses can also be viewed as models of body-size evolution, where species are assumed to form a star phylogeny (cf. Schluter 1990). Regardless, we use the term "assembly" for brevity. Note, however, that our analyses of the rate of body-size evolution provide a more realistic analysis of community asssembly through evolutionary diversification (see below). First, in a random assembly model, the probability of occurrence of a certain body size in a local assemblage (here, Jamaica and Hispaniola) is directly proportional to the frequency of that body size within the source pool. We use mainland (South American) hylids as the species pool, given that the Caribbean species clearly are derived from South American species (Wiens et al. 2006b; this study) and to avoid the "Narcissus effect" of assembly models (i.e., a reduction in the power of the methods due to potentionally sampling from a post-competition pool when the pool is restricted to

those species that actually arrived; see Colwell and Winkler 1984). We used the hypergeometric distribution as our model of random assembly (Sokal and Rohlf 1995; see Appendix 2). Under this distribution, species are assumed to be sampled without replacement from a larger treefrog species pool, which we categorized into four body-size classes based on Duellman (2001; small: $X < 30$ mm, medium: $30 \leq X < 50$ mm, large: $50 \leq X < 80$ mm, and very large: $X \geq 80$ mm). For the species pool, we used maximum reported SVL for each species, obtained from literature sources for all nine Caribbean species as well as for 445 of the 453 South American species of the family Hylidae listed in Frost (2007). SVL data and references are presented in Table A2.3 of Appendix 2. Hypergeometric probabilities of body-size distributions for Jamaica and Hispaniola were calculated by hand. Specific details of the analysis, including the derivation of the probability models, can be found in Appendix 2.

In an alternative model, the frequency of different body-size classes in a community may significantly differ from those expected based on the source pool. For example, body sizes that are underrepresented in the mainland source pool may have a greater chance of becoming established in the island community, either through in situ evolution or dispersal. This “biased assembly” of the community may occur because of competition among species of similar body sizes (e.g., although very large species of treefrogs are relatively rare, they may have greater odds than medium-sized species of invading or evolving in a community in which a medium-sized species already exists). One can view this “biased assembly” model as a test of random versus biased dispersal or body-size evolution. To assess the probability of a biased assembly model, one must

incorporate parameters that differentially weight the odds of different body sizes occurring in the assembled community (i.e., the "bias" parameters; see below). For example, if relatively many small species occur in a resulting community but relatively few small species occur in the overall source pool, small species have been sampled from the source pool more frequently than the random expectation. A model that can account for this "sampling bias" is termed the non-central hypergeometric distribution (McCullagh and Nelder 1989; see Appendix 2). In our implementation of this model, three sampling bias parameters were estimated, each representing the sampling bias of one body-size category relative to the largest body-size category (see Appendix 2 for the justification of this parameterization). Thus, a significant departure from 1.0 for any of these parameters indicates a sampling bias in favor of a certain body size relative to another. Maximum-likelihood estimates (MLEs) and confidence intervals of the bias parameters were calculated in MatLab (ver. 6.5, The MathWorks Inc., Natick, MA), with the bias parameters (ψ_i) for a given size assumed to be equal across the two islands. MatLab code is available from the authors upon request.

The two models were compared via a likelihood ratio (*LR*) test, which can be used to compare nested models. These two models are nested because the non-central hypergeometric distribution becomes the hypergeometric distribution when all the bias parameters (as parameterized here) equal one. The *LR* is asymptotically distributed as $\chi^2_{p,\alpha}$, where p is the number of free parameters differing between the two models and α is the desired level of statistical significance. In this case, $p = 3$ and we set $\alpha = 0.05$.

One criticism of this approach would be that previous phylogenetic analyses indicated that most of the Caribbean species form a clade (Faivovich et al. 2005; Wiens et al. 2006b), and thus an assembly model assuming multiple invasions from South America or a model of evolution under a star phylogeny is not realistic (see Losos 1990 for a similar example). Although we concur with this criticism, we emphasize that this test is only documenting the low probability of seeing the even body-size spacing in Caribbean communities, given the frequencies of possible hylid body sizes; it is not meant to realistically model the actual assembly or evolution of Caribbean communities. The results of this test show that distributions of body sizes in West Indian treefrogs species differ from those in South American treefrogs and in a way that is consistent with competititively driven divergence to achieve a wide array of body sizes. We also provide a test of community assembly through random body size evolution in the section on rates of body-size evolution. This latter test complements the community assembly analyses and presents a more realistic scenario, given our phylogenetic results (see below).

PHYLOGENETIC ANALYSES

We estimated the phylogenetic relationships of *Osteopilus* to test whether the body-size extremes of species on Jamaica and Hispaniola each evolved in replicate. Seven of eight treefrog species on these two islands are within *Osteopilus*, and they represent both the largest and smallest treefrog species on each island. If the phylogeny suggests that both islands were each colonized once by *Osteopilus*, and the one

colonizing lineage gave rise to both the largest and smallest species on that island, then body-size diversification has occurred independently on the two islands. Alternatively, multiple colonizations of an island, with each species sharing a most recent common ancestor with a similar-sized species from another island, would support the idea that the body-size extremes on Jamaica and Hispaniola did not evolve independently. Note that island monophyly is not necessarily required for replicate body-size diversification. For example, if the species of one island were paraphyletic with respect to a monophyletic set of species on the other island, there might still be replicate evolution of body-size extremes on each island.

To test these scenarios, we estimated the phylogenetic relationships within *Osteopilus* using a partitioned Bayesian analysis of combined nuclear and mitochondrial DNA sequence data. We generated new sequence data using standard protocols for five mitochondrial (12S, cyt *b*, COI, ND1, ND2) and four nuclear genes (*c-myc*, POMC, RAG-1, TNS3) for all nine Caribbean species and for 14 other species of the hylid clade Lophiohylini (sensu Faivovich et al. 2005), in which *Osteopilus* is nested. To extend our sampling of Lophiohylini beyond those species available to us, additional taxa (13 species) and genes [one mitochondrial (16S), three nuclear (TYR, RHO, SIA)] were obtained from Faivovich et al. (2005), but there was also overlap between studies for ten species and three genes. Sequence data from the current study and previous studies were combined into a single matrix.

Our primary estimate of phylogeny was based on a partitioned Bayesian analysis of all the genes combined, but parsimony analyses were also conducted. We generally

prefer Bayesian analyses over parsimony because Bayesian analyses are model-based and therefore better able to account for the heterogeneous substitution processes of the 13 different genes analyzed here. Molecular and phylogenetic methods generally followed recent phylogenetic analyses of hylid frogs (cf. Smith et al. 2005, 2007; Wiens et al. 2005, 2006b). Expanded methods are available in Appendix 2, including methods of taxon sampling, molecular data collection, partitioning strategies, and phylogenetic analysis.

Because we needed phylogenies with branch lengths to estimate the rate of body-size evolution in non-*Osteopilus* hylids, we also conducted Bayesian analyses to estimate phylogenies of Cophomantini, the *Dendropsophus* clade (sensu Wiens et al. 2006b), Phyllomedusinae, and the *Scinax* clade (sensu Wiens et al. 2006b). We used data from the 325-taxon data set for hylid frogs and outgroups assembled by Wiens et al. (2006b), which had been analyzed using only parsimony.

RATE OF BODY-SIZE EVOLUTION

To test whether the rate of body-size evolution is accelerated in *Osteopilus*, we estimated the rate of body-size evolution within this clade and then compared it to tropical South American clades. *Osteopilus* are derived from a predominantly South American clade (Lophiohylini) and understanding the evolution of *Osteopilus* communities may offer insights into the early stages of the evolution of older treefrog assemblages, such as those in South America (see DISCUSSION).

Comparing rates of evolution requires trees with comparable branch lengths (i.e., in the same units) for all the relevant clades. Because somewhat different molecular data sets were available for different clades (e.g., Lophiohylini vs. other clades), we obtained comparable branch lengths across all clades by estimating a chronogram separately for each clade and then combining branch lengths across the tree by using time as a common currency (see Wiens et al. 2006a). We converted the molecular branch lengths from the Bayesian analysis of the combined data into units of time using a penalized likelihood method (PL; Sanderson 2002) in the program *r8s* (version 1.6 for Unix; Sanderson 2003). Wiens et al. (2006b) estimated a chronogram for 124 hylids using 9 fossil calibration points, including all relevant hylid fossils. However, the taxon sampling for each clade was limited. We estimated a Bayesian phylogeny for each relevant South American clade and then used the age of that clade estimated by Wiens et al. (2006b) to calibrate the ultrametric trees produced by *r8s* (Table 2.3). Wiens et al. (2006b) presented two sets of dates (age of Neobatrachia of 100 or 160 million years), and we used both to estimate two sets of divergence times for each clade. Individually-estimated Bayesian phylogenies and chronograms were manually added to the dated "backbone" chronogram from Wiens et al. (2006b) to produce a complete tree of the South American Hylidae (see Figs. A2.1 and A2.2 in the appendix).

To calculate rates of body-size evolution, we used the likelihood method of O'Meara et al. (2006) in the program *Brownie*. The parameter calculated by this method (σ^2) is the variance of character change that accumulates at each step of a Brownian motion random-walk model of trait evolution (Felsenstein 1985). Because this

parameter influences the rate at which the overall character variance in a clade accumulates, it can be thought of as the rate of morphological evolution (Martins 1994; Collar et al. 2005). Rates were calculated for (1) *Osteopilus*, (2) Lophiohylini exclusive of *Osteopilus*, (3) Cophomantini, (4) *Dendropsophus*, (5) the *Scinax* clade, (6) Phyllomedusinae, and (7) all major South American clades combined, exclusive of *Osteopilus* (i.e., groups 2–6 above).

To test for a significantly higher rate of body-size evolution in *Osteopilus*, we conducted a censored test (O'Meara et al. 2006) between *Osteopilus* and other South American hylids, from which *Osteopilus* is derived. Censored tests prune the clade of interest (here, *Osteopilus*) from the tree, estimate rates for the pruned subtree and for the larger tree without the subtree, and then compare the likelihoods of the one-rate (for the entire tree) and two-rate (as above) models. To compare the likelihoods, we used a likelihood ratio (*LR*) test. We used maximum SVL (snout-vent length) of the species as a standard index of body size (i.e., regardless of sex). Analyses using only male maximum SVL yielded similar results. SVL data were ln-transformed prior to analysis. These analyses of the rate of body-size evolution are explained in further detail within Appendix 2.

A significantly higher rate of body-size evolution in *Osteopilus* would imply a higher probability of seeing the observed body-size extremes than if body size evolved in *Osteopilus* under the lower rate for all South American and Caribbean hylids. However, we note that this, by itself, is not a direct test of how unlikely it is that we see such extremes. Thus, we calculated a simple odds ratio of the probability of seeing

such extremes given the rate of body-size evolution from the two-rate model (a separate rate is estimated for *Osteopilus*) versus the one-rate model (one rate for all South American and Caribbean hylids). This analysis provides a more realistic test of random community evolution than the community assembly models described above. Instead of simply comparing the body sizes in West Indian treefrogs to those in South American, we now ask: what is the probability of seeing the observed range of body sizes in West Indian treefrog assemblages given the rate of evolution in the South American clades? To do this, we calculated the probability of obtaining body sizes equal to or more extreme than the smallest and largest species on Jamaica and Hispaniola (four total) by sampling from a normal distribution with mean equal to the mean of all *Osteopilus* and variance obtained in one of two ways. In both cases, the variance was calculated as the product of the root-to-tip distance on the ultrametric *Osteopilus* phylogeny and the rate of evolution. In the first case, we used the rate estimated for *Osteopilus* in the above two-rate model of evolution. In the second, we used the rate estimated from the one-rate model. We then calculated an odds ratio (simply the ratio of the two probabilities) to compare the probability of seeing the observed body size extremes within the Caribbean based on the two rates. Note that although we used this test because it may be more intuitive than the rates analyses per se, it is not independent of the rates analyses, as the body-size extremes tested here were used to estimate the rates.

Results

REPEATED EVOLUTION OF BODY-SIZE EXTREMES IN TREEFROG ASSEMBLAGES AROUND THE WORLD

Combining data on local and regional species composition with body-size data from treefrogs around the world revealed similar body-size extremes in nearly every major region. Most regional assemblages (7 of 8) have a smallest species ≤ 30 mm and a largest species ≥ 100 mm, despite differing species numbers and ages (Table 2.1). This pattern is also present in local assemblages ranging from four species (Jamaica; Schwartz and Henderson 1991) to 36 species (Santa Cecilia, Ecuador; Duellman 1978). However, within the single temperate region (Holarctic), this pattern did not hold (Table 2.1), in that very large species (>80 mm) are absent. Because regions were chosen as areas of independent diversification (based on phylogenetic information), our results indicate that the large body size range characteristic of tropical assemblages has evolved a minimum of seven times, including in the Caribbean, South America, Middle America, Southeast Asia and India, sub-Saharan Africa, Madagascar, and Australasia (Fig. 2.1).

MORPHOMETRIC ANALYSES

Principal components analysis (PCA) indicated that overall body size is the major source of morphometric variation among species within *Osteopilus*. The first PC axis (PC1) accounted for 97.7% of the variation, with all other axes each accounting for < 1% of the total variation. The loadings for PC1 were all positive and similar for all

variables (mean = 0.2887, range = 0.2829–0.2913), so we consider this axis as a measure of overall body size. Thus, body size seems to be the major axis of morphometric differentiation within *Osteopilus*. Given that all other variables were strongly correlated with SVL (results not shown) and that SVL data were available for hundreds of hylid species (whereas data from PC1 were only available for *Osteopilus*), we simply used SVL as a standard proxy for body size in subsequent analyses.

DIVERGENCE IN DIETARY RESOURCE USE

Within *Osteopilus*, we found many different prey types (13 orders/classes total), but most species consumed a high proportion of coleopterans (beetles) and orthopterans (crickets, grasshoppers). We found a strong correlation between the number of prey items found within each species and the prey diversity for that species (Pearson correlation (r) = 0.94, P = 0.0017; Spearman's rank correlation (r_s) = 0.90, P = 0.0056; Fig. 2.2a). Prey overlap was generally quite high among species (Table A2.1 in the appendix), with the exception of *O. pulchrilineatus* (which had no coleopterans, but few samples; N = 6) and *O. wilderi* [which consumed many homopterans, which are generally much smaller (here, < 4.73 mm) than the smallest prey consumed by the individuals of most other species; Fig. 2.2]. These observations support the idea that *Osteopilus* are dietary generalists that utilize the same general prey types. Finally, across all individuals sampled (i.e., across and within species), we found a strong correlation between body size and prey size within *Osteopilus* (Fig. 2.2b; N = 89; minimum prey size: r = 0.55, P < 0.0001; r_s = 0.60, P < 0.0001; mean prey size: r =

0.56, $P < 0.0001$; $r_S = 0.63$, $P < 0.0001$; maximum prey size: $r = 0.55$, $P < 0.0001$; $r_S = 0.61$, $P < 0.0001$). This correlation remained strong in interspecific correlation analyses of mean treefrog body size and prey size (standard correlation: $r = 0.90$, $P = 0.0053$; PGLS: $r = 0.90$, $P = 0.0053$).

COMMUNITY ASSEMBLY ANALYSES

A comparison of the body-size distributions of species on Jamaica and Hispaniola with that of South American hylids in general suggests that Caribbean assemblages have a more even representation of species across body-size classes than expected by random assembly or by evolution. Although the *LR*-test was not significant (Table 2.2), two of the individual bias parameters were significantly different from 1, indicating a statistically significant bias in favor of oversampling the underrepresented very large species and undersampling the highly represented small and medium species (Table 2.2). Thus, in Caribbean assemblages, fewer species than expected under the random assembly model occur within the small and middle size classes, whereas more species than expected occur within the very large body-size category. The discrepancy between the significance of the bias parameters and the lack of support for the overall biased model is most likely due to a lack of statistical power as a consequence of the small number of species on each island in the Caribbean (e.g., artificially doubling the number of species in the Caribbean assemblages produced both highly similar bias parameters and a significant *LR*-test in favor of the biased assembly model).

PHYLOGENY WITHIN MAJOR SOUTH AMERICAN CLADES

Bayesian analyses of Cophomantini, the *Dendropsophus* clade, the *Scinax* clade, and Phyllomedusinae are generally congruent with previous analyses of these clades based on parsimony (Faivovich et al. 2005; Wiens et al. 2006b). Bayesian posterior probabilities (Pp) were high throughout most trees for Cophomantini, *Scinax*, and Phyllomedusinae, whereas resolution was weakly supported for some deep nodes within the *Dendropsophus* clade. The phylogenies for these clades are depicted in Figures A2.1 and A2.2 of Appendix 2.

PHYLOGENY OF *OSTEOPILUS* AND COMMUNITY ASSEMBLY WITHIN THE CARIBBEAN

Of 9618 base pairs (bp) of combined data, we excluded 419 due to ambiguous alignment in the 12S and 16S genes. Of the remaining characters, 2590 were parsimony-informative. Separate Bayesian analyses of the 4172 bp of nuclear data and the 5446 bp of mitochondrial data were mostly congruent, with no strongly supported incongruence (Fig. 2.3). Separate parsimony analyses of the two data sets were generally concordant with the Bayesian results. Additionally, the Bayesian analysis of the combined data produced a topology with many strongly supported nodes that were congruent with trees from the separate analyses of the nuclear and mitochondrial data (Fig. 2.3). Parsimony bootstrap proportions generally were low for deep nodes, but most previously recognized subclades (Faivovich et al. 2005) were strongly supported (Fig. 2.3).

Osteopilus and an *Osteocephalus-Tepuihyla* clade were strongly supported as sister taxa. Congruent with the topology of Faivovich et al. (2005), we found strong support for a clade of *Trachycephalus* and *Phrynohyas*, but with each genus polyphyletic. This result supports the proposed synonymy of *Phrynohyas* with *Trachycephalus* (Faivovich et al. 2005).

Osteopilus was strongly supported as monophyletic by both Bayesian Pp and parsimony bootstrap. Within *Osteopilus*, most nodes were strongly supported by Bayesian Pp, but only the sister relationship of *O. brunneus* and *O. crucialis* was strongly supported by parsimony. The low parsimony support seems to be associated with the mitochondrial data; parsimony analysis of the nuclear data alone gives a tree similar to the combined Bayesian phylogeny, and with relatively strong support (results not shown). Based on the Bayesian analysis of the combined data, the species of Jamaica are monophyletic and nested within a paraphyletic grouping of Hispaniolan *Osteopilus*, and the Cuban species *O. septentrionalis* is sister to the Jamaica-Hispaniola clade. These results suggest that body-size diversification on Jamaica and Hispaniola occurred in replicate on each island, as predicted under the model of competitively driven divergence (Fig. 2.4).

RATES OF BODY-SIZE EVOLUTION

Comparison of rates of body-size evolution within *Osteopilus* and South American treefrog clades showed a highly elevated rate within *Osteopilus*. The rate within *Osteopilus* (0.0150) was more than twice that of any other South American hylid group

[range = 0.0019–0.0072; all rates presented here are for the younger set of divergence dates and are in units of $(\ln mm)^2$ per million years; see Table 2.3 for full results]. A likelihood ratio test indicated that a two-rate model for body-size evolution within South American and Caribbean hylids, with one rate for *Osteopilus* and one for the other hylids, significantly fit the data better than a model with a single rate for the entire group ($LR = 9.79 > \chi^2_{1,0.05} = 3.84$, $P = 0.0016$; two rates: *Osteopilus* = 0.0150, SA hylids = 0.0040; single rate: 0.0045).

The odds ratios indicated that it was much more likely for the extreme body sizes on Hispaniola and Jamaica to evolve when *Osteopilus* had its own rate of evolution than under the common rate for South American and Caribbean hylids together. For the younger set of divergence dates, the odds in favor of the two rate model were $1.52 * 10^{32}$ to 1. For the older dates, the odds were $1.36 * 10^{36}$ to 1. That is, if we assume in the West Indian treefrogs the rate of body-size evolution estimated for all treefrogs , there is a very low probability of observing the extreme body sizes we see in *Osteopilus*. Thus, taking an evolutionary view of community assembly, the body-sizes observed in the West Indian treefrogs are more divergent than expected.

Discussion

Competition is thought to be an important force driving divergence among species (Taper and Case 1985; Doebeli 1996; Schluter 2000b). However, experimental studies of this phenomenon may be problematic in that the taxa that have diverged the most by this process are expected to compete the least today. As a result, phylogeny-based

investigations that link replicated patterns in communities to the evolutionary processes that produce them offer an important but underutilized approach to reveal the role of different processes as they relate to present-day phenotypic diversity (Losos 1994, 1996). Here, we introduce the idea of studying the evolution of body-size extremes within and among assemblages as a way to infer past competition. Competitive diversification of a trait should be in the direction of extreme trait values (e.g., away from an intermediate initial phenotype; Taper and Case 1985; Doebeli 1996), leading to the prediction that communities in which competition has been historically important are expected to converge on similar body-size extremes. In this study, we examine the evolution of body-size extremes in treefrogs in order to link community patterns to the mechanisms that might be producing them.

We have shown that body-size extremes are similar across tropical treefrog assemblages around the world (Fig. 2.1; Table 2.1). Furthermore, the extremes of body size within these assemblages have been realized through convergent body-size evolution a minimum of eight independent times (six outside the Caribbean and two within).

We can begin to understand the evolutionary origins of the typical body-size extremes in treefrog communities through examining body-size diversification within the simplified system offered by Caribbean treefrogs. Based on studies of other treefrogs (e.g., Duellman 2005), we predicted that *Osteopilus* species were dietary generalists that overlapped substantially in prey type (e.g., different insect orders), but which avoid dietary overlap by consuming prey of different sizes, depending on their body sizes.

Our analyses of diet are consistent with the idea that *Osteopilus* species diverge in body size to utilize prey of different sizes. Our community assembly analyses suggest that Caribbean communities have more very large and fewer small- and medium-sized species than expected based on the body-size distribution of South American treefrogs (Table 2.2). This result illustrates that we see very large species (i.e., those representing the upper size extremes) despite the fact that very large species are rare among the South American hylids from which *Osteopilus* is derived. Conversely, we see fewer small- and medium-sized species, despite the fact that such species have evolved the most frequently in South America. Furthermore, the phylogeny of *Osteopilus* shows that the diversification of body sizes on Jamaica and Hispaniola each occurred in replicate, with species on the same islands more closely related than species of similar body size on different islands (Fig. 2.4). In particular, our phylogeny suggests that Jamaica and Hispaniola were each colonized only once by *Osteopilus* species, and that each colonizing lineage evolved to produce both the largest and smallest species on their respective islands. Concordant with these results, the rate of body-size evolution is very high in *Osteopilus* relative to all other major South American hylid clades, considered individually and together (Table 2.3). Our results suggest rapid, deterministic phenotypic diversification in *Osteopilus* following colonization of a region in which hylid treefrogs did not previously occur, leading to a range of extreme body sizes among species similar to those seen in older communities in South America and elsewhere around the world.

CAUSES OF BODY-SIZE DIVERSIFICATION WITHIN THE CARIBBEAN

We suggest that our results are most consistent with the idea that competitive interactions may have been the primary force driving body-size diversification in treefrogs, or at least within *Osteopilus*. Other processes besides competition, such as diversification driven by predators or by physiological differences, seem to be less parsimonious explanations for the overall patterns of body-size evolution (discussed in detail below). Many theoretical (e.g., Slatkin 1980; Taper and Case 1985, 1992; Doebeli 1996; Dieckmann and Doebeli 1999) and empirical (e.g., Schluter 2000a; Gray and Robinson 2002; Bolnick 2004) studies have demonstrated the effects of competition on phenotypic diversification. Upon invading a new habitat, such as an island in the Caribbean, abundant ecological opportunity may be present. As competition intensifies within the ancestral colonizing body size (i.e., from an increasing number of individuals within a species or from multiple species of similar size), selection for larger or smaller individuals may exist to exploit underutilized resources (Simpson 1953; Schluter 1988, 1996, 2000a,b; Losos et al. 2006). This selection would favor an expansion of the body-size range among or within species regardless of the size of the original colonist, since expanding the body-size range within a community can be the result of decreasing minimum size, increasing maximum size, or both. Note, also, that the idea of ecological release suggests that a lack of competition experienced by an ancestral colonizing species may allow for “exploration” of the resource spectrum, with drift leading conspecifics or other species to different sizes initially (Arthur 1987).

Ecological studies to further test the competition hypothesis are also important. For example, one could conduct a manipulative experiment in which degree of body-size similarity among species is compared to a fitness proxy under resource-limited conditions (e.g. for food; see below). Alternatively, one could estimate selection on body size in different populations of a widespread species which occurs both allopatrically and sympatrically with other species of *Osteopilus* (e.g. *Osteopilus brunneus*), with the expectation that stabilizing selection may be stronger in populations that co-occur with both larger and smaller species than in populations that are allopatric. Unfortunately, many of the most interesting and relevant ecological studies of *Osteopilus* would be difficult given the recent declines and current rarity of many of the largest and smallest Hispaniolan and Jamaican species (IUCN et al. 2006). The few studies of competition in adult frogs have shown dramatic effects of interspecific competition on the abundance of species with similar habitat and resource use (Inger and Greenberg 1966), including studies in hylid treefrogs (Meshaka 2001). In particular, exotic populations of *Osteopilus septentrionalis* in Florida may compete strongly with co-occurring hylid species (Meshaka 2001). If body-size divergence is still an ongoing process within *Osteopilus*, we might expect to see current evidence of competition. However, we also emphasize that while current competition among species would further support the role of competition in body-size evolution, this would not directly demonstrate what happened in the deep history of *Osteopilus*. That is, it does not directly follow that processes that occurred millions of years ago are still important agents of selection today, especially given a dramatic evolutionary response to that past

selective pressure. For example, a deep history of body-size divergence might be the case if the divergence was associated with speciation in *Osteopilus* and occurred at a similar point in the past.

Given our hypothesis of competitive diversification in Caribbean treefrogs, for what resource might they be competing? We suggest that competition for food may be the primary driver of body-size diversification. In amphibians in general and treefrogs in particular, prey size is strongly associated with body size (e.g., Toft 1980, 1985; Lima and Moreira 1993; Duellman 2005) and few instances of prey specialization have been documented (Inger and Greenburg 1966; Toft 1981, 1985; Duellman 2005; but see Lima and Magnusson 1998). We found similar results in *Osteopilus*, with no discernible specificity in diet among species and prey sizes that are strongly positively correlated with body size [see also Meshaka (2001) for similar results in *Osteopilus septentrionalis* alone]. Thus, resource partitioning in *Osteopilus* is most likely to be determined by prey size rather than type. Because gape width may limit the size of the largest prey item consumed by an individual, larger body size allows an individual to potentially consume a greater range of prey items (Schoener and Gorman 1968; Gittleman 1985). At the other end of the size spectrum, small body size may confer a selective advantage in feeding on small prey, as it is energetically inefficient for sit-and-wait predators (such as treefrogs; Duellman and Trueb 1986) to consume prey that are small relative to their body size (Griffiths 1980). Because the positive prey-size/body-size relationship holds for many insectivorous tetrapods (e.g., birds: Brandl et al. 1994; lizards: Roughgarden 1974; Schoener 1967, 1968; Vitt et al. 2000, 2005; Duellman 2005; mammals: Fisher

and Dickman 1993; Churchfield et al. 1999; salamanders: Burton 1976; Krzysik 1979; Toft 1985), competitive diversification along a body-size continuum may be a general phenomenon (e.g., Losos 1994; Radtkey et al. 1997; Melville 2002; Kozak et al. 2005).

We acknowledge that multiple agents of selection may have influenced body-size evolution in *Osteopilus*. However, other factors seem unlikely to explain the repeated evolution of extreme body sizes, for a variety of reasons. For example, all other things being equal, larger body size generally confers higher resistance to evaporative water loss in frogs (Shoemaker 1992). Thus, species of different body sizes might partition habitats based on humidity, with smaller species constrained to remain within more mesic habitats and large species allowed to utilize comparatively drier habitats. However, on both Hispaniola and Jamaica, the largest and smallest species are the most restricted in geographic distribution, occurring primarily within montane mesic forest, with only the intermediate-sized species inhabiting the xeric areas of each island (Schwartz and Henderson 1991).

A second alternative explanation is predation. For example, large body size may offer a refuge from small predators (Sondaar 1977), and small body size may have evolved to facilitate hiding from predators. However, even though predation has been shown to affect morphological diversification (e.g., Hendry et al. 2006; Langerhans et al. 2007), it is not clear how predation would lead to evolution of a dramatic range of body sizes in sympatry, as the body size morph that experiences the most predation would presumably be lost. Indeed most previous studies have demonstrated the influence of predation on morphological divergence between populations in different locations (e.g.,

Hendry et al. 2006; Langerhans et al. 2007), but have not shown that it yields a range of different phenotypes in sympatry (as we see in *Osteopilus* and other treefrogs; but see Nosil and Crespi 2006).

Third, body-size evolution could be a consequence of reproductive character displacement (sensu Gerhardt and Huber 2002) during speciation or secondary contact after speciation, given that body size may be important in reproductive isolation in frogs through its effects on the dominant frequency of mating calls (Ryan 1988). Indeed, body-size divergence has been associated with reproductive character displacement in frogs (Hoskin et al. 2005; Pfennig and Pfennig 2005). However, in these cases, body size changes are much smaller than we see across *Osteopilus* (20% in Hoskin et al. 2005; ~8% in Pfennig and Pfennig 2005; but an average of 57% between successively larger *Osteopilus* species; Table A2.6 in the appendix). Thus, it appears that reproductive isolation can be achieved with minor changes in body sizes, and that reproductive character displacement is unlikely to explain the vast range of body sizes that has evolved repeatedly in *Osteopilus*. Furthermore, both cases involve changes primarily in male size (Hoskin et al. 2005; Pfennig and Pfennig 2005). In *Osteopilus*, the large range of body sizes has evolved in both sexes (Jamaica: males = 27.3–100 mm, females = 28.7–122 mm; Hispaniola: males = 39.5–108.8 mm, females = 42.8–141.9 mm). Additionally, the rate of body-size evolution in male *Osteopilus* is similar to that for females (0.0103 vs. 0.0150, respectively; DSM, unpublished), especially compared to the rates for South American clades (range: 0.0019–0.0072; see RESULTS). These patterns are consistent with body size changing to reduce competition in diet, but not

reproductive character displacement. Finally, we are unaware of any evidence that assigns a primary role to reproductive character displacement in structuring the body sizes of entire assemblages, particularly in the case in which body-size distributions are convergent. Thus, although reproductive character displacement might have played some role in the history of body-size evolution in *Osteopilus*, we do not expect this process to have played a major role in producing the large range of body-sizes in both males and females that we see today.

Finally, other explanations for trends in body-size evolution on islands, such as selection for smaller size due to resource limitation on islands (Wassersug et al. 1979; Lomolino 1985), typically focus on unidirectional size changes between island and mainland populations, rather than the diversification of a range of body sizes on a single island, and are thus unlikely to apply here. Although a combination of factors could also have an important influence on body size evolution, it seems less likely that this would lead to similar patterns around the world than a simpler explanation that is also consistent with this pattern (i.e., competitively-driven divergence).

We have asssumed that competition within and between Caribbean hylid species was important in driving their body-size evolution, as was the absence of other hylid clades in the Caribbean. Competition (or lack thereof) with other groups of organisms seems unlikely to have been important. For example, the only arboreal frogs in the West Indies are hylids and *Eleutherodactylus* (Schwartz and Henderson 1991), and we have no evidence that *Eleutherodactylus* have influenced patterns of body size

evolution in *Osteopilus*. Furthermore, *Eleutherodactylus* co-occur with hylids in South and Middle America as well (e.g., Duellman 2001, 2005).

COMPETITION AS A CONSTRAINT ON FURTHER BODY-SIZE DIVERSIFICATION

While our analysis of Caribbean treefrogs suggests that competition may drive body-size divergence, it also suggests that competition may constrain body-size divergence within South America. The hylids of Hispaniola and Jamaica show similar ratios between the body sizes of successively larger species (results not shown), with only a single instance of the evolution of each general body size class on each island. An examination of the mean body size and rates of evolution in the major hylid clades of South America (Table 2.3) indicates that although body size is diverse across clades, its rate of evolution has been low within clades. Thus, in South American hylids, body size apparently diversified in the early history of the major clades, but has evolved little since; species of different body-size classes are largely confined to distinct clades. At most localities in South America, the smallest species are of the genera *Dendropsophus* and/or *Scinax*, and the largest species are from Cophomantini, Phyllomedusinae, and/or Lophiohylini (e.g., Duellman 1978; 2005; Heyer et al. 1990). Because all of the South American communities we reviewed here contain members of these major clades, we expect that this general taxonomic composition of communities may be very old. Thus, the long sympatry of many hylid clades, each filling a different generalized body-size role within a community, may have led to limited selection for body-size diversification

within the major clades of hylids in South America. In this way, competition may be secondarily acting to constrain body-size diversification.

Despite the limited body-size divergence within South American hylid clades over time, there has been considerable diversification of species within these clades (all South American groups in Table 2.3 have at least 55 species). Our results add to the increasing number of studies which have found a pattern of species diversification with limited phenotypic diversification after an initial diversification of morphotypes, including studies of lizards (Losos et al. 2006) and *Desmognathus* salamanders (Kozak et al. 2005). In many cases, the recent species diversification has been shown to have occurred primarily as allopatric speciation with relatively little phenotypic differentiation. In the same such cases, the phenotypically undifferentiated species have remained allopatric, such that sympatric species still show no ecological overlap (see Losos et al. 2006 for an extensive discussion of this phenomenon). In contrast, in South American hylid treefrogs, many species of the same clade and body-size class co-occur within present-day assemblages (see, for example, Duellman 1978, 2005; Heyer et al. 1990). Thus, the pattern in hylid treefrogs seems to be different from those documented previously. The generality of this pattern in hylids could be studied in other regions in which hylids are the predominant treefrogs, such as Middle America and Australasia. In both regions, hylids have diversified to the typical body-size extremes (Table 2.1) and have speciated extensively (Wiens et al. 2006b).

UNRESOLVED QUESTIONS

Our finding of the similarity of body-size extremes across tropical treefrog assemblages opens up a number of interesting questions for future research. What ecological, evolutionary, and developmental factors influence the extremes of body size that are so common across treefrog communities? For example, why do we often see ~20-30 mm as the smallest size and ~100 mm as the largest size? Why are there no species within the largest size class in temperate regions?

Similarly, other aspects of Caribbean treefrog diversification present interesting unanswered questions. First, how did speciation happen within *Osteopilus*? Given the within-island diversification found in this study, extensive distributional overlap of Caribbean treefrogs (Schwartz and Henderson 1991), and little evidence for vicariance events on Jamaica and the main landmass of Hispaniola (Glor et al. 2003; Losos 2004), it would seem that Caribbean treefrogs may be a candidate for sympatric speciation and divergence (see also Hedges 1989 for *Eleutherodactylus* and Losos 2004 for *Anolis*). However, there are relatively few strongly-supported cases of sympatric speciation (Coyne and Orr 2004), and more evidence is necessary to rule out the possibility of allopatric divergence (Losos 2004).

Second, given four species of treefrogs on both Jamaica and Hispaniola, why are there no native treefrogs on Puerto Rico and only one on Cuba? This is particularly surprising given that opportunities for allopatric speciation (in the form of vicariance) are well-documented for Cuba (Glor et al. 2004). Additionally, *Osteopilus septentrionalis* is

the most basal species of *Osteopilus*; thus, relative to other *Osteopilus*, this species has had ample “time for speciation” (Stephens and Wiens 2003).

Finally, at a larger scale, why are there so few species of treefrogs within the Caribbean? This is surprising given the extensive diversification of other Caribbean taxa, such as *Anolis* lizards (143 species; Williams 1983; Losos and Schluter 2000), *Sphaerodactylus* geckoes (75 species; Hass 1991), and *Eleutherodactylus* frogs (147 species; Hedges 1989; IUCN et al. 2006; Heinicke et al. 2007). Wiens et al. (2006b) found a strong correlation between species richness and the timing of colonization of regions in which hylid frogs occur, with the Caribbean being one of the most recent regions to be invaded by hylids. Further research should examine whether this relationship occurs within the Caribbean across different groups of organisms, such as *Anolis* and *Eleutherodactylus*.

CONCLUSIONS AND PROSPECTS

In this paper, we develop a general methodology to study the role of past competition in explaining evolutionary divergence among species. Our approach is complementary to experimental studies of the role of competition in character divergence, but may be particularly applicable to cases in which competition is currently weak, absent, or difficult to measure. We apply this four-part approach to the evolution of body-size extremes in treefrog communities and find support for a strong role of competition in the evolutionary divergence of body size in *Osteopilus*. Although we cannot prove that competition caused selection for extreme body sizes over millions of

years, our data and analyses suggest that it is the best-supported explanation for the pattern of body-size divergence among extant Caribbean treefrog species. The replicate evolution of similar body-size extremes may be relevant to many systems, including communities that no longer show classic signatures of competition in body size (e.g., even spacing) or clades that consist of a single ecomorph that has diversified in body size. Additionally, although we focus on body-size evolution here, our approach can be extended to many other characters. In particular, our approach can be used in any system in which significant niche-partitioning among species may be achieved through divergence in a single, quantitative character (e.g., trophic morphology, habitat use).

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Table 2.1. Summary of literature review of body-size extremes in worldwide treefrog assemblages. Most regional assemblages have a smallest species < 30 mm and a largest species > 100 mm; similar body size extremes also occur in most of the local communities presented here. Clade ages are estimated crown-group ages of the predominant treefrog clades in each region (Caribbean: *Osteopilus*; South America: Hylidae; Middle America: Middle American Clade; Holarctic: *Hyla*; SE Asia and India: Rhacophoridae; Australasia: Pelodryadinae; Africa: Brevicipitidae sensu Bossuyt et al. (2006); Madagascar: *Boophis*). The one exception is *Boophis*, for which we present the stem-group age (due to limited taxon sampling). The ages for the first five regions correspond to those estimated using the younger and older root calibration points in Wiens et al. (2006b) and the current study. The ages for SE Asia and India and Madagascar correspond to smallest and largest estimates of Bossuyt et al. (2006) (their "estimate 2" and "estimate 3"). The age for Africa is from Fig. 3 of Bossuyt et al. (2006).

Region[a]	Body size (mm)			Species richness[b]	Age of predominant clade (mya)		Reference
	Smallest	Largest	Difference				
Caribbean	28.7	141.9	113.2	9	24.35	32.51	
Hispaniola	42.8	141.9	99.1	4			Schwartz and Henderson 1991
Jamaica	28.7	122	93.3	4			Schwartz and Henderson 1991
South America	15.8	135	119.2	453	64.97	92.90	
Boracéia, Brazil	25	104	79	26			Heyer et al. 1990
Santa Cecilia, Ecuador	23	132	109	36			Duellman 1978
Middle America	22.1	110.4	88.3	153	44.72	60.65	
Barro Colorado Island, Panamá	27.8	113.7	85.9	10			Rand and Myers 1990
Chamela, Jalisco, México	28	113.7	85.7	8			Duellman 2001
Holarctic	33	70	37	31	31.85	41.65	
Okefenokee Swamp, United States	44	70	26	5			Wright 2002
Ishigakijima and Iriomotejima, Japan	37	67	30	4			Goris and Maeda 2004
Australasia	16	141	125	174	42.37	60.40	
Magela Creek system, Australia	16	110	94	15			Tyler et al. 1983

Huon Peninsula, Papua New Guinea	40	141	101	12			Zweifel 1980
Southeast Asia and India	16	115	99	283	60.00	62.80	
Phong Nha-Ke Bang National Park, Vietnam	32	115	83	11			Ziegler et al. 2006
Nanga Tekalit, Sarawak, Borneo	35	90	55	10			Lloyd et al. 1968
Madagascar	23	103	80	65	63.10	66.70	
Ranomafana National Park	29	103	74	10			Andreone 1994
Andohahela National Park	32	103	71	13			Nussbaum et al. 1999
Africa	20	110	90	242	91.00		
Arabuko-Sokoke Rain Forest, Kenya	21	90	69	12			Drewes 2007
Impenetrable Forest, Uganda	21	62	41	15			Drewes and Vindum 1994

[a]Extremes for entire region includes only species endemic to that region, whereas local assemblage (indented) extremes include all species.
[b]Includes only number of native treefrog species

Table 2.2. Results of community assembly analyses: non-central model parameter estimates (MLE), 95% confidence intervals for each parameter, and results of model comparisons using the likelihood-ratio (LR) test. *p* denotes the number of free parameters in each model, whereas *P* is the traditional *P*-value. MLEs of the bias parameters indicate that very large species are more common in Caribbean communities relative to their frequency in South America compared to small, medium, and large species. Bias parameter confidence intervals which exclude 1.0 indicate statistical significance (i.e., when all $\psi_i = 1.0$, the non-central model collapses to hypergeometric). This result suggests that the even distribution of body sizes observed within the Caribbean is not expected by chance. The lack of statistical significance of the *LR*-test is likely due to the small number of species within the Caribbean (see RESULTS for details).

Parameter	MLE	95% CI
ψ_0	0.099	(0.006,0.790)
ψ_1	0.108	(0.012,0.668)
ψ_2	0.180	(0.023,1.112)

Model	ln likelihood	*p*	*LR*
Hypergeometric	-7.95	0	6.24
Non-central Hypergeometric	-4.83	3	

$P = 0.10$

Table 2.3. Mean of maximum snout-to-vent length (SVL) of species within a clade and maximum-likelihood estimates of rates of body-size (maximum SVL) evolution in clades of South American and Caribbean treefrogs. Despite considerable diversity in SVL across South American groups, rates of body-size evolution are substantially lower within South American groups than within *Osteopilus*, considered both individually (individual rate estimates) and together (*LR*-tests).

		Ages[b]		Rates[c]	
Group	SVL[a]	Younger root	Older root	Younger root	Older root
Cophomantini	53.3 ± 17.4	51.67	73.55	0.00330	0.00227
Dendropsophus	28.9 ± 8.4	35.65	50.02	0.00193	0.00138
Phyllomedusinae	62.0 ± 22.7	34.39	49.76	0.00621	0.00429
Scinax clade	33.9 ± 8.5	53.77	75.95	0.00237	0.00169
Lophiohylini (without *Osteopilus*)	57.1 ± 24.5	35.90	48.59	0.00720	0.00522
Osteopilus	86.3 ± 46.1	24.35	32.51	0.01500	0.01128
South American hylids[d]	45.3 ± 20.6	64.97	92.90	0.00404	0.00284
			LR[e]	9.79	10.62
			P =	0.0016	0.0008

[a]Reported as mean (± one standard deviation) SVL of entire clade, calculated as the average of the maximum reported SVL of each species within each clade.
[b]Ages of the most recent common ancestor of all the species sampled within this study, in millions of years ago.
[c]Root categories refer to the two sets of root dates used to calibrate the chronograms for clades (see text for details).
[d]Includes the Cophomantini, *Dendropsophus*, Phyllomedusinae, *Scinax* clade, and Lophiohylini (without *Osteopilus*)
[e]Likelihood ratio tests (*LR*, as defined in Appendix 2) refer to a comparison of a two-rate model (one for *Osteopilus*, one for South American hylids) to a one-rate model (a single rate for both groups)

1

Figure 2.1. Body-size extremes of treefrog assemblages around the world. Dashed lines delineate approximate boundaries of regions of independent treefrog evolution (see Materials and Methods). Body sizes of cartoon frogs are directly proportional to the body size of the largest and smallest species within the each group (corresponding to Table 1). Note that lines leading from each legend point to arbitrary locations within regions. We use Brevicipitidae sensu Bossuyt et al. (2006).

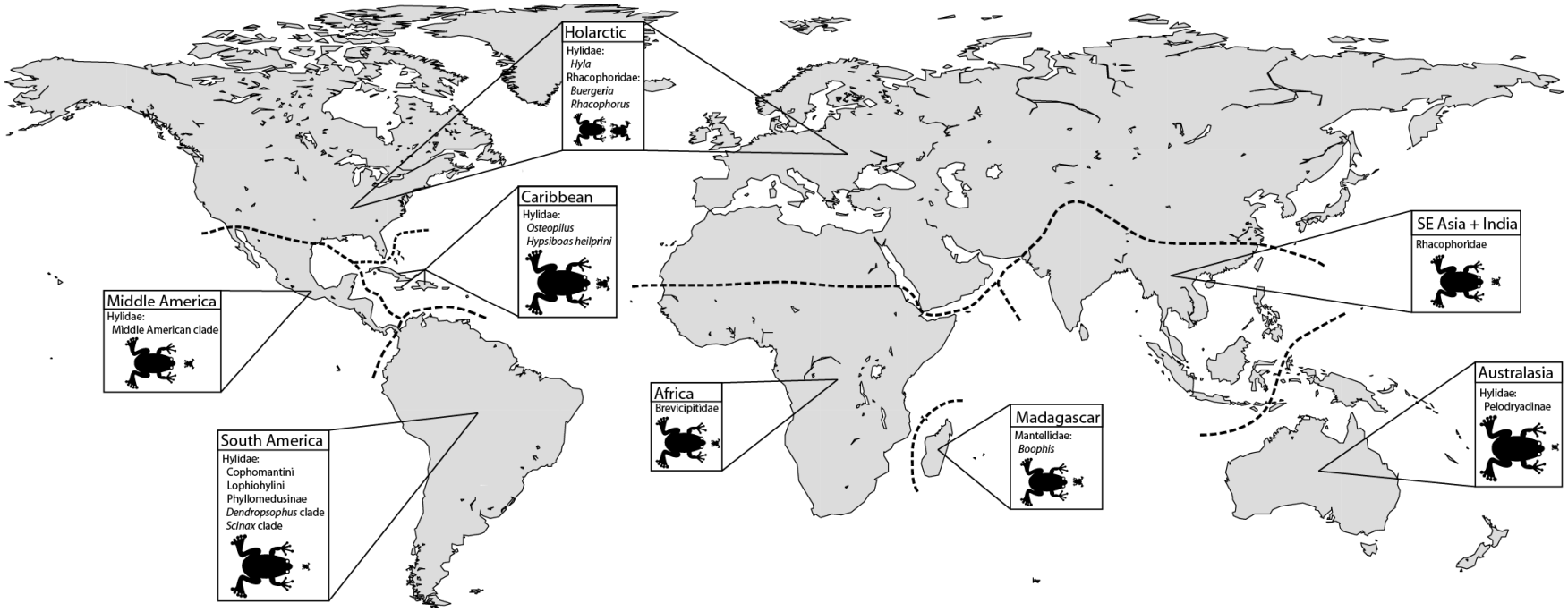


Figure 2.2. (a) Plot of total number of prey items sampled versus the number of different types of prey (identified to taxonomic order or class) found for each species. (b) Plot of body size versus mean prey size for resource use analysis. Body size is represented as ln(snout-to-vent length in mm), and prey size is additionally ln-transformed. Bars represent one standard error of the mean for both body size and prey size.

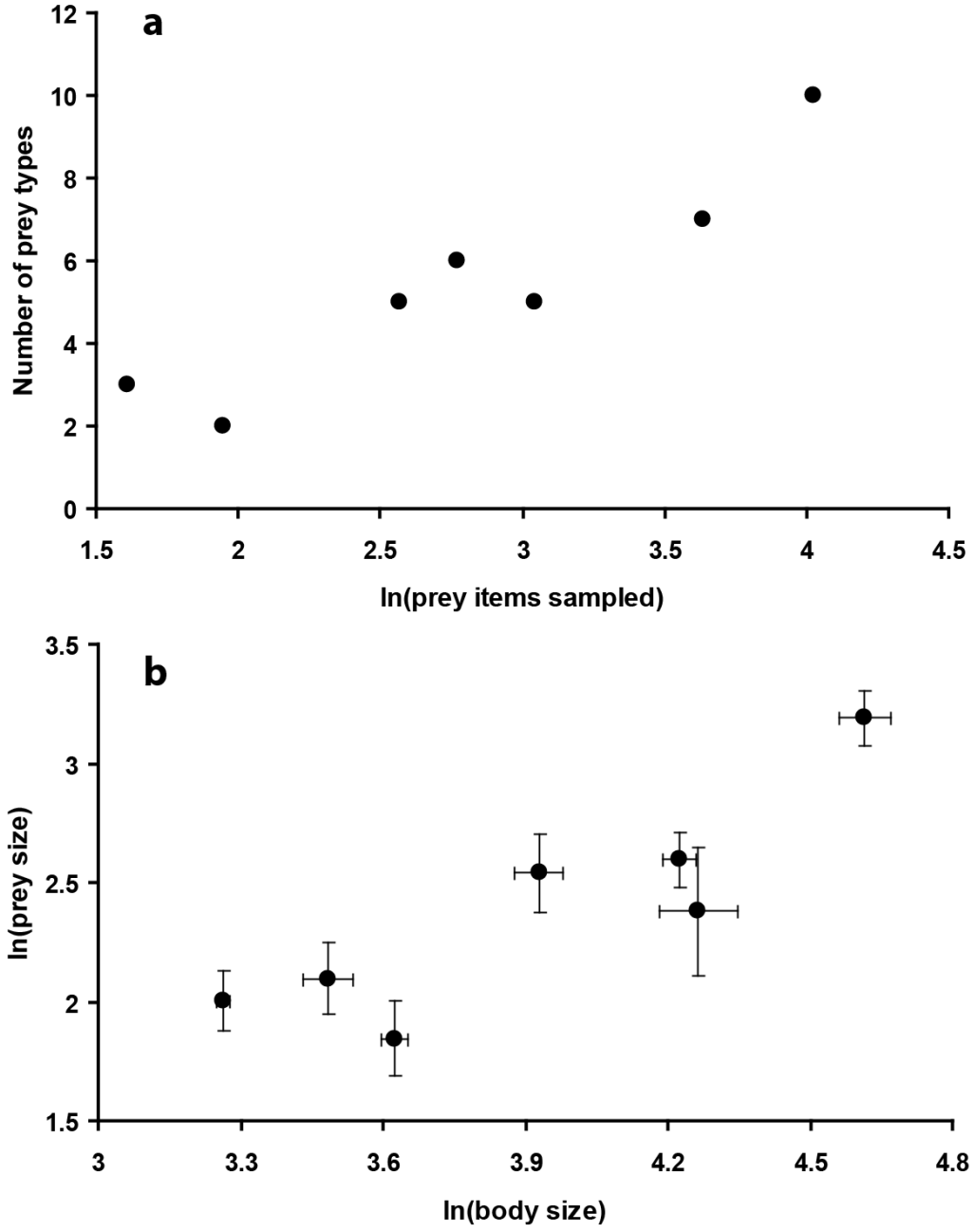


Figure 2.3. Phylogeny of Lophiohylini (Hylidae) based on combined Bayesian analysis of seven nuclear and six mitochondrial genes. Values above branches indicate the Bayesian Pp, and those below branches indicate parsimony bootstrap proportions for concordant clades. Nodes that were also recovered in separate Bayesian analyses of the mitochondrial and/or nuclear data are labeled with symbols. Unlabeled nodes were unique to the combined data analysis.

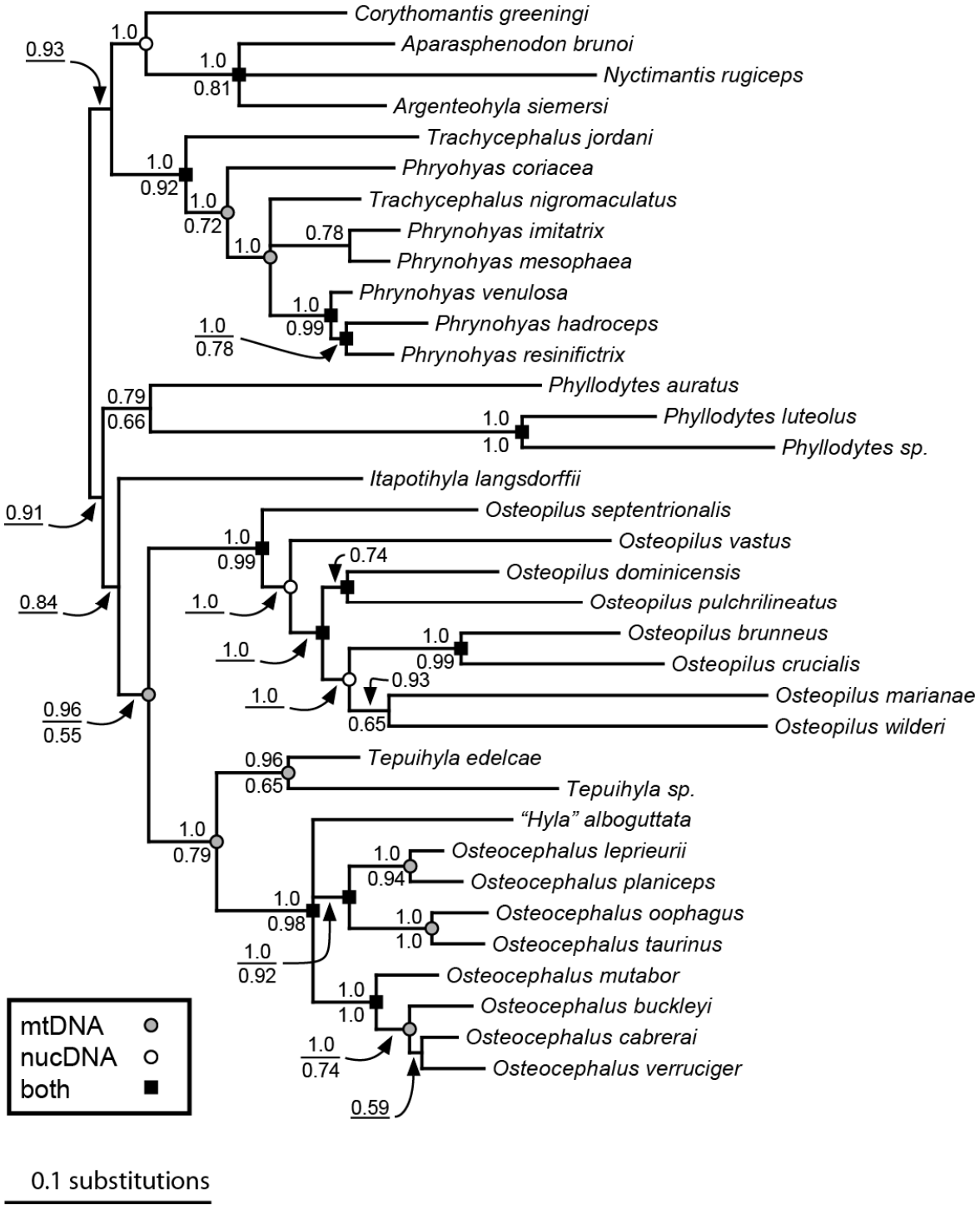
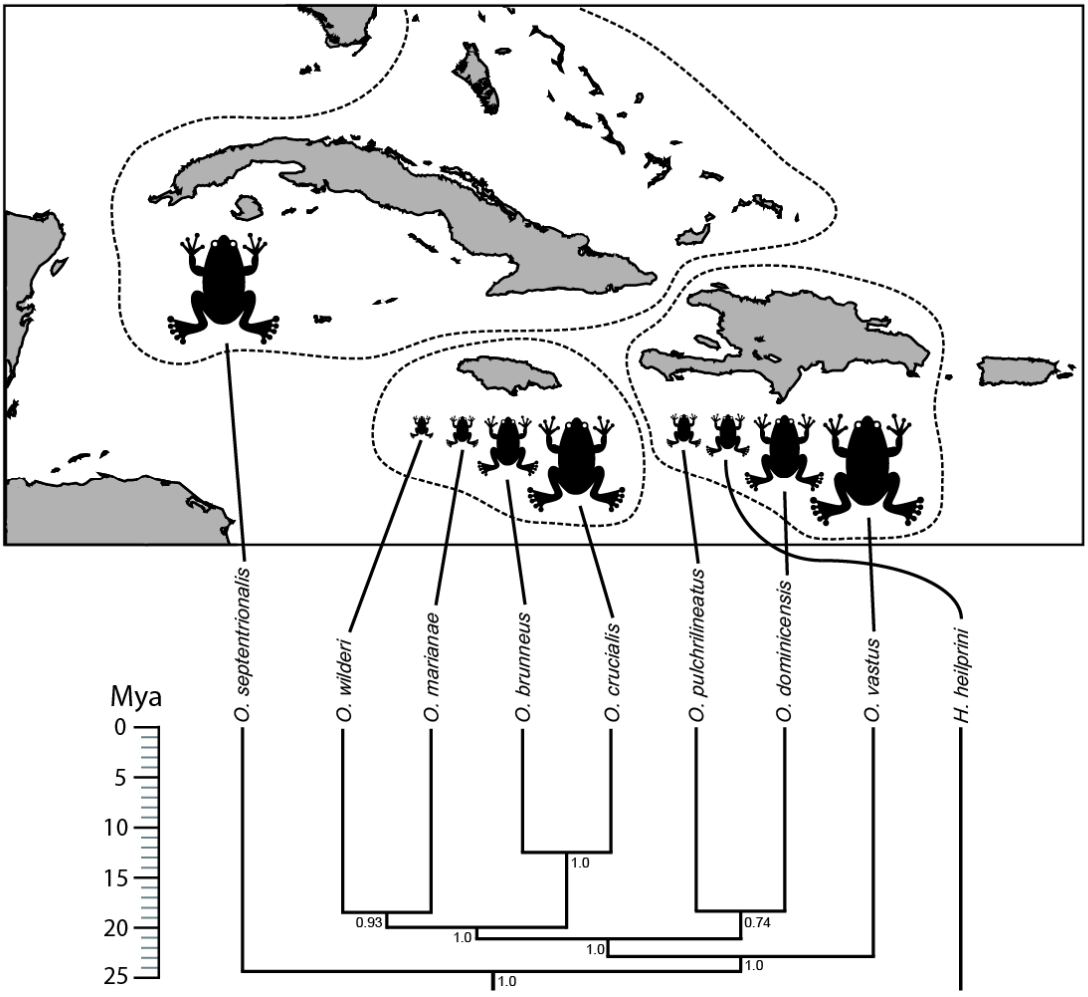


Figure 2.4. Body-size evolution and biogeography of Greater Antillean treefrogs (*Osteopilus* and *Hypsiboas heilprini*). The phylogeny is from the Bayesian analysis of the combined data (Fig. 2.3), with branch lengths proportional to time (as determined using penalized-likelihood analysis). The scale bar indicates branch lengths resulting from the younger calibration point in dating analyses, in millions of years ago (MYA). Note that the branch leading to *Hypsiboas heilprini* stems from the South American clade Cophomantini and is not drawn proportional to time (this branch is actually much longer), but it is included to illustrate all native species of hylids inhabiting the Greater Antilles. Body sizes of cartoon frogs are directly proportional to the maximum body size of each species, demonstrating the diversity of body sizes within islands and among closely-related species.



Chapter 3: Community assembly through evolutionary diversification and dispersal in Middle American treefrogs

Introduction

A major goal of evolutionary ecology is to understand the origins of ecological communities. Specifically, how does a set of species with a given set of ecological traits come to exist together in the same place? In recent years, there has been growing appreciation for the importance of using phylogenies to understand how communities have originated through evolutionary, ecological, and biogeographical processes (e.g., special issues of *Ecology* in 1996 and 2006 and reviews in Webb et al. 2002; Emerson and Gillespie 2008). Many recent studies have focused on the phylogenetic relatedness of co-occurring species, and have used these patterns of relatedness to infer ecological processes (e.g., Webb 2000; Cavender-Bares et al. 2004; Horner-Devine and Bohannan 2006; Kembel and Hubbell 2006; Lovette and Hochachka 2006; Webb et al. 2006; Vamosi et al. 2009). In this paper, we use a phylogenetic approach to infer the relative roles of trait evolution and biogeographic dispersal in creating patterns of community structure (defined here as the set of co-occurring species and their ecologically relevant character states).

Many different ecological and evolutionary processes may determine the structure of a community. However, in general, only two major processes seem likely to add a species with a given character state to a specific community. First, character states may be added through in situ evolution within the community (in situ evolution or ISE hereafter). In situ evolution may be determined by abiotic conditions and by interactions with co-occurring species (e.g., selection to exploit underutilized resources and reduce competition). Second, character states may be added through dispersal of lineages into the community that evolved these states elsewhere and retained them

over time (ecologically conservative dispersal or ECD; Stephens and Wiens 2004). The ability of a species to invade and persist in a given community will be determined by the characteristics of the dispersing species and the abiotic and biotic conditions present there (Morin 1999).

To what extent is community assembly determined by ISE versus ECD? Addressing this question requires combining information from ecology, phylogeny, and biogeography. Previous studies have found evidence for both ISE (e.g., Losos et al. 1998; Ackerly 2004; Gillespie 2004) and ECD (e.g., Ackerly 2004; Stephens and Wiens 2004). However, these studies did not quantify the influence of these processes on community assembly, nor have they quantitatively addressed what might explain the preponderance of a particular process in a given community or biota.

What factors determine the extent to which communities are assembled through ISE versus ECD? We make four predictions that address such factors. (1) Systems (e.g., regions, communities) that are relatively closed to biogeographic dispersal are likely to be dominated by ISE, as species diversify to fill open niches (e.g., adaptive radiations on islands; Losos et al. 1998; Schluter 2000; Gillespie 2004; Harmon et al. 2008; Moen and Wiens 2009). Though often documented on islands, similar processes may be important in continental systems as well, given that biogeographic dispersal may be limited by climate as well as by physical separation (Janzen 1967; Wiens and Donoghue 2004; Lomolino et al. 2006). For example, mountain ranges may form islands of distinct climates within a region and may be important centers for ISE. Therefore, even in more open biogeographic systems, we might expect more ISE in montane regions relative to lowlands and on different isolated mountain ranges. (2)

Given the potential constraints of climatic tolerances on biogeographic dispersal, we expect most ECD to occur between locations with similar climatic regimes. (3) Competition may also limit ECD, in that lineages from outside a region may be unable to invade communities in which the relevant niches are already "filled" (e.g., Morin 1999). Thus, ECD might only occur if lineages have character states dissimilar to those of species already present (although some theory predicts that ecological similarity might instead allow for long periods of co-occurrence; Leibold and McPeek 2006; Scheffer and van Nes 2006). (4) Competition may also prevent dispersing lineages from expanding into new niches (e.g., Schluter 2000), and so may determine whether or not invading lineages undergo ISE (but see Kozak et al. 2009). Thus, we may expect more ISE in the first lineage to colonize a region and conservatism in lineages that arrived later. We test these four hypotheses for the first time here.

In this paper, we combine ecological, phylogenetic, and distributional data to quantify the relative importance of regional dispersal and in-situ evolution in 39 hylid frog communities in Middle America (Mexico to Panama), and to address the hypotheses described above. Middle American hylids offer an attractive study system because an extensive monograph (Duellman 2001) describes the morphology, geographic distribution, and natural history of each species. Furthermore, new phylogenies (Faivovich et al. 2005; Smith et al. 2005, 2007; Wiens et al. 2005, 2006b) provide a framework for analyzing patterns of biogeography and character evolution. Hylids are a monophyletic group (Faivovich et al. 2005; Wiens et al. 2005) and a distinctive ecological guild; they are the dominant group of arboreal frogs in Middle America, and the only arboreal frogs that utilize aquatic habitats for breeding (excepting

the more geographically restricted centrolenids and hemiphractids; Duellman 2001; Savage 2002).

In order to illustrate our approach, we focus on two ecologically important characters, adult body size and larval habitat. In general, hylids are dietary generalists (on arthropods), in which prey size is strongly associated with body size (e.g., Meshaka 2001; Duellman 2005; Moen and Wiens 2009). Thus, body size seems to determine whether different species consume the same prey items. Furthermore, body size appears to be the main axis of morphological diversification in hylid frogs (see Results). In Middle American hylids (Duellman 2001), larvae may be deposited in standing water ("ponds" hereafter), streams, or in arboreal sites (e.g., bromeliads, treeholes), depending upon the species. Larval habitat determines whether or not larvae of different species may potentially co-exist and compete, and seems to be strongly associated with microhabitat preferences of adults (Zimmerman and Bierregaard 1986; Donnelly and Guyer 1994; Duellman 2001; Ernst and Rödel 2008), at least during the breeding season (i.e., pond-breeding hylids are usually found on vegetation in or near ponds, whereas stream-breeding hylids are found on vegetation near streams; Duellman 2001).

In this study, we develop simple indices to quantify the relative importance of ISE and ECD at the regional and local scales. In order to examine the origins of character states (traits) at the regional scale, we map character evolution and biogeographic shifts onto phylogenies. If an ecological character changed after dispersal into the region, then we consider this a character-state origin through ISE. If a lineage dispersed into the region with a character state that evolved before the dispersal event, we consider

this dispersal event a case of ECD. Using these criteria, we quantify for each character the number of trait origins in the region through ISE and ECD. We also trace the origin of character states in 39 local communities to ISE or ECD at the regional scale, assigning the character state of each species in each community to ISE or ECD within Middle America. We then quantify the proportion of species having their character states through ISE or ECD and test whether the proportion of ISE in each community is related to the elevation of that community (with the expectation that higher elevation communities will be isolated by their climate and therefore dominated by ISE). We also examine how widespread each trait origin has become among communities, and whether some communities are characterized by unusually widespread or locally restricted character-state origins (e.g., are some geographically isolated communities dominated by local ISE?). Finally, we also address (a) the rate of ISE in each lineage relative to its timing of colonization of Middle America, (b) whether ECD occurs from areas of similar or dissimilar climatic regimes outside the region, and (c) whether invading lineages are able to colonize communities in which ecologically similar species are already present.

Materials and Methods

LOCAL COMMUNITY STRUCTURE AND CHARACTER DATA

We considered 39 local-scale hylid communities, most of which were described by Duellman (2001). We define a community as the assemblage of species within a single locality. The exact spatial limits of these sites have not been strictly defined, but each

consists of a single collecting locality within an area of no more than a few square kilometers. Each consists of a single general habitat type (e.g., cloud forest) but encompasses multiple microhabitats within that habitat (e.g., forest, stream edge). For many lowland communities, community composition is relatively homogeneous across localities (Duellman 2001; appendix Table A3.1), so that the exact area should have little impact. For highland communities, species composition may change dramatically among localities over a smaller spatial scale, but this is related to differences in habitat types (e.g., cloud forest vs. pine forest vs. montane rainforest), whereas we focus on localities encompassing a single habitat type. Overall, these sites have been visited repeatedly by herpetologists over several decades, and some sites have been the subject of long-term studies. Thus, we are confident that the hylid fauna at each site has been adequately documented.

Data on species composition were taken mostly from Duellman's (2001) Table 73 and distributional appendices. However, nine communities in that table were excluded, because species data were unavailable or the precise location of the site was uncertain. Twelve communities were added to increase representation of northern Mexico (nine sites; from Duellman 2001) and Honduras (three sites; from McCranie and Wilson 2002). These 39 communities collectively include 115 of the 161 currently described hylid species in Middle America. Given that there is little evidence for major geographic variation in body size in these species (see below) and none for larval habitat, we assigned species to character states for these communities based on Duellman's (2001) overall characterizations for these species. Species composition of communities and character states of these species are given in appendix Table A3.1.

Some species in these communities were not represented in our phylogeny. We dealt with this in two ways. First, all species in Middle America were assigned to monophyletic genera by Faivovich et al. (2005), given the phylogeny of the sampled species and assigning unsampled species to genera based on traditional taxonomy. Subsequent phylogenetic analyses (Smith et al. 2007) with additional Middle American species corroborate this taxonomy. In most cases, the generic designation allowed us to unambiguously assign a species' character states to ISE or ECD, particularly when all congeners shared the state. For example, if all species in a genus are stream-breeding, which arose after colonization of Middle America, then we ascribe the presence of stream-breeding in every congener to ISE, even if some species were not included in the phylogeny. If the genus was variable for the character in question, we assumed that species shared their states with close relatives due to common ancestry, without postulating additional instances of ISE. However, if the species did not share the same state with its congeners, then we assumed an additional instance of ISE. As an alternate approach, we calculated the indices assuming all unsampled species as unknown (i.e., we excluded them from community totals). However, the results from the two approaches were qualitatively the same. We present results derived only from the first procedure.

Because communities in close geographical proximity may be similar in species composition (and therefore non-independent in our correlation analyses), we tested for spatial autocorrelation among communities. We expect communities separated by very long distances to be relatively independent, so we only conducted analyses within Mexico (with 23 of 39 communities), and within Costa Rica and Panama (with 10 of 39).

In other words, given our intention to test whether nearby communities are sufficiently dissimilar, the distinctness of distant communities is irrelevant and potentially misleading.

We first calculated a “least-cost” distance between communities using the PATHMATRIX extension (Ray 2005) in ArcView GIS 3.3 (Environmental Systems Research Institute, Redlands, CA). This distance is simply the shortest distance over land between each pair of communities. The least-cost distance is equal to the Euclidean distance in cases where the straightline distance between communities did not cross the Caribbean Sea or Pacific Ocean, but is longer otherwise.

Second, we calculated all pairwise similarities in species composition across communities using the Sørensen coefficient of similarity

$$C_S = 2a / (2a + b + c)$$

where a is the number of species found in both communities, b is the number of species in the first community but not the second, and c is the number of species found only in the second community (Sørensen 1948; Legendre and Legendre 2003). This similarity index ranges from 0 (communities completely different) to 1 (communities identical). Finally, using the PopTools toolbox (Hood 2006) in Excel (Microsoft Professional Edition, 2003), we conducted a Mantel test for a correlation between community distance and similarity, with 999 permutations of the geographic distance matrix. We found no evidence for an effect of geographic proximity on similarity of species composition (Mexico: $r = 0.004$; $P = 0.970$; Costa Rica and Panama: $r = -0.058$; $P = 0.654$). Thus, we did not account for geographic proximity of communities in subsequent analyses.

ANCESTRAL STATE ESTIMATION

The Middle American hylid fauna is dominated by a large clade consisting of 16 genera and ~167 species (Faivovich et al. 2005; Wiens et al. 2005, 2006b; Smith et al. 2007). This clade is primarily endemic to the region and referred to as the Middle American clade (MAC) or Hylini (but three genera occur in North America and one extends into Europe and Asia). Other hylid clades make up ~20% of the ~160 species in the Middle American hylid fauna (Wiens et al. 2006b). Our phylogenetic sampling (see below) included 60 species of the MAC in Middle America (~47%) and almost all Middle American hylid species outside of this clade. Many montane species have not been sampled, largely because of recent declines and extinctions in montane communities (e.g., Lips et al. 2004). However, our sampling for low-elevation taxa is nearly complete. Most importantly, 71% of the species in the 39 communities are included in the phylogeny.

We mapped biogeographic shifts and character evolution onto a hylid phylogeny based on combined Bayesian analyses of 10 nuclear and mitochondrial genes. The primary phylogeny used is based on a detailed phylogeny of the MAC (Smith et al. 2007). For other hylid clades, we used a composite chronogram from Moen and Wiens (2009), based primarily on data from Wiens et al. (2006b). Briefly, Wiens et al. (2006b) estimated phylogeny and divergence times for 124 hylid species, incorporating all relevant hylid fossils and geological calibration points. Moen and Wiens (2009) expanded taxon sampling within 5 individual clades (Phyllomedusinae, Cophomantini, Lophiohylini, *Scinax* clade, and *Dendropsophus* clade), and estimated the phylogeny

and branch lengths using Bayesian analysis. Branch lengths were then converted into units of time using penalized likelihood analysis (Sanderson 2002) with r8s (Sanderson 2003), using the estimated ages of each clade from the 124-taxon chronogram of Wiens et al. (2006b) as root ages. Chronograms for individual clades were added to this "backbone" tree to produce an overall chronogram (see Appendix Figs. S1–S3). We used this overall chronogram from Moen and Wiens (2009) and added the phylogeny of the MAC from Smith et al. (2007). This approach (from Wiens et al. 2006a) allowed us to obtain comparable branch lengths in units of time throughout the phylogeny, without estimating a chronogram for all 283 taxa simultaneously (large trees with heterogeneous branch lengths can be difficult for r8s). Further, preliminary results from an unpublished likelihood tree for 362 hylid taxa (from RAxML; Stamatakis 2006) with divergence dates (from BEAST; Drummond and Rambaut 2007) yields a very similar topology and age estimates (r = 0.89 with divergence dates in Table 3.4 and almost all dates within 3.5 million years (My) of those for each node).

Wiens et al. (2006b) calibrated their 124-taxon chronogram with two separate root ages (Neobatrachia 100 and 160 million years ago [Mya]); thus, we generated two chronograms, one for each set of divergence dates from Wiens et al. (2006b). We conducted all analyses using both sets of branch lengths, but results did not qualitatively differ. Unless indicated otherwise, we only present results using the younger dates.

Biogeographic reconstructions were performed using the stochastic model of geographic range evolution of Ree and Smith (2008). We first assigned each species to one of seven major biogeographic regions (e.g., Middle America, South America, North

America, West Indies; see Figs. S1–S3) and then estimated changes in geographic ranges in the program *lagrange* (Ree and Smith 2008). We constrained all range sizes to be composed at most of two regions, as no current species occupies more than two of our regions. We specified an "area adjacency matrix" to allow only contiguous composite ranges, thus excluding unrealistic ranges (e.g., Northern South America + Eurasia). We also conducted analyses using standard parsimony and likelihood ancestral-state estimation methods (see Wiens et al. 2006b), but all methods gave similar results. For brevity, we only present results from the more realistic Ree and Smith (2008) approach.

We obtained data on larval habitat and body size from various literature sources (see appendix Table A3.2), but most data on species from Middle America were obtained from Duellman (2001). Data were obtained for 278 of the species in our 283-taxon phylogeny (Figs. S1–S3) and for 32 additional Middle American hylids not included in the tree. We used snout-vent length (SVL) as an index of body size, which is standard in anuran studies. Given that body sizes generally are similar between males and females but are not necessarily identical (Duellman 2001), we analyzed data from males only (which are more commonly collected than females). We used maximum SVL within a species, to reduce potential confounding of mature and immature specimens when using average sizes. Geographic variation in male body size is generally limited. For example, Duellman (2001; vol. 1) presented data on geographic variation in male body size from 15 species of hylid frogs in Middle America, and these data suggest limited size variation within species. However, we also conducted an analysis of variance (ANOVA; Sokal and Rohlf 1995) on these data to

examine the relative amount of within- versus among-species variation in body size. We found most variation to be among, rather than within, species (n = 29–441, mean n = 139.5; $F_{14,2077}$ = 4548, P < 0.0001; s^2_{among} = 0.1811, proportion of total variation (p_{total}) = 97.2%; s^2_{within} = 0.0053, p_{total} = 2.8%; analysis on $\log_e$-transformed data). Thus, overall variation in adult male body sizes within species is limited relative to variation across species, suggesting that use of mean, minimum, or maximum body size should have limited impact on the results. Furthermore, we focus here on very broad categories of body sizes (i.e., >20 mm). Appendix Table A3.2 lists raw data and specific literature sources for both larval habitat and body size.

Previous studies (e.g., Moen and Wiens 2009) suggest that body size should be the major axis of morphological variation in hylids. To test this hypothesis, we measured 135 museum specimens (numbers and data in appendix Table A3.3) representing all genera of Hylidae. We measured 14 variables typically used to quantify morphometric variation in frogs (e.g., Duellman 2001): (1) snout-to-vent length (SVL; tip of snout to anterior margin of cloaca); (2) tibia length (tip of knee to tip of heel); (3) foot length (proximal edge of inner metatarsal tubercle to tip of fourth toe); (4) head length (posterior corner of jaw to tip of snout); (5) head width (distance between posterior corners of jaw); (6) interorbital distance (width of bone between two orbits); (7) internarial distance (distance between narial openings); (8) eye-to-nostril distance (posterior tip of nostril to anterior corner of eye); (9) eye diameter (distance between anterior and posterior corners of eye); (10) hand length (proximal edge of outer palmar tubercle to tip of third finger); (11) thumb length (insertion point of thumb into hand to tip of thumb); (12) radioulnar length (elbow to distal edge of outer palmar tubercle); (13)

maximum width of terminal digit of finger 3; and (14) tympanum width (anterior to posterior extent). All measurements were conducted on males.

We performed a principal components analysis (PCA; Manly 1994) on the correlation matrix of these variables. PC1 accounted for 91.2% of the variation, and represented overall size (sensu Jolicoeur 1963; i.e., all PC1 loadings on the original variables were nearly identical in sign and magnitude; appendix Table A3.4). Other PC axes each accounted for less than 2.5% of the variation. Furthermore, when only Middle American hylids are included, PC1 accounted for 92.9% of the variation (appendix Table A3.4). Thus, we used SVL as an overall measure of size, given that data on SVL are available for almost all hylid species (but data on PC1 are not), and that SVL and PC1 are strongly correlated among these 51 species (r = 0.991).

Ancestral values of larval habitat were estimated using parsimony and maximum likelihood in the program Mesquite (Maddison and Maddison 2004). Most species can be unambiguously coded as breeding in ponds, streams, or arboreal habitats (Duellman 2001). However, a few species utilize both ponds and streams, and we defined an additional state (pond and stream) for these species. For parsimony analyses, we used a step-matrix to make transitions between either “pond” or “stream” breeding and “pond and stream” breeding one half step (as opposed to one step between all other states). States were otherwise unordered. For likelihood, all transitions between states were considered equally likely. Overall, parsimony and likelihood gave the same results for all nodes except five; in all five cases, one method gave ambiguous results consistent with the other method’s resolution. Thus, we assigned those nodes the state which was consistent with both methods.

Ancestral values of body size were estimated using the linear generalized least-squares method of Martins and Hansen (1997) implemented in COMPARE version 4.6 (Martins 2004). Body-size data were $\log_e$-transformed prior to ancestral-state estimation to better meet the assumptions of the least-squares method. After reconstruction as a continuous character, species and ancestral nodal values were assigned to body size categories following Duellman (2001; small: $X < 30$ mm, medium: $30 \leq X < 50$ mm, large: $50 \leq X < 80$ mm, and very large: $X \geq 80$ mm). This categorization allowed us to assign changes in body size in the same manner as changes in larval habitat (i.e., as character-state origins; see below). Because these size categories are somewhat arbitrary, we also conducted analyses using an alternate set of body-size categories (from Savage 2002; small: $X < 30$ mm, medium: $30 \leq X < 60$ mm, large: $60 \leq X < 200$ mm). We found qualitatively similar results in all analyses using the different sets of categories, so we present results only using the size categories of Duellman (2001).

We acknowledge that there can be considerable uncertainty in reconstructing both biogeographic changes and character evolution, and this uncertainty may influence the accuracy of our estimation of ISE and ECD (see below). However, despite various potential issues in ancestral character reconstruction (e.g., Cunningham et al. 1998; Oakley and Cunningham 2000; Wiens et al. 2007), many of the patterns that we document are obvious merely from the examination of the phylogeny and the states of extant taxa, without the need for highly accurate ancestral reconstructions (e.g., given that all species of an endemic genus breed in streams but have a large range of body

sizes, it is clear that the ancestor was stream breeding and that there was considerable in situ evolution in body size).

ESTIMATING THE ROLES OF ISE AND ECD

We first estimated the relative importance of ISE and ECD at the regional scale for each ecological character. Throughout the paper, we use "origin" to describe the addition of a given character state to a region or local community through either dispersal or in situ evolution. For example, although two species may share the same character state (e.g., pond breeding), the state may have appeared (originated) in the region in two different ways, evolving within Middle America in one species and through dispersal from South America in the other. The same character state may be added to the region many different times through each process, and each instance of evolution or dispersal is counted as a separate origin in the region.

We used the ecological and biogeographic reconstructions to distinguish ISE and ECD events. If a state evolved after a biogeographic shift into Middle America, then this regional origin was considered to be through ISE (Fig. 3.1). If the state evolved before dispersal into Middle America, then the dispersal of that lineage into the region was considered to be an origin of that state through ECD (Fig. 3.1). In two cases (of 74 total origins), a shift in biogeography occurred on the same branch as a change in one of the characters. In such cases, it is not possible to distinguish between ISE and ECD. We arbitrarily lumped these few cases into the ISE category, given the assumption that these character-state changes most likely occurred in response to a new selective regime encountered in a new region. However, assigning them to the ECD category

had negligible impact on the overall results [e.g., r = 0.71 between ROTIs (see below) of the four relevant communities when categorizing these as ISE versus ECD]. Finally, a limited number of species occur in both Middle America and North or South America; in all cases, biogeographic reconstruction allowed us to resolve the direction of colonization for these species. Figure 3.3 shows the inferred colonizations of Middle America, as well as character states for species and estimated character states at the internal nodes for Middle American hylid frogs.

For each character, we quantified the number of character-state origins in the region and assigned them to either ISE or ECD. We then determined the relative importance of regional ISE and ECD for the structure of local communities by developing several simple indices. We calculated indices separately for each character (i.e., body size and larval habitat). First, for each species in each community, we traced the origin of the species' character states to ISE or ECD at the regional level (Fig. 3.1). Second, we divided the number of species within a given community whose character state originated in Middle America through ISE by the total number of species in the community. This value varies from 0 to 1, with higher values indicating a greater proportion (within a community) of species whose character states originated within Middle America via in situ evolution, relative to dispersal from elsewhere. We call this the Regional Origin Trait Index (ROTI; Fig. 3.1). Additionally, we counted the number of independent ISE events represented in each community and divided this by the total number of independent ISE and ECD events. We call this index the Proportion of ISE Events (PIE). Although similar to the ROTI, the PIE reflects the relative importance of in situ evolution in terms of the overall number of regional-scale dispersal and character

evolution events represented in a given community, rather than the proportion of species that have a character-state whose origin was by ISE (as in the ROTI). For example, even though there may be 10 species in a community, their states may have originated through only two ISE events and one ECD event, given that speciation may occur after dispersal or character evolution. Although the PIE is distinct from the ROTI in what it quantifies, we expect these two indices to be correlated (Fig. 3.1).

We also estimated the spread of each character-state origin among the surveyed communities within the region. We developed the Trait Origin Dispersal Index (TODI), which is the proportion of communities to which each origin (either through regional ISE or ECD) of each character state has spread among the included communities (Fig. 3.1). For example, a character state that has evolved in the common ancestor of two species that together occur in 9 of the 39 communities would have a value of 0.23. We acknowledge that this is a relatively simplistic measure, because it only considers the number of sampled communities and not actual dispersal distances.

In order to identify communities having many character-state origins with limited dispersal, we also calculated the Community Trait Dispersal Index (CTDI). The CTDI is simply the average of TODI across species in a community for a given character (Fig. 3.1).

Finally, we note that one could develop probability models or a permutation procedure to examine whether a community's ROTI or CTDI was significantly small or large (i.e., close to 0.0 or 1.0, respectively). Because we are primarily interested in overall broad patterns (e.g., with elevation) and not the statistical significance of individual index values per se, we have not extensively explored such methods here.

However, we examine one type of null model for the ROTI. We also examined the influences of species incidence across communities, community size, and regional pool size on the statistical significance of different ROTI values under this model.

In brief, we asked whether an individual community's ROTI was significantly different from the random expectation based on the total number of ISE and ECD events represented among all species in the region (Middle America). To assess significance, we used the hypergeometric probability distribution (Sokal and Rohlf 1995), a model of sampling without replacement. Under this distribution, one can assess the probability of obtaining a given community's ROTI value under the expectation based on random assembly from the regional pool of species and then compare this to the case when it is more likely that one type of event (i.e., ISE or ECD) is predominantly represented among the species within a community. The two models (random vs. non-random) are then compared using a likelihood-ratio test. This procedure is directly analogous to simulating community assembly from a regional pool but has the advantage of directly calculating the probabilities that a simulation would only approximate. See Appendix S2 (Supplementary Materials) for full model details, as well as our qualitative variations on the regional species pool (see above).

CORRELATION ANALYSES

If dispersal among high elevation communities is limited by climatic differences in intervening lowlands (see Introduction), we expect to see significant relationships between elevation and our indices. First, we predict that higher elevations may be hotspots for diversification and may show more ISE (i.e., higher ROTIs in high elevation

communities). Similarly, we predict that there will be a significant negative relationship between elevation and the CTDI, indicating relatively isolated ISE events and limited disperal among communities.To address these predictions, we examined correlations between elevation and our community indices. All correlations presented are based on the Spearman's rank correlation coefficient (r_S), as many indices were not normally distributed. Rank correlations were calculated in JMP IN (Version 4.0.4, SAS Institute, Inc., Cary, NC, 2001). In many cases, the colonization of Holarctic *Hyla* into high elevation areas of northern Middle America resulted in outliers (statistically and biologically) in these elevation analyses, as this re-invasion into Middle America (Smith et al. 2005) represents the only high-elevation ECD event. In analyses in which these outliers had an impact on the results, we present results both including and excluding data from the three *Hyla*-dominated communities (localities 3, 6, 12; appendix Table A3.1). Unless otherwise noted, the sample size for all correlation analyses is $n = 39$ (reflecting our 39 communities).

SIMILARITY OF CO-OCCURRING SPECIES

The principle of competitive exclusion predicts that establishment of a species in a new community may be limited by the similarity of the colonizing species to species already occurring there (Morin 1999). If competitive exclusion limits establishment in communities, we expect that species will not share identical states for characters that may affect competitive interactions, especially in cases in which South American lineages have recently invaded a community that contains ecologically similar incumbent species of the MAC. Thus, we tallied the number of species in each

community that have the same states for the two characters under consideration. We considered pairs of species whose body size differs by less than 5 mm and with the same larval habitat to be ecologically similar. We consider this criterion as a conservative estimate of ecological similarity (i.e., we require that species be similar in both body size and larval habitat, and the body sizes must be very similar). That is, if the result of ECD is to add a species which is ecologically similar (by our conservative criterion) to another within the community, then it would appear that competitive exclusion does not necessarily prevent the co-occurrence of ecologically similar hylid species in the community. We also examined the impact of using different body-size similarity cutoffs, continuously varying the criterion from 0 to 10 mm.

Finally, we note that these frogs do not differ in activity time (all are nocturnal; Duellman and Trueb 1986) and have the same seasonal activity (e.g., environmental breeding cues are similar for most species, at least within larval habitat type; Duellman 2001). Thus, as noted in the Introduction, adult body size and larval habitat are likely the most important characters affecting ecological interactions among Middle American treefrogs.

CLIMATE AND COLONIZATION

We hypothesized that many of the colonizations of Middle America involved dispersal between regions with similar climatic regimes. Thus, we expected a general positive correlation between the climatic distribution of a given lineage in Middle America and its likely ancestral climatic distribution. For this analysis, we focused on the more recent invasions of the region and not the original invasion of Middle America

by the MAC, as the ancestor of the MAC seemingly diversified to occupy every habitat and climatic zone inhabited by hylid frogs in the region.

Estimating the climatic distribution of these lineages within Middle America was straightforward. We obtained localities for the relevant species from museum and literature records (especially Duellman 2001) and then used ArcView GIS 3.3 to generate climatic data for each locality using the WorldClim database (Hijmans et al. 2004, 2005). We focused on annual mean precipitation (Bio1) and annual mean temperature (Bio12) as two obvious descriptors of the climatic niche. For colonizations that consisted of a single species, we averaged the values of each variable across localities within each region to obtain the estimates for that species in each region. For colonizations that diversified in situ into two or more species, we used the average of the average values for each species (most multi-species invasions consisted of few species, such that a formal ancestral reconstruction would likely give very similar results to averaging among species).

To approximate the ancestral climatic distribution associated with each colonization event, we assumed that the ancestral climatic regime of the colonist was most likely to be represented by its closest relatives occurring in the ancestral region. Temperature seasonality shows strong phylogenetic signal in Hylidae (Wiens et al. 2006b), as does mean temperature of the coldest month within the MAC (Smith et al. 2005), so we expect this to be the case for other environmental variables. Therefore, we obtained average values of the same climatic variables for the sister species or clade of each colonizing lineage (given that the sister taxon occurred in the inferred ancestral region). Localities were obtained from literature and museum records. The

sister species were inferred from the 283-taxon tree for all hylids (see above), and the ancestral region was determined by our biogeographic reconstructions (see above). Several cases involved species with populations both in Middle America and outside the region (typically South America), and we simply compared the two sets of populations as if they were different species. Finally, we used a Spearman's rank correlation (r_s) to estimate the relationship between the climatic regimes of each colonizing clade in Middle America and in the ancestral region.

We included 12 hylid lineages in this analysis, each representing a separate colonization of Middle America. Localities per species (or per species within a region) ranged from 2 to 83 (mean = 11.6). These lineages (and the sampled species) were (1) *Hyla eximia* group (Middle American lineage = *Hyla euphorbiacea*, *Hyla plicata*; North American = *H. wrightorum*), (2) *Hyla arenicolor* [it is unclear whether this species represents an independent colonization of Middle America (the biogeographic reconstruction of its most recent ancestor was ambiguous), but results were similar excluding it; Middle America (MA) and North America], (3) *Trachycephalus venulosus* [MA and South America (SA)], (4) *Dendropsophus microcephalus* (MA and SA), (5) *Dendropsophus ebraccatus* (MA*;* SA = *D. bifurcus, D. leucophyllatus, D. sarayacuensis, D. triangulum*), (6) *D. robertmertensi* and *D. sartori* (MA; SA = *D. leali, D. rhodopeplus*), (7) *Scinax boulengeri* (MA; SA = *S. garbei, S. sugillatus*), (8) *S. staufferi* and *S. elaeochrous* (MA; SA = *S. fuscovarius, S. nasicus, S. ruber*), (9) *S. ruber* (MA and SA), (10) *Hypsiboas rufitelus* (MA; SA = *H. pellucens*), (11) *Hypsiboas rosenbergi* (MA and SA), and (12) *Hypsiboas boans* (MA and SA). We did not include the two lineages of *Hyloscirtus* because our sample sizes of localities per species were very small (e.g., *n* =

1). We also excluded phyllomedusines, given the seemingly complex biogeographic relationships between Middle and South American lineages in the phylogenetic neighborhood of *Agalychnis* (Wiens et al. 2006b). Nevertheless, preliminary analyses including these three lineages gave qualitatively similar results to those using 12 lineages.

DATES OF COLONIZATION EVENTS

The Middle American hylid fauna is dominated by one species-rich clade (MAC) and many less-diverse invasions from other hylid clades. We compared the relative ages of these clades (and how the frequency of ISE is related to the timing of colonization; see below) using the chronogram described above. The minimum age of colonization of a given region can be estimated from the timing of the oldest splitting of a clade of species that are endemic to that region (i.e., the crown group age of the endemic clade). The putative maximum age can be estimated as the age of the endemic species' common ancestor (i.e., the stem group age of the endemic clade), although we acknowledge that the colonization could be somewhat older in some cases. We present both the minimum and maximum dates of colonization for these endemic clades.

Unfortunately, estimating the ages of single-species invasions (i.e., one species occurs in the region and its sister species occurs in the ancestral region) is much more uncertain. For example, the timing of colonization could be much more recent than the timing of the split between these two species. Therefore, in these situations we present estimated ages of species that appear to have colonized Middle America as a single

invasion, assuming that the colonization of Middle America did not occur before the origin of those species. The ages of these species could also be overestimated because of incomplete taxon sampling of South American species within the relevant clades. In addition, many single-species invasions have populations in both regions. Colonization dates for these species are uncertain without detailed phylogeographic sampling, but we use the timing of their split from their sister species as a crude estimation of the maximum age of the colonization event.

For the determination of colonization dates, we used two chronograms. The first was the 283-taxon phylogeny used for ancestral-state estimation [i.e., branch lengths corresponding to the 100 Mya root from Wiens et al. (2006b); see above]. The second chronogram had the same topology, but branch lengths were estimated using the set of divergence dates corresponding to the 160 Mya root.

RATES OF IN SITU EVOLUTION

Our interest in the ages of colonization events was related to their propensity for ISE. For example, are there lower rates of ISE in the lineages that colonized more recently? We first estimated the rate of ISE for each colonizing lineage for each character as the number of ISE events divided by the age of the colonizing lineage. For simplicity, we used the midpoint of the age of the branch on which the colonization event is inferred to have occurred (the average of the stem and crown group age estimates for the clade). We conducted these analyses using both the 100 and 160 Mya root ages. However, since results were qualitatively the same, we report only results using 100 Mya (given that we are interested in relative timing, not absolute

timing). This comparison of rates is compromised somewhat by the many single-species colonization events (no body size or life history differences expected); however, our results comparing the MAC only to multi-species colonizations were qualitatively similar (see below).

Alternatively, the opportunity for evolutionary events may be more a consequence of the sum of branch lengths within a clade (i.e., character evolution is modeled as occurring along phylogenetic branches, not as a function of time per se; O'Meara et al. 2006). Thus, we also conducted these analyses dividing the number of ISE events for clades by the sum of branch lengths within those clades, using the 100 Mya-rooted chronogram, as above. These analyses were only conducted on multi-species invasions of Middle America.

Results

A graphical summary of the distribution, ecological traits, and dispersal histories of hylid clades in Middle America is provided in Fig. 3.2. Ancestral reconstructions of biogeographic history and trait evolution are presented for the Middle American clade (MAC) and non-MAC lineages in Middle America in Figs. 4 and 3, respectively. A graphical summary of the geographic location, clade composition, and ecological structure of each community is provided in Fig. 3.4.

There have been 27 origins of larval habitat types among Middle American hylids, 10 through in-situ evolution (ISE) and 17 through ecologically conservative dispersal (ECD; Table 3.1). Most origins through ECD represent colonization of lowland pond-dwelling lineages from South America (14 of 17; black circles on the lower bars in

Fig. 3.2), many of which have spread throughout the Middle American lowlands (e.g., *Dendropsophus*, phyllomedusines, *Trachycephalus, Scinax*). There were also two invasions of highland stream-dwelling lineages into highland habitats in lower Central America (*Hyloscirtus colymba* and *H. palmeri*), and one invasion of a pond-dwelling lineage from temperate North America (*Hyla arenicolor* and the *Hyla eximia* group) into montane areas of Mexico and Guatemala (Fig. 3.2). Within the MAC, there was an early origin (ISE) of stream-dwelling (Fig. 3.3b), which spread to most montane communities in the region (Figs. 2, 5). There has also been in situ evolution of pond-breeding (from stream-breeding ancestors; Fig. 3.3b) that spread into many low elevation communities (i.e., *Diaglena, Isthmohyla, Smilisca, Tlalocohyla, Triprion*). Two lineages within this pond-breeding clade have secondarily become stream breeding in lower Central America (*Isthmohyla, Smilisca*). There have been four origins of arboreally-breeding hylids in the region (two from pond breeders, two from stream breeders), all representing in situ evolution within the MAC.

The proportion of stream breeding species in communities increases with elevation (all data: $r_S = 0.592$, $P < 0.001$; *Hyla* excluded: $r_S = 0.787$, $P < 0.001$), whereas the proportion of pond breeding species decreases with elevation (all data: $r_S = –0.482$, $P = 0.002$; *Hyla* excluded: $r_S = –0.709$, $P < 0.001$). Too few communities had arboreal-breeding species to examine a correlation between elevation and proportion of arboreal species, but a two-tailed Wilcoxon two-sample test shows that communities with arboreal-breeding species are on average higher in elevation than communities with no arboreal breeders ($U_S = 197$,$t_S = 2.06$, $P = 0.039$).

There have been 44 origins of different body size classes in Middle America, most through ISE (29 of 44; Table 3.1) and a smaller number through ECD (15 of 44). Small, medium, large, and very large body sizes have each evolved repeatedly in situ. Within the MAC, a large range of body sizes is present within most major clades (i.e., the *Plectrohyla*, *Ptychohyla*, *Charadrahyla,* and *Smilisca* clades all include species ranging in size from small to large or very large; Fig. 3.2). Most in situ changes are within the MAC, but 7 of 29 in situ changes involve species from South American lineages, including species of small, medium, and very large body sizes.

The relative importance of regional ECD and ISE for the assembly of individual communities differs considerably among characters and communities. The regional origin trait index (ROTI) ranges between 0.0 and 1.0 for both characters across different communities (Table 3.2). Across all 39 communities, the average ROTI is 0.574 for body size and 0.579 for larval habitat (i.e., on average slightly more than half of the species within a given community trace their character states to in situ evolution within Middle America). The Proportion of ISE Events (PIE) was very similar to the ROTI (Table 3.2; correlation between ROTI and PIE for body size: $r_S = 0.808$, $P < 0.001$; larval habitat: $r_S = 0.901$, $P < 0.001$). Thus, further analyses were only conducted on the ROTI.

There is a weak relationship between the ROTI for larval habitat and that for body size, but this relationship is primarily due to the influence of the three *Hyla*-dominated communities (all data: $r_S = 0.315$; $P = 0.051$; *Hyla* excluded: $r_S = 0.170$; $P = 0.322$). Elevation shows a positive correlation with the ROTI for larval habitat (all data: $r_S = 0.403$; $P = 0.011$; *Hyla* excluded: $r_S = 0.693$; $P < 0.001$) and a negative correlation

with the ROTI for body size (r_S = –0.401; P = 0.012), indicating that higher-elevation communities are dominated by larval habitat character states that evolved within Middle America and by body-size character states that evolved outside of Middle America. Most body-size evolution in the MAC occurred in clades that secondarily invaded the low elevations, whereas montane communities have many species of medium body size, a trait which originated through ECD in the ancestor of the Middle American clade (Fig. 3.3b).

The trait-origin dispersal index (TODI) for body size ranges between 0.00 and 0.74, with an average of 0.110 (i.e., a single character-state origin is represented in an average of 4.29 of the 39 local communities; Table 3.1). Origins of body-size classes through ISE have spread to an average of 10.1% of sampled communities, whereas origins of size classes through ECD have spread to an average of 12.6% of sampled communities. Origins of larval habitat through ISE and ECD have each spread on average to 16.7% and 13.4% of communities, respectively (overall average 14.6%, Table 3.1). The community trait-dispersal indices (CTDI) for body size range between 0.103 and 0.615 and for larval habitat between 0.128 and 0.697. The body size CTDI is not correlated with elevation (r_S = 0.056, P = 0.736). In contrast, community elevation is strongly but negatively correlated with the CTDI for larval habitat (r_S = –0.486, P = 0.002), indicating limited dispersal of larval habitat character-state origins at higher elevations.

Twenty-nine of the 39 communities (74%) include pairs of ecologically similar species (same larval habitat and body size within 5 mm). Of the total of 77 ecologically similar species pairs, 31 pairs (40%) consist of species from lineages that independently

invaded Middle America (e.g., a MAC species and a species from a South American clade). For example, many lowland communities contain both small, pond-breeding species of the MAC (e.g.,*Tlalocohyla picta*) and small, pond-breeding species from South America (e.g., *Dendropsophus microcephalus, Scinax staufferi*), and we have observed them in microsympatry in many localities in Mexico (Wiens, unpubl.). Even when we increased the stringency for ecological similarity by reducing the body-size similarity cutoff, we still found many examples of co-occurring species that were very similar (e.g., in 15 of the 39 communities, there are 26 instances of co-occurrence of species that have the same larval habitat and adult body size within 2 mm of each other; Fig. S5).

There is a mixed relationship between the climatic distribution of lineages in Middle America and the climatic distribution of conspecific populations and closely related species in the inferred ancestral region. A strong positive correlation exists for precipitation (r_s = 0.755; P = 0.005; n = 12) but not temperature (r_s = 0.406; P = 0.191; n = 12). Note, however, that the lack of strong temperature correlation is mostly a consequence of the similarity in temperature values among most colonizing lineages, with limited variation between lineages that colonized warm areas and those that colonized cooler areas (Table 3.3). Most of the colonizing lineages dispersed from lowland tropical habitats in South America into similar habitats in Middle America, but biogeographic reconstruction indicated one invasion of relatively cool, dry montane habitats in Middle America from temperate montane habitats in semi-arid western North American.

The estimated ages of species and clades show that the MAC is by far the oldest invasion of Middle America, and that all other invasions are considerably younger (Table 3.4). The MAC has undergone extensive in situ diversification since its colonization of the region, with 20 and 9 ISE events in body size and larval habitat, respectively, within Middle America. The other 17 hylid colonizations of Middle America have only resulted in a total of 9 body-size and 1 larval habitat ISE events. Additionally, the rate of in situ evolution is 0.355 body-size and 0.160 larval-habitat ISE events/My for the MAC. The average rate of in situ evolution for all other colonizations is 0.039 and 0.003 events/My (range: 0–0.222 and 0–0.051) for body size and larval habitat, respectively. When the MAC rates are statistically compared to those of the 16 subsequent colonizations, the former are significantly higher (body size: $t_s = 17.82$, $P < 0.0001$; larval habitat: $t_s = 44.44$, $P < 0.0001$). Although these comparisons are compromised by the many single-species colonization events (for which dates are uncertain and ISE unlikely), the rates for the MAC are still substantially higher than for all six other multi-species colonization events (body-size ISE: mean = 0.055, range = 0–0.153; larval habitat ISE: mean = 0.009, range = 0–0.051), a difference that is also statistically significant (body size: $t_s = 10.50$, $P = 0.0001$; larval habitat: $t_s = 16.41$, $P < 0.0001$). Overall, these results suggest that rates of ISE are lower in the lineages that colonized Middle America more recently.

However, when we estimated the rate of ISE per unit branch length, we did not find the MAC to be different when compared to the six more recent colonizations for rate of ISE in both body size (MAC = 0.023 ISEs/My; $\text{Others}_{\text{mean}} = 0.019$, SE = 0.009; $t_s = 0.329$, $P = 0.755$) and larval habitat (MAC = 0.010; $\text{Others}_{\text{mean}} = 0.003$, SE = 0.003; $t_s =$

2.069, *P* = 0.093). This result suggests that the rate of ISE in the MAC may not be exceptional, but the greater number of ISEs within that clade (relative to more recent colonizations) is due to its longer residence within the region and greater number of species.

Discussion

To what extent is local community structure determined by in situ evolution or ecologically conservative dispersal of character states from outside the region? In this paper, we address this question quantitatively for the first time, by developing new indices and applying them to the hylid frogs of Middle America. We find that the average regional origin trait index (ROTI) among communities is 0.574 for body size and 0.579 for larval habitat, indicating that on average just over half of the species present in each community can trace their character states to in situ evolution within the region. However, the proportion of character states in each community originating through each process varies considerably between characters and communities, with the proportion varying from 0 to 1 for each character, depending upon the community. We also found that patterns of in situ evolution (ISE) and ecologically conservative dispersal (ECD) at the regional scale may not predict patterns at the local scale. For example, even though more origins of larval habitat in the region are through ECD (Table 3.1), within the local communities sampled, more communities are dominated by character-state origins through ISE. This disparity arises because many origins of larval

habitat through ECD are somewhat limited in geographic extent, whereas two of those arising through ISE are widespread within the region.

Variation among communities in the proportion of character-state origins by ECD and ISE (i.e., the ROTI) is seemingly explained by complex patterns of trait evolution and dispersal. Biogeographic analysis suggests that the Middle American clade of hylids (MAC) were the first hylid treefrogs to enter Middle America, ~55–80 million years ago (Table 3.4). This lineage then diversified into three montane stream-breeding clades (Fig. 3.3b), which have spread to many communities and diversified considerably in body size (Fig. 3.2). One clade within this montane, stream-breeding lineage evolved to utilize lowland ponds (*Isthmohyla*, *Smilisca* clade, *Tlalocohyla;* Fig. 3.3b) and also diversified considerably in body size (Figs. 2, 4). The pond-breeding clade then secondarily invaded streams in lower Central America (*Isthmohyla, Smilisca*), where most other stream-breeding clades are absent. The lowland clade also invaded temperate North America, Europe, and Asia, and then re-invaded the Middle American highlands, likely from the western North American highlands (Smith et al. 2005). More recently (~20–30 Mya or later), the lowlands of Middle America were invaded by various South American hylid clades. These invasions consisted mostly of lowland pond breeders and included a broad range of body sizes. Some of these invasions spread throughout the Middle American lowlands (*Dendropsophus,* phyllomedusines*, Trachycephalus, Scinax*), whereas others remained in lower Central America (most *Hypsiboas*, some *Scinax*). There were also two invasions of Middle American highlands from a lineage of South American montane stream breeders (*Hyloscirtus*), but these two invasions were limited in their biogeographic extent, and are only represented in one of

the 39 sampled communities. These recent invasions from South America show relatively little ISE, apart from some minor shifts in body size.

PRINCIPLES OF COMMUNITY ASSEMBLY

Despite this complexity, we suggest that a limited number of general principles may explain many of these patterns and that these principles may apply to many other organisms and regions. First, the temporal staggering of colonizations may explain which lineages have undergone extensive ISE and which have not. The MAC almost certainly was the first lineage to invade Middle America (Table 3.4), and it underwent extensive ISE in both body size and larval habitat. Other lineages invaded more recently, and most have undergone relatively limited diversification in body size and larval habitats within Middle America. Because rates of ISE were not higher for the MAC when we calculated ISE per unit branch length (see Results), our results suggest that the time available for speciation and ecological diversification within a colonizing group may be more important for ISE than ecological opportunity per se. The temporal staggering of hylid invasions was likely caused by the separation of Middle and South America during most of the Tertiary, and their more recent reconnection (Lomolino et al. 2006). We note that some of our estimated clade ages (Table 3.4) imply that treefrogs dispersed prior to the terrestrial reconnection of Middle and South America, but overwater dispersal of frogs no longer seems implausible (e.g., Vences et al. 2003; Evans et al. 2003).

Second, elevation seems to play an important role in driving patterns of community assembly, even though the relationship between elevation and the ROTI is

not simple. Most highland communities are dominated by species of the in situ radiation (MAC), but both ECD and ISE contribute to both lowland and highland communities. For example, some species of the MAC are present in many lowland communities. Conversely, some South American clades extend into lower montane communities (e.g., 1,000 m). Furthermore, a clade from North America (*Hyla*) has dispersed into many communities in northern Middle America, and these are the only hylids present in some high-montane communities.

Ecological differences between lineages inhabiting different elevations also play a role in driving patterns of community structure. For example, stream-breeding lineages dominate mid-elevation cloud forest habitats (where ponds may be rare) and pond-breeding lineages dominate lower elevation communities (where high-gradient streams may be rare). There is also a trend for higher-elevation communities to lack species of the largest body sizes (maximum male size of the largest species in each community decreases with elevation; $r_s = -0.677$, $P < 0.001$; see also Fig. 3.4). This is associated with the negative correlation between elevation and the body-size regional origin trait index (ROTI), because most body-size evolution in the endemic MAC occurred at low elevations. High-elevation communities are dominated by moderate-sized species, which was the ancestral body size category of the MAC. We note that high latitude hylid communities also lack very large species (Moen and Wiens 2009), suggesting selection against large body sizes in cooler climates (but see Ashton 2002). The causes of these patterns in body-size evolution and distribution are unclear and deserve further study.

Elevation may also strongly influence community assembly through its effects on dispersal. The larval habitat community trait-dispersal index (CTDI) is strongly negatively correlated with elevation, indicating that montane origins of larval habitat are not generally widespread, in contrast to larval habitat origins at low elevations. This result suggests that a dispersal gradient may exist across elevations, with the most dispersal in the lowlands and the least dispersal in the highlands.

Third, limited climatic tolerances (i.e., niche conservatism) may help explain many patterns of dispersal and community assembly. Most cases of ECD involve invasion from climatically similar regions, such as the multiple invasions of tropical lowlands in Middle America from tropical lowlands of South America, the invasion of cool, dry montane habitats (e.g., pine forest) from temperate North America (*Hyla*), and two invasions of tropical montane Central America from tropical montane South America (*Hyloscirtus*). Conversely, there were no invasions from the temperate lowlands of North America into tropical lowlands of Middle America, and only two invasions of temperate North America from Middle America (Smith et al. 2005; Wiens et al. 2006b). Furthermore, the general distinctness of lowland and highland communities may reflect specialization to different climatic regimes (although the different life history modes of lowland and montane species may also be important). The climatic insularity of high elevation habitats may also explain why there seems to be more limited dispersal of character-state origins among montane communities relative to lowland communities, based on the community trait dispersal index (CTDI).

Fourth, ECD of lineages into communities is not precluded by the presence of ecologically similar species in those communities. Instead, we find many cases where

species with similar body size and larval habitat co-occur. Of course, these species pairs may be differentiated in other characters besides these two, and more precise measurements of even these two characters might reveal important differences (but see Materials and Methods). We simply point out that overlap in these two characters does not seem to prevent co-occurrence, contrary to our initial expectations based on the principle of competitive exclusion (Morin 1999). In fact, some ecological theory suggests that ecological similarity among sympatric species may facilitate their co-occurrence under some conditions (e.g., Leibold and McPeek 2006; Scheffer and van Nes 2006). Additionally, previous research on ecologically similar frog species suggests that competition may affect abundance, but need not preclude co-occurrence (Inger and Greenburg 1966). Finally, our results are consistent with those of Ernst and Rödel (2008), who suggested that similarity in breeding habitat did not influence community assembly in a South American hylid frog assemblage.

THE POTENTIAL ROLE OF COMPETITION

We see three major roles that competition might play in the assembly of Middle American hylid communities that should be addressed in future studies. First, competition may limit dispersal between different communities and different climatic regimes. For example, lineages invading from lowland South America may not extend into higher elevation communities because these communities are already occupied by hylid species, and resources may be too limited to support additional species (or simply too limited to favor niche expansion). We note that most communities have ~8 species (Smith et al. 2007), and that most species belong to the MAC in higher elevation

communities but less than half do at lower elevations (appendix Table A3.1). However, as mentioned above, limited climatic tolerances and differences in larval habitat may also constrain elevational shifts.

Second, in a similar vein, competition may limit niche shifts within communities. For example, stream-breeding evolved in *Isthmohyla* and *Smilisca* only in lower Central America, where many other stream-breeding lineages are absent (e.g., *Charadrahyla* clade, *Plectrohyla* clade). Furthermore, we found that recently invading lineages showed reduced amounts of ISE, possibly because species of the MAC already evolved to occupy much of the available niche space, reducing selection for divergence in the more recent colonists (for other possible examples see Losos et al. 1998; Wiens et al. 2006a; but see Kozak et al. 2009). However, this might also be a consequence of less time for speciation and ecological diversification in these more recently colonizing clades (i.e., rates of ISE are not higher in younger lineages when summed branch lengths are used).

Third, competition may drive trait divergence within communities, as suggested by the ecological theory of adaptive radiation (Schluter 2000). The repeated evolution of extreme body sizes within major lineages of the MAC may reflect divergence driven by competition (e.g., Moen and Wiens 2009), coupled with the general separation of highland and lowland faunas and the shifting mosaic of lineages present in different highland communities (see Table A3.1). Intriguingly, despite the potential role of competition in causing and/or constraining evolutionary changes in these characters, we found little evidence that competition prevents the co-occurrence of species having similar values for these traits.

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Table 3.1. Summary of the origins of each character state in Middle America (through in situ evolution or dispersal). The trait-origin dispersal index (TODI) indicates the spread of each trait origin among the sampled communities.

Character-state origins	Number of character-state origins	TODI range	TODI mean
In situ evolution (ISE)			
Body size			
Medium to small	8	0.00–0.23	0.063
Medium to large	7	0.00–0.74	0.223
Medium to very large	2	0.00–0.08	0.038
Large to medium	8	0.00–0.10	0.051
Large to very large	3	0.05–0.15	0.103
Overall	28	0.00–0.74	0.101
Larval habitat			
Pond to stream	3	0.07–0.36	0.188
Pond to arboreal	2	0.02–0.15	0.090
Stream to pond	2	0.03–0.72	0.372
Stream to arboreal	2	0.08–0.10	0.090
Pond to pond & stream	1	0.00	0.000
Overall	10	0.00–0.72	0.167
Ecologically conservative dispersal (ECD)			
Body size			
Small	3	0.05–0.26	0.188
Medium	7	0.00–0.62	0.136
Large	1	0.026	0.026
Very large	4	0.03–0.26	0.090
Overall	15	0.00–0.62	0.126
Larval habitat			
Pond	16	0.00–0.62	0.149
Stream	2	0.00–0.03	0.013
Arboreal	0	-	-
Overall	18	0.00–0.62	0.134

Table 3.2. Properties of communities included in this study. The regional trait origin index (ROTI), proportion of ISE events (PIE), and community trait dispersal index (CTDI) are defined in the text.

Locality number	Elevation (m)	Number of species in community	Latitude	Longitude	Body Size			Larval Habitat		
					ROTI	PIE	CTDI	ROTI	PIE	CTDI
1	597	3	29.22	-110.133	1.00	1.00	0.547	0.66	0.50	0.684
2	9	5	23.22	-106.417	1.00	1.00	0.369	0.80	0.50	0.697
3	2603	1	23.8	-105.4	0.00	0.00	0.103	0.00	0.00	0.179
4	11	8	19.53	-105.083	0.75	0.71	0.279	0.63	0.40	0.519
5	412	5	19.02	-102.1	1.00	1.00	0.369	0.80	0.50	0.697
6	2240	1	19.3	-99.117	0.00	0.00	0.103	0.00	0.00	0.179
7	2078	8	17.47	-100.196	0.50	0.50	0.333	1.00	1.00	0.359
8	2	6	15.85	-97.07	0.66	0.67	0.158	0.33	0.20	0.449
9	1768	8	16.2	-97.129	0.75	0.75	0.212	1.00	1.00	0.359
10	53	4	16.33	-95.233	1.00	1.00	0.481	0.50	0.33	0.596
11	361	3	23.05	-99.15	0.66	0.67	0.376	0.33	0.33	0.410
12	2007	3	20.37	-98.73	0.00	0.00	0.274	0.33	0.33	0.128
13	2253	4	20.18	-98.25	0.25	0.50	0.474	0.75	0.50	0.314
14	767	4	19.21	-96.81	0.75	0.75	0.468	0.75	0.50	0.622
15	1369	7	19.14	-96.99	0.43	0.75	0.487	1.00	1.00	0.374
16	2093	4	18.7	-97.32	0.50	0.67	0.340	0.75	0.50	0.314
17	1041	9	18.87	-97.03	0.56	0.57	0.447	0.55	0.50	0.382
18	1015	6	18.57	-95.17	0.83	0.80	0.462	0.83	0.75	0.441
19	350	8	18.58	-95.1	0.63	0.57	0.420	0.63	0.40	0.571
20	876	9	17.85	-96.33	0.44	0.80	0.499	0.88	0.75	0.330
21	30	8	18.09	-96.12	0.50	0.50	0.385	0.38	0.17	0.484
22	1942	6	17.15	-93.01	0.67	0.75	0.269	1.00	1.00	0.359
23	30	7	20.7	-88.47	0.57	0.50	0.469	0.57	0.25	0.571
24	254	8	17.23	-89.61	0.63	0.57	0.446	0.50	0.20	0.542
25	1324	8	15.08	-88.92	0.75	0.86	0.330	0.88	0.80	0.369

26	1085	8	15.08	-88.93	0.63	0.80	0.468	0.75	0.66	0.558
27	2	7	15.8	-84.3	0.57	0.57	0.403	0.43	0.80	0.516
28	1132	4	15.63	-86.79	0.75	0.75	0.365	1.00	1.00	0.449
29	10	6	15.78	-86.78	0.50	0.50	0.397	0.50	0.25	0.500
30	2802	5	10.13	-84.1	0.00	0.00	0.615	1.00	1.00	0.323
31	1172	11	9.85	-83.43	0.36	0.50	0.485	0.63	0.50	0.420
32	54	12	10.42	-83.95	0.58	0.60	0.289	0.33	0.14	0.452
33	38	11	8.7	-83.48	0.73	0.67	0.238	0.27	0.22	0.303
34	13	6	10.33	-85.2	0.50	0.50	0.291	0.33	0.33	0.303
35	1349	10	8.8	-83	0.40	0.57	0.431	0.70	0.67	0.300
36	27	7	9.22	-80.02	0.43	0.50	0.282	0.14	0.17	0.308
37	643	9	8.6	-80.13	0.56	0.57	0.221	0.33	0.38	0.231
38	490	7	7.7	-77.58	0.57	0.50	0.282	0.14	0.17	0.330
39	31	10	9.17	-79.83	0.60	0.63	0.276	0.20	0.25	0.319

Table 3.3. Summary of selected climatic niche characteristics of hylid lineages that have colonized Middle America and of their close relatives (or conspecific populations) that occur in their inferred ancestral geographic range.

Clade	Bio 1 (Annual mean temperature; ºC)		Bio12 (Annual mean precipitation; mm)	
	Middle American lineage	Extralimital lineage	Middle American lineage	Extralimital lineage
Hyla eximia group	13.9	8.4	983.7	584.4
Hyla arenicolor	17.3	12.8	811.7	430.4
Trachycephalus venulosus	25.8	24.6	2190.2	2163.6
Dendropsophus microcephalus	24.9	26.7	2426.4	1491.7
Dendropsophus ebraccatus	23.9	25.4	3147.9	3039.4
Dendropsophus sartori-D. robertmertensi	27.1	25.3	1553.1	2845.9
Scinax boulengeri	25.9	25.7	3169.3	4333.6
Scinax staufferi	24.9	21.9	2589.3	1846.0
Scinax ruber	26.6	25.8	2511.7	2541.8
Hypsiboas rufitelus	25.7	23.8	3598.8	3246.0
Hypsiboas rosenbergi	26.3	23.8	2835.3	3317.0
Hypsiboas boans	26.0	24.3	2184.0	2591.4

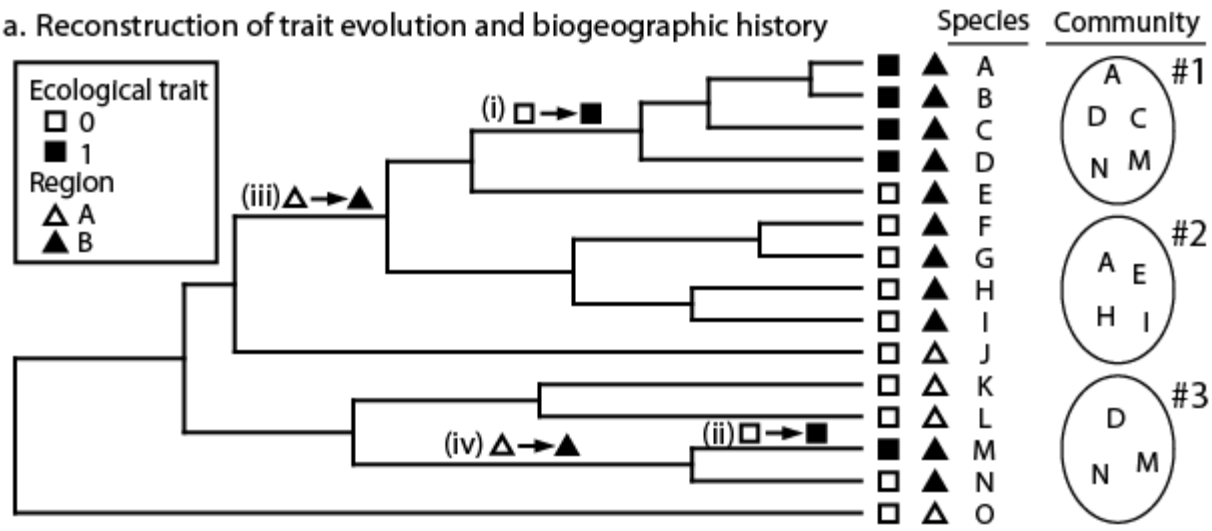
Table 3.4. Estimated ages of dispersal events for hylid frogs colonizing Middle America from South America, showing that the Middle American clade colonized the region far earlier than any other hylid clade. Estimates are based on two potential root ages for Neobatrachia (100 Mya and 160 Mya). We present an interval of ages for each clade, with the more recent date indicating the crown-group age of the clade and the earlier date indicating the stem-group age. Thus, these intervals potentially bracket the date of colonization of Middle America, as inferred from our ancestral area reconstructions. Single species are those that either occur in both Middle and South America or are Middle American-endemic species that are nested within South American clades. Each represents a separate colonization event. The dates for these species merely indicate the estimated age of these species (i.e., the split from their putative sister species), and suggests only the earliest date at which they are likely to have colonized Middle America. See Methods for various caveats associated with these dates. Note that the date associated with *Cruziohyla calcarifer* is likely grossly overestimated, given that this species seemingly has a close relative in South America and only a limited distribution in Middle America.

Clade or species in Middle America	100 Mya	160 Mya
Clades		
Middle American clade	55.30–57.53	77.28–81.11
Agalychnis-Pachymedusa-Hylomantis clade	23.50–28.67	34.00–41.49
Dendropsophus robertmertensi-D. leali clade	16.30–18.80	23.34–26.83
Hyloscirtus colymba- H. simmonsi clade	19.79–25.71	27.83–36.43
Middle American *Hyla*	18.06–21.05	21.42–24.79
Scinax boulengeri-S. sugillatus clade	2.63–16.37	3.63–22.72
Scinax elaeochrous-S. staufferi clade	19.89–23.84	27.63–33.10
Single species		
Cruziohyla calcarifer	34.39	49.76
Dendropsophus ebraccatus	18.94	27.21
Dendropsophus microcephalus	18.80	26.83
Hyloscirtus palmeri	19.33	27.57
Hypsiboas boans	13.80	19.67
Hypsiboas crepitans	12.33	17.41
Hypsiboas rosenbergi	12.33	17.41
Hypsiboas rufitelus	9.01	12.89
Scinax ruber	13.72	18.86
Trachycephalus venulosus	6.76	9.50

Figure 3.1. Diagrammatic example of our approach to quantifying the relative importance of in situ evolution (ISE) and ecologically conservative dispersal (ECD) in determining patterns of community structure within a region, based on hypothetical data. (a) First, we use ancestral state estimation to examine both biogeographic dispersal into the region of interest (here, region B) and ISE of an ecologically relevant character-state within the region. Dispersal of a lineage into the region without subsequent change in that character is an ecologically conservative dispersal (ECD) event. Evolution of the character state after the lineage disperses into the region is considered in situ evolution (ISE). Numbered changes (i–iv) in regions and ecological traits correspond to the ISE (i, ii) and ECD events (iii, iv). (b) Second, all character-state origins in the region, whether by evolution or dispersal, are examined. Species within the region are assigned to these origins, and the proportion of communities in which the descendents of a given origin occur is the Trait-Origin Dispersal Index (TODI). For example, descendants of the ISE event (i) are present in all three communities, and so this origin has a TODI score 1.0. (c) Finally, descriptive statistics are calculated for each community. The Regional Trait-Origin Index (ROTI) is the proportion of species within each community whose character state is the consequence of an ISE event within the region. For example, in Community 1, four of the five species (A, C, D, M) have state 1 through ISE events (i and ii). The Proportion of ISE Events (PIE) is calculated by tallying the total number of independent regional ISE and ECD events that contributed to each community, and then dividing the number of ISE events by the total events (ISE and ECD). The Community Trait Dispersal Index (CTDI) is the average TODI within the community, and indicates the extent to which a community is dominated by geographically restricted trait origins.

Figure 3.1

a. Reconstruction of trait evolution and biogeographic history



b. Character-state origins for region B

Type	New state (origin)	Taxa	TODI
ISE	0 to 1 (i)	A,B,C,D	1.00
	0 to 1 (ii)	M	0.67
ECD	0 (iii)	E,F,G,H,I	0.33
	0 (iv)	N	0.67

c. Community statistics

Community	Taxa	ROTI	PIE	CTDI
1	A,C,D,M,N	0.80	0.67	0.87
2	A,E,H,I	0.25	0.50	0.50
3	D,M,N	0.67	0.67	0.78

Figure 3.2. Elevational and latitudinal distribution of hylid clades in Middle America, including a summary for each clade of the range in maximum male body size among species (circle size) and types of larval habitat use (circle color; note that different colors only indicate presence of different character states, and not their relative frequencies). Widths of horizontal lines indicate latitudinal ranges, and the height of the line indicates the elevational midpoint of the clade (i.e., mean of the elevational midpoints of the species in each clade; Smith et al. 2007). Heavy lines indicate subclades within the Middle American clade, and phylogenetic relationships among these subclades are shown in gray. Thin lines indicate lineages of the predominately South American clades, where each line represents a separate hypothesized dispersal event into Middle America. Note that these latter lines are not positioned based on their elevational midpoints; rather, these lines are clustered by the larger clade to which they belong. Elevational midpoints of the Middle American species of these predominately South American clades are indicated in parentheses.

Figure 3.2

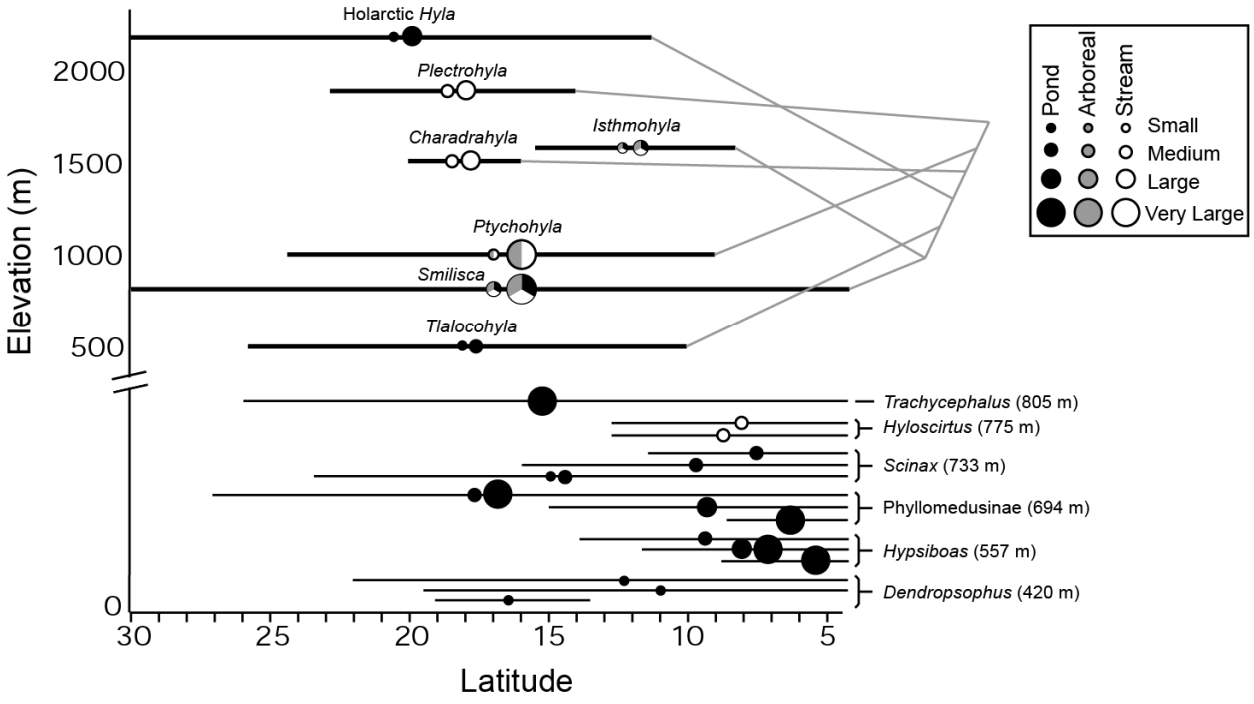


Figure 3.3. Cropped phylogeny figures showing ancestral character-state estimates for (1) body size, (2) larval habitat, and (3) biogeographic region, estimated by maximum likelihood (for the first two) and the DEC likelihood model (for the third). Phylogenies shown were chosen to illustrate the ISE and ECD events for Middle American treefrogs, but the entire phylogeny (Figs. A3.1–A3.3) was used to estimate ancestral states. Branch lengths indicate estimated ages of lineages based on penalized likelihood analysis using the younger set of calibration dates (see Materials and Methods for details). Branch colors reflect biogeographic designations (for species at tips) and ancestral-state estimates (for internal nodes), estimated under the DEC model of Ree and Smith (2008). This model distinguishes between range evolution along branches and changes that occur at cladogenesis events; thus, we show changes as occurring mid-branch (for changes along branches) or as vertical branches differing from their common ancestor (for changes at cladogenesis). Note that the position of changes along branches is arbitrary and was chosen for visual clarity. Branch colors reflect maximum-likelihood estimates (MLEs) of states, and dashed branches represent cases where alternative reconstructions fell within two $\log_e$-likelihood units of the MLE (Ree and Smith 2008). In most of these latter cases the displayed resolution still had a much higher likelihood than all other possible resolutions, with the exception of the nodes in the vicinity of the Middle American *Hyla* in Figure 3b. Because of the extreme amount of ambiguity in this case (no potential resolution had a normalized likelihood higher than 0.44 and 3–5 alternative resolutions were possible), we considered it most likely that *Hyla* recolonized Middle America only once. However, considering this clade as representing multiple colonization events did not influence our results (not shown). In Figure 3b we magnify two changes in ancestral range simply because they may be difficult to visualize at the original scale of the figure. Tips with no circles indicate taxa for which either body size, larval habitat, or both types of data were unavailable. The two colors of *Hyla arenicolor* represent both pond and stream breeding in this species. Finally, the circle left of *Ecnomiohyla miliaria* and *E. minera* is for both taxa and their common ancestor (all the same states), but has been moved to facilitate visualization of the terminal branch lengths for these taxa.

Figure 3.3a

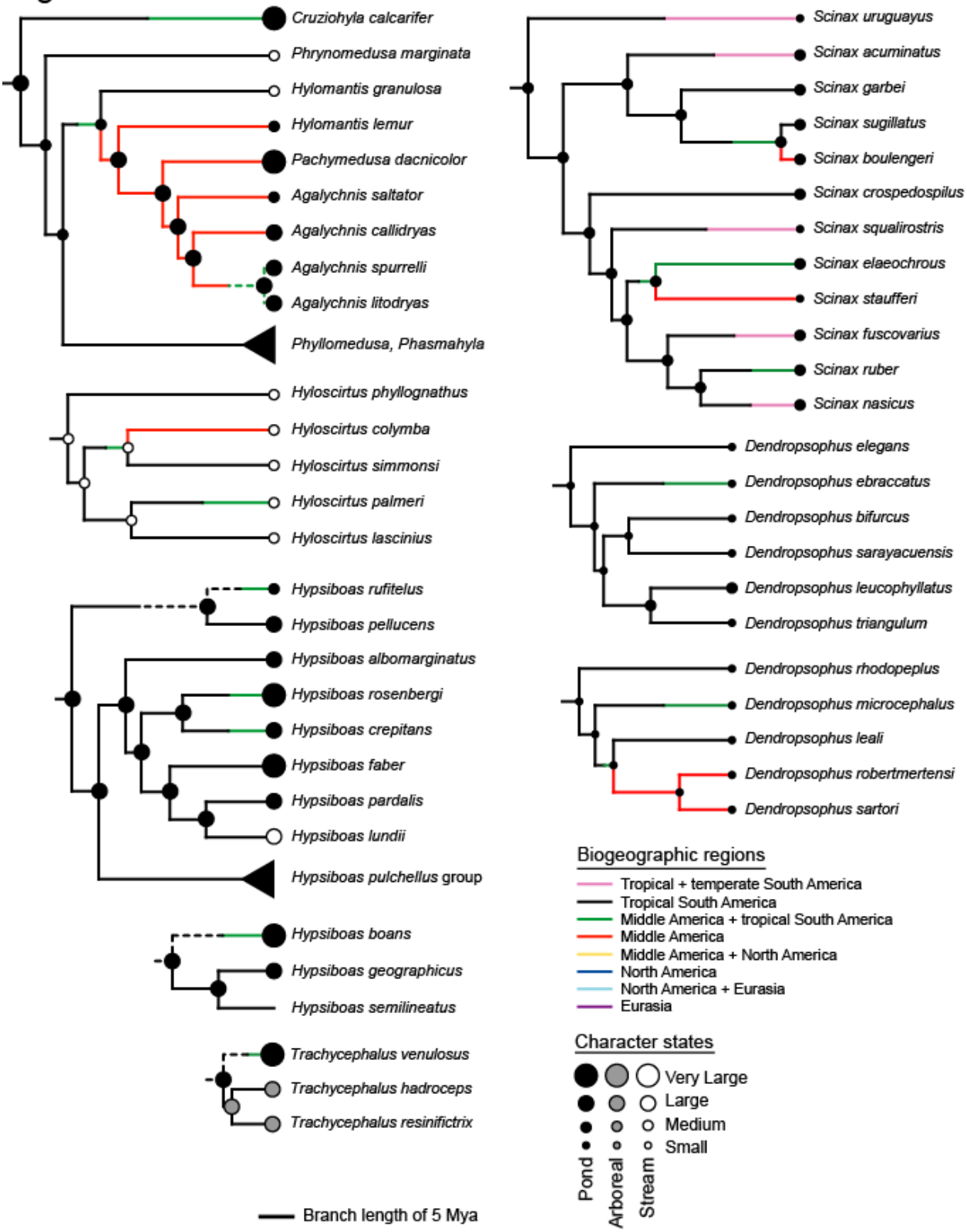

Cruziohyla calcarifer
Phrynomedusa marginata
Hylomantis granulosa
Hylomantis lemur
Pachymedusa dacnicolor
Agalychnis saltator
Agalychnis callidryas
Agalychnis spurrelli
Agalychnis litodryas
Phyllomedusa, Phasmahyla
Hyloscirtus phyllognathus
Hyloscirtus colymba
Hyloscirtus simmonsi
Hyloscirtus palmeri
Hyloscirtus lascinius
Hypsiboas rufitelus
Hypsiboas pellucens
Hypsiboas albomarginatus
Hypsiboas rosenbergi
Hypsiboas crepitans
Hypsiboas faber
Hypsiboas pardalis
Hypsiboas lundii
Hypsiboas pulchellus group
Hypsiboas boans
Hypsiboas geographicus
Hypsiboas semilineatus
Trachycephalus venulosus
Trachycephalus hadroceps
Trachycephalus resinifictrix
Branch length of 5 Mya
Scinax uruguayus
Scinax acuminatus
Scinax garbei
Scinax sugillatus
Scinax boulengeri
Scinax crospedospilus
Scinax squalirostris
Scinax elaeochrous
Scinax staufferi
Scinax fuscovarius
Scinax ruber
Scinax nasicus
Dendropsophus elegans
Dendropsophus ebraccatus
Dendropsophus bifurcus
Dendropsophus sarayacuensis
Dendropsophus leucophyllatus
Dendropsophus triangulum
Dendropsophus rhodopeplus
Dendropsophus microcephalus
Dendropsophus leali
Dendropsophus robertmertensi
Dendropsophus sartori
Biogeographic regions
Tropical + temperate South America
Tropical South America
Middle America + tropical South America
Middle America
Middle America + North America
North America
North America + Eurasia
Eurasia
Character states
Very Large
Large
Medium
Small
Pond
Arboreal
Stream

Figure 3.3b

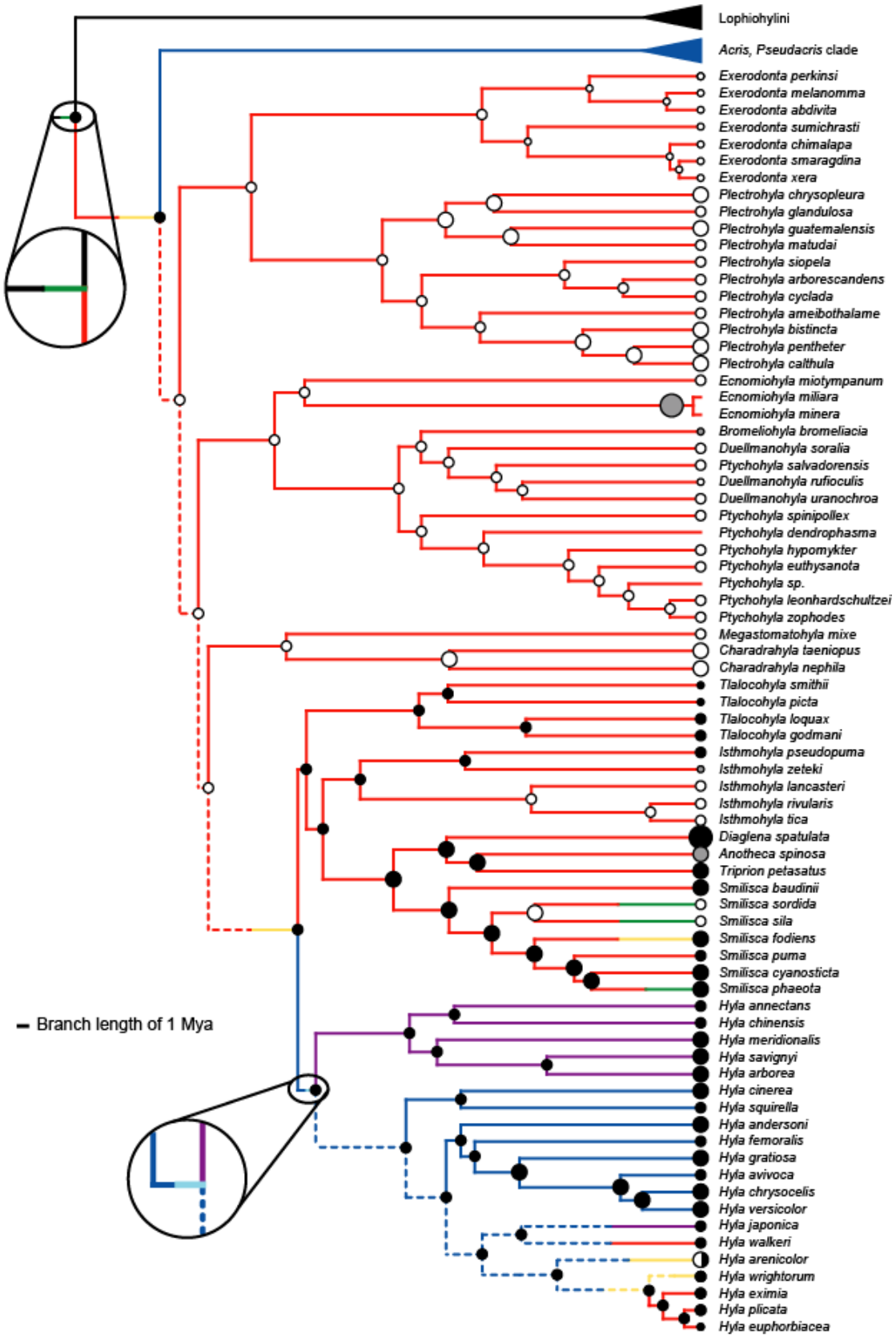
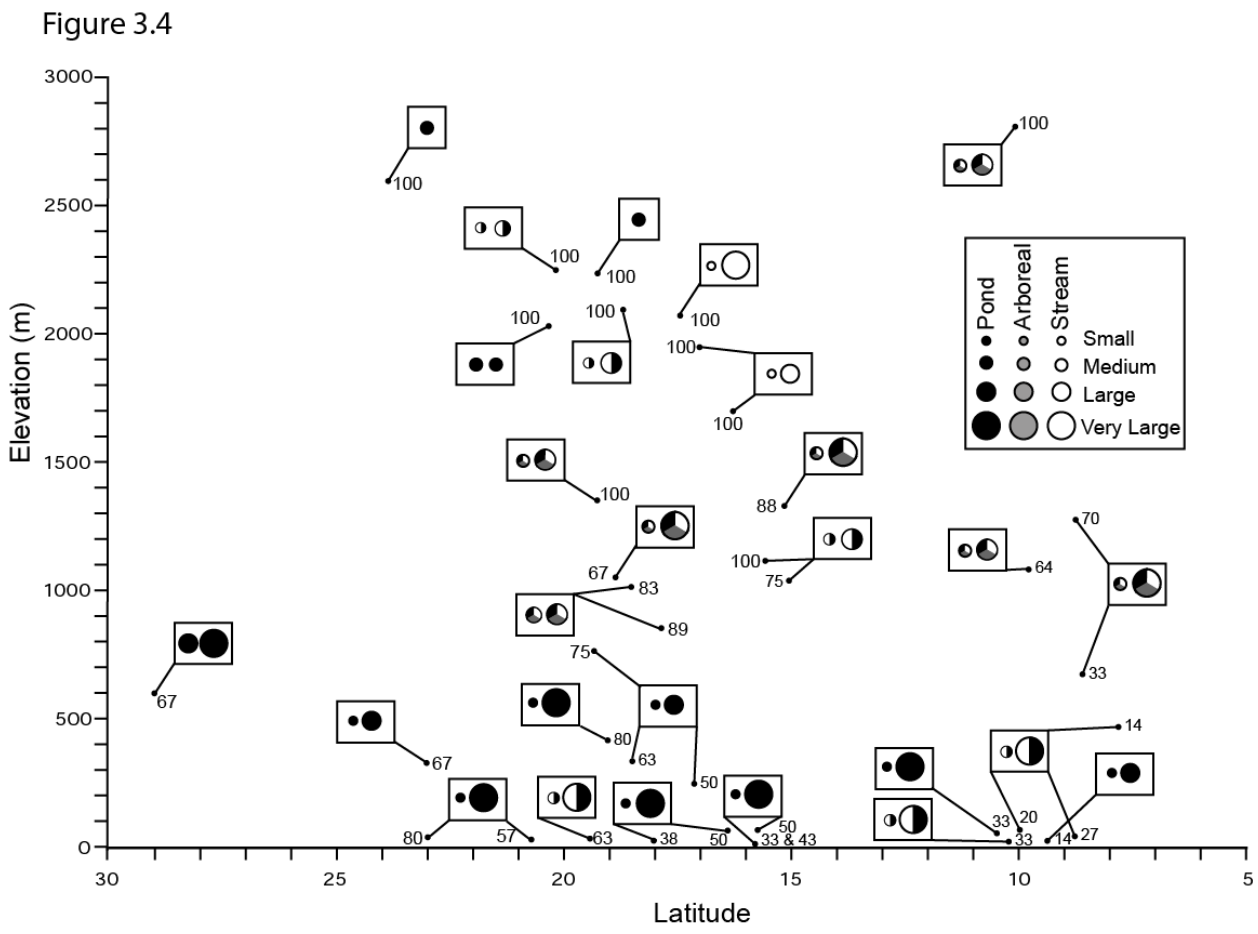

Lophiohylini
Acris, Pseudacris clade
Exerodonta perkinsi
Exerodonta melanomma
Exerodonta abdivita
Exerodonta sumichrasti
Exerodonta chimalapa
Exerodonta smaragdina
Exerodonta xera
Plectrohyla chrysopleura
Plectrohyla glandulosa
Plectrohyla guatemalensis
Plectrohyla matudai
Plectrohyla siopela
Plectrohyla arborescandens
Plectrohyla cyclada
Plectrohyla ameibothalame
Plectrohyla bistincta
Plectrohyla pentheter
Plectrohyla calthula
Ecnomiohyla miotympanum
Ecnomiohyla miliara
Ecnomiohyla minera
Bromeliohyla bromeliacia
Duellmanohyla soralia
Ptychohyla salvadorensis
Duellmanohyla rufioculis
Duellmanohyla uranochroa
Ptychohyla spinipollex
Ptychohyla dendrophasma
Ptychohyla hypomykter
Ptychohyla euthysanota
Ptychohyla sp.
Ptychohyla leonhardschultzei
Ptychohyla zophodes
Megastomatohyla mixe
Charadrahyla taeniopus
Charadrahyla nephila
Tlalocohyla smithii
Tlalocohyla picta
Tlalocohyla loquax
Tlalocohyla godmani
Isthmohyla pseudopuma
Isthmohyla zeteki
Isthmohyla lancasteri
Isthmohyla rivularis
Isthmohyla tica
Diaglena spatulata
Anotheca spinosa
Triprion petasatus
Smilisca baudinii
Smilisca sordida
Smilisca sila
Smilisca fodiens
Smilisca puma
Smilisca cyanosticta
Smilisca phaeota
Hyla annectans
Hyla chinensis
Hyla meridionalis
Hyla savignyi
Hyla arborea
Hyla cinerea
Hyla squirella
Hyla andersoni
Hyla femoralis
Hyla gratiosa
Hyla avivoca
Hyla chrysocelis
Hyla versicolor
Hyla japonica
Hyla walkeri
Hyla arenicolor
Hyla wrightorum
Hyla eximia
Hyla plicata
Hyla euphorbiacea
Branch length of 1 Mya

Figure 3.4. Simplified summary of the structure of 39 hylid frog communities in Middle America. Points indicate the latitude and elevation of each community, circles in boxes indicate the range of maximum male body sizes among species (circle size) and range of larval habitats (circle color) in each community. Boxes with only one circle indicate sites with only one species. The numbers next to each point indicate the percentage of species in the community belonging to the Middle American clade. In some cases, one box (summarizing body size and larval habitat) summarizes the ecological traits of two or more communities with similar trait ranges, as indicated by boxes connected to multiple points.



Chapter 4: Convergence and conservatism in the evolution of ecology, morphology, and performance across continents in frogs

Introduction

When we look around the world, we see convergent evolution of general "ecotypes" (similar ecology and morphology) reflected in many groups of organisms. Well-recognized examples include the parallel evolution of species of mammals similar in ecology and body form that are replicated in both placental mammals around the world and their marsupial counterparts in Australia, as well as stem-succulent plants of the families Cactaceae and Euphorbiaceae that have independently evolved similar solutions for thriving in dry climates (Futuyma 1998). In many ways, this is not surprising – if the environment and associated selection pressures are similar in different parts of the world, we may expect to see convergent changes in relatively similar (e.g. all plants, all mammals) but somewhat unrelated taxa.

Such expected convergence forms the basis of studies of adaptive radiations, lineages that speciate rapidly while diversifying ecologically to occupy a diverse array of environments (Schluter 2000). Such radiations have been documented across the tree of life, from Hawaiian silverswords (Baldwin and Sanderson 1998) to African cichlids (Kornfield and Smith 2000). Some, such as the *Anolis* lizards of the Greater Antilles (Losos 2009) and the littoral and benthic species pairs of freshwater fishes (Robinson and Wilson 1994; Schluter 2000; Snorasson and Skúlason 2004), have been replicated in many geographic locations, a phenomenon called replicate adaptive radiation (Schluter and McPhail 1993; Losos et al. 1998). Furthermore, such replicate adaptive radiations can lead to convergent community structure, meaning similar characteristics of communities (such as ecological and morphological diversity) in their constituent species (Schluter 1986; Schluter and Ricklefs 1993).

Yet aside from some well-supported examples (Glor 2010), strong evidence of replicated adaptive convergence has been documented less than we might expect, and where such replicated adaptive radiation has been well documented, it has so far has only been found on a relatively small geographic scale (Losos 2010). Despite this, we know that many clades of organisms around the world are ecologically diverse, and this diversity has evolved from a common ancestor with a specific ecological role. Although this ecological diversification may not fit the definition of adaptive radiation, it is nonetheless important. To characterize (and study) this phenomenon, we can more generally study ecological radiations, which we define herein as ecological diversification within a group of organisms that share a common ancestor.

A number of questions about the ecological diversification of organisms remain unaddressed. First, does ecological diversification necessarily lead to parallel changes in other aspects of the phenotype, such as morphology or performance? Though adaptive radiations lend support to this idea (by definition), their relative infrequency suggests that they likely lie on one end of a continuum of possible evolutionary outcomes. Indeed, a number of studies have now shown cases of "incomplete convergence" (Leal et al. 2002; Herrel et al. 2004; Langerhans et al. 2006), cases where there is evidence for some adaptive evolution but the end result is not what has traditionally been considered convergence. For example, Stayton (2006) found that not all herbivorous lizard lineages were clustered in morphospace to the exclusion of their closest relatives, yet when compared to their sister groups, they had evolved toward the same area of morphospace (which implicitly represented an "optimal" phenotype). In this case, adaptive divergence seemed to occur, yet "complete convergence" may have

been prevented by inherent differences among adapting lineages, such as different genetic or developmental systems, different adaptive landscapes, or differences in time spent adapting in a given environment up to the present day (e.g. analogous to the "time-for-speciation effect" of Stephens and Wiens 2003).

Second, although convergent evolution as a general phenomenon seems to be widespread (Schluter 2000), it does not necessarily translate into convergent community structure (Price et al. 2000; Losos 2010). However, convergent community structure has long been noted by ecologists in many organisms in many places (e.g. Orians and Paine 1983; Schluter 1986; Kelt et al. 1996), which in turn points to the fact that convergent community structure is not necessarily tied to replicated adaptive radiation. Instead, this structure can develop as a result of two processes (Losos 1996; Stephens and Wiens 2004). First, as discussed above, adaptive evolution within a geographic location can produce ecological diversity. Alternatively, ecological diversity in a given location could be the result of biogeographic dispersal with little or no accompanying changes in ecology, morphology, or other phenotypic traits (ecologically conservative dispersal; Losos 1996; Ackerly 2003; Stephens and Wiens 2004). Overall, it is reasonable to assume that in most cases, what we see in the world today is a mixture of both in situ adaptive diversification and ecologically conservative dispersal. However, few studies have directly asked whether for a given group of organisms one or both processes have been important (Stephens and Wiens 2004; Moen et al. 2009), and none has explicitly conducted a comparison on a global scale.

Third, most global-scale tests of adaptive convergence thus far have primarily focused on patterns of morphological convergence (e.g. Winemiller 1991; Stayton 2006;

Revell et al. 2007b). While these studies have been very useful, whole-organism performance capacities (e.g. locomotion, feeding) are expected to be the target of selection in comparisons of fit to the environment, with morphology only selected upon indirectly (Arnold 1983; Wainwright 1991; Irschick et al. 2007, 2008). Furthermore, the relationship between morphology and performance may not often be one-to-one (Koehl 1996; Wainwright et al. 2005; Vanhooydonck et al. 2006), and this decoupling may allow for morphological diversity where little exists in performance, or vice versa (Collar and Wainwright 2006; Wainwright 2007). As a consequence, a growing literature (e.g. Alfaro et al. 2005; Vanhooydonck et al. 2006) suggests a need for data on performance in ecologically relevant behaviors (e.g. locomotion, feeding) in addition to morphological data in order to adequately characterize phenotypic diversification (Arnold 1983; Irschick et al. 2007).

Frogs represent an excellent group for addressing questions of ecological diversification. Around the world, frogs use many types of microhabitats (Duellman and Trueb 1986), and arboreal, burrowing, semi-aquatic, and terrestrial species occur in most tropical assemblages (e.g. Glaw and Vences 1994; Inger and Stuebing 1997; Duellman 2005). Furthermore, some studies have shown diversification of these forms within single clades (Bossuyt and Milinkovitch 2000; Young et al. 2005), yet other groups show relatively few microhabitat transitions despite large species diversity (e.g. the mostly arboreal hylids; Wiens et al. 2005). Given these diverse patterns of microhabitat use and diversification, frogs are an excellent group in which to examine the diverse processes that may lead to ecological radiation and convergent community structure.

Herein we compare phenotypic diversity in three assemblages of frogs from around the world that show diverse patterns of microhabitat evolution and biogeographic dispersal. We first compare diversity in morphology and performance across assemblages, and then examine the relationships among microhabitat use, morphology, and performance. We then ask whether lineages that have undergone biogeographic dispersal with no changes in microhabitat use (i.e., ecologically conservative dispersal) have evolved in morphology and performance, or if instead such lineages show little change despite biogeographic dispersal over great distances. We finally examine the evolution of morphology and performance in association with ecological diversification within a given geographic location. We ask whether previous adaptation to an ancestral microhabitat restricts the evolution of morphology and performance in the face of microhabitat diversification, or if instead convergence with other, ecologically similar species around the world has occurred despite the relatively short timescale over which ecological diversification has occurred. We show that despite emphases in the literature on the contrast between adaptive radiation and niche conservatism (e.g. Losos 2008; Wiens 2008), both processes have been important in these assemblages of frogs.

Materials and Methods

LOCALITIES AND FROG COLLECTION

Three localities were chosen to maximize representation of the phylogenetic history of microhabitat changes in frogs. These locations were Yunnan Province, China (where aquatic and semi-aquatic frogs are most diverse and have a deep history;

Roelants et al. 2007; Wiens 2007; Amphibiaweb 2008), the Amazon rainforest near Leticia, Colombia (where arboreal and terrestrial frogs are the most diverse and have a deep history; Roelants et al. 2007; Wiens 2007; Amphibiaweb 2008), and the wet tropics of northern Australia near Darwin (only two major clades, Myobatrachidae and Hylidae, the latter of which is in situ radiation to use diverse microhabitats; Young et al. 2005). The latter location is particularly interesting, because many of the diverse microhabitat specialists here were likely derived from an ancestor that was itself a microhabitat specialist (arboreal), allowing us to address the potential imprint of past adaptation, and compare this to assemblages where this is not the case. In principle we could have also included communities that represented the Nearctic and Palearctic frog faunas. However, our broader analyses of the evolution of microhabitats in frogs suggest that we would not capture any more information than we already do with the current localities (e.g., North American faunas have members of the same clade of arboreal hylids that reached China from South America [Smith et al. 2005], and the same clade of microhylids that reached South America from the Old World [Savage 2002] is also represented in North America by *Gastrophyrne*).

Work in all three localities was done during the wet season (June-July in China, December-March in Colombia, and November-January in Australia). Frogs in China were collected in the general vicinity of Baoshan, Yunnan (25º 6.724' N, 99º 9.688' E), and performance trials were conducted at the Kunming Institute of Zoology, Chinese Academy of Sciences, in Kunming, Yunnan. Frogs in Colombia were primarily collected near Km. 11, Via Tarapacá (which runs north out of Leticia, Dept. of Amazonas; 4º 7.160' S, 69º 57.020' W), with some species found on the grounds of the Hostal Mahatu,

Leticia. Performance trials were carried out within the Laboratorio de Productos Naturales at the Universidad Nacional de Colombia Sede Amazonia. Work in Australia was conducted at the University of Sydney's Tropical Ecology Research Facility (TERF) near Fogg Dam, Northern Territory, Australia (12º 34.735' S, 131º 18.862' E). While individuals were collected from various sites near the TERF, all species examined in Australia are syntopic (e.g. all can be found at Heather and Jerry's Pond; M. Greenlees, pers. comm.). Across all sites, all frogs were collected with appropriate permits (see Acknowledgements) and all work was conducted under Stony Brook University IACUC# 2011-1876 - NF.

At each site frogs were encountered primarily during dusk and into the evening via searches on foot (along forest paths, up streams, in ponds) or along the road. Frogs were collected by hand and placed in either cloth or plastic bags and transported directly to the laboratory after each evening's search. Upon arrival, frogs were individually housed within small plastic containers. Each container had abundant air holes and wet paper towels or grass to maintain moisture and provide shelter. In China and Colombia, containers were housed within the laboratory, whereas in Australia containers were placed in an outdoor shed.

Performance data were collected from each individual over the course of about one week, and afterward all individuals were sacrificed and preserved (see below). The sex of all individuals was internally verified through inspection of gonads, and morphological data were measured from each individual (see separate sections below for more detail on performance and morphological methods).

Frog species were chosen so as to maximize sampling of microhabitat use, though search success limited which species were actually studied. As a consequence, not all microhabitat use specialists were sampled from China and Colombia (though all types occur at each site; see Lynch 2005; Yang and Rao 2008). The species used in this study and microhabitat use of each (see below) are listed in Table 4.1.

As the extra weight related to egg mass in females may affect jumping performance (Kuo et al. 2011), we primarily collected male frogs. However, due to low abundance in the field for some taxa or the inability to externally sex individuals, in some cases females were used. Preliminary data analyses indicated that sex did not influence performance, so we pooled data across sexes for all analyses.

PERFORMANCE

Overview

For each individual we collected data on performance in jumping, swimming, and clinging. These behaviors were chosen because they are likely to be divergent across species using different microhabitats. Jumping is arguably important for almost all species of frogs (Gans and Parsons 1966; Zug 1978; Emerson 1979, 1981), but variation among species might be seen if trade-offs exist with other performance variables (e.g. swimming; Nauwelaerts et al. 2007). We expect swimming to be particularly important for semi-aquatic species, and clinging should be important in arboreal or rock-climbing species (Emerson and Diehl 1980; Emerson 1991). Importantly, data on these three performance behaviors were measurable for all species despite differences in microhabitat use, whereas data on other potentially relevant

behaviors such as burrowing were not collected because we simply could not elicit this behavior from most species.

In the case of jumping and swimming, we collected data on velocity, acceleration, and power (see details below). While endurance may be important in some species (Taigen et al. 1982; Taigen and Pough 1985), we did not measure this as most species use rapid, maximal efforts during predator escape and prey capture (Duellman and Trueb 1986; but see Taigen et al. 1982) and hence tire quickly (Bennett and Licht 1973, 1974).

Jumping

Each individual frog underwent 3–5 jumping sessions, starting the day after collection. In each session, individuals were tested until performance was visibly reduced (i.e., leading to exhaustion), usually 4–5 individual jumps. Jumping sessions were conducted every other day (with swimming performance trials conducted on days in-between; see below). To control for potential activity differences due to time of day, all individuals were tested at least once each in the morning (0800–1200h), afternoon (1200–1800h), and evening (1800–0200h). The order of testing individuals was randomized within a given jumping session. Over all sessions and trials, only the single jump that represented maximum effort of each individual over all jumping sessions was used as data for further analysis (see below).

The complete takeoff phase of each jump was recorded on a TroubleShooter TS250MS (Fastec Imaging Corporation, 2004) high-speed video camera at 250 frames per second. This framing rate is generally appropriate for filming the jumps of small

vertebrates (Kuo et al. 2011). Complete jumps were not captured on film (e.g. to measure total distance, height of jump, etc.) because achieving a wider angle would have contributed to digitization error, thus potentially inflating the error for estimating velocity and acceleration profiles; Walker 1998). Jumping trials were conducted within an arena constructed of two Plexiglas panels (85 cm long by 60 cm wide, 14 cm apart), which served to form a lane through which frogs jumped parallel to the camera so as to avoid underestimating velocity and acceleration. The substrate of the arena was cardboard, though fine-grained sandpaper (1000-grit) was overlaid for toads of the genera *Rhinella* and *Duttaphrynus* because their relatively dry skin did not gain traction on cardboard. We elicited maximum effort by placing frogs within the arena and either slapping a hand on the ground just behind the frog or lightly tapping the frog's back. We also placed a dark box at the end of the track to give each frog a "goal" to elicit escape behavior.

In China and Colombia, frogs were taken directly from their cages for performance trials, as they were also housed within the laboratory. In Australia, frogs were placed within the laboratory 1h before the start of performance trials to acclimate to ambient temperature. At the time of the start of each jumping session for each frog, ambient temperature near the frog's cage in the laboratory was noted. This temperature was always within temperature range in which frogs were collected in the field for this study (results not shown; laboratory temperature ranges [in ºC] were 24.2–27.1 in Australia, 21.8–25.2 in China, and 23.5–27.6 in Colombia). These temperatures are also within the range of peak performance for tropical frogs (see review in Navas et al. 2008, their Fig. 3), and in general performance seems to be less temperature

sensitive than muscle physiology per se (Hirano and Rome 1984, James et al. 2007). Most importantly, an analysis of a subset of the data (Australian frogs) showed almost no relationship between temperature and peak velocity, peak acceleration, and peak power (effect of temperature across all species: $P \geq 0.395$ in all analyses; temperature within species: $P \geq 0.301$ for peak velocity and acceleration). The one exception to these insignificant results was a significant interaction between species and temperature (i.e., within-species effect of temperature; $P = 0.050$) on peak power, driven largely by a negative relationship between temperature and peak power in *Litoria nasuta*. However, this association was in the direction opposite of that expected and also the only significant factor of 36 estimated parameters across these three models, suggesting that it may not be more than chance. Finally, there was no tendency for the best effort for a given individual (i.e. the data that were eventually used for statistical analyses) to occur at a particular temperature (results not shown).

Swimming

The general methodology for swimming followed that for jumping (i.e., frequency of trials, time of day, and temperature). Burst swimming performance was elicited by releasing frogs at one end of a long aquarium (120 cm long by 30 cm wide by 50 cm tall) filled with water to a depth of 30 cm. Swimming performance was captured from above using the same camera as for jumping performance but at 125 frames per second, due to the slower speeds and accelerations associated with swimming. As some species had a tendency to dive instead of swim horizontally on the surface, the

angle of all dives was noted so as to convert the distance traveled in the plane of the camera to actual distance traveled (i.e., $D_{actual} = D_{camera} / \cos(\theta)$).

Clinging

We designed a clinging apparatus by gluing a metal hinge to the bottom of a Teflon®-coated non-stick frying pan (28.5 cm diameter, 6 cm deep). This surface was used because high molecular weight plastics (including Teflon®) have a similar coefficient of friction to the waxy leaves typical of rainforests (Emerson 1991; see also Burton and Bhushan 2006; and Walker 2004, p. 139). Frogs were placed on the pan when it was level, and the pan was gradually inverted from 0º up to 180º. The angle of the pan was noted at the moment in which each individual lost traction (via either sliding or falling, depending on the angle). Each frog was tested 3 times to ensure accurate estimation of maximum adhesive performance (Emerson 1991). Data used for subsequent analyses were only the maximum angle attained by each individual across all trials. As in jumping, we do not expect temperature to have strongly affected our maximum clinging angle estimates. Wet adhesion, as is used by frogs to cling to surfaces (Emerson and Diehl 1980), is governed by two primary forces (Bikerman 1971). First, Stefan adhesion is related to viscosity of the fluid, which is directly related to temperature. However, this type of adhesion likely plays a very small role frog adhesion (Emerson and Diehl 1980). The second force, capillarity, is temperature independent, and this plays the largest role in frog adhesion (Emerson and Diehl 1980; Emerson 1991). Hence, we do not expect differences in temperature across different locations to influence our estimates of clinging angle.

Data extraction from videos and performance variables

The tip of the snout was digitized in each video frame for the takeoff phase in jumping and burst-effort in swimming (i.e. complete swimming stroke). This was generally 2 frames before each effort and several frames (usually 4–5) after, thus allowing for adequate characterization of all aspects of jumping performance during take-off (e.g. maximum horizontal velocity and acceleration are not alterable after takeoff; Marsh 1994). Digitization was done in ImageJ (Ver. 1.42, Rasband 1997) using the "Figure Calibration" plug-in (F. V. Hessman, unpublished). Changes in vertical and horizontal position of digitized coordinates between frames were then converted into straight-line distance traveled between each frame. Distance-time plots were then uploaded into QuickSAND (Walker 1998) to smooth the plots and subsequently calculate velocity and acceleration profiles via numerical derivatives, using quintic spline algorithms from Woltring (1985). These algorithms smooth through distance-time data by optimizing smoothness not only in the original distance-time plots but also in the derivatives, based on the expectation that animal performance curves (such as those of velocity and acceleration) should be relatively smooth. Ideally one would use an objective criterion to smooth through the data. However, the only fully-automatic smoothing algorithm in QuickSAND (generalized cross-validation; GCV) frequently seemed unstable and produced biologically unrealistic curves (e.g. positive acceleration after jumping takeoff or during gliding in swimming; Fig. 4.1). Therefore, we manually adjusted the smoothing parameter until we achieved the least amount of smoothing possible while also reaching velocity and acceleration profiles that were realistic (see Fig. 4.1 for

examples of these characteristics; also see Marsh and John-Alder 1994; James and Wilson 2008).

We examined the following jump variables, following Toro et al. (2003) and Kuo et al. (2011): (1) takeoff angle (measured directly in ImageJ), (2) peak takeoff velocity, (3) peak acceleration during takeoff, and (4) peak mass-specific power during takeoff (maximum value of the product of the instantaneous velocity and acceleration profiles; Toro et al. 2003). In swimming, we calculated (1) peak velocity, (2) peak acceleration, and (3) peak mass-specific power. Finally, as mentioned above, our sole performance variable for clinging was maximum clinging angle.

We averaged maximum values for the above variables among individuals of a species to obtain a mean value for each performance variable for each species (Appendix Table A4.1). Although variables characterizing maximum performance were generally consistent within individuals (e.g. peak velocity and peak acceleration for a given individual were achieved in the same video), this was not always the case. However, because of the inter-dependence of many of these performance variables (i.e. a combination of the "best" values may not be biologically possible for an individual in a single effort), we chose to use the single effort characterized by the peak velocity of a given individual as its maximum effort instead of taking the maximum values across all videos. Nonetheless, species means were nearly identical regardless of how we characterized an individual's maximum effort (e.g. jumping peak velocity: $r = 0.9991$; jumping peak acceleration: $r = 0.9949$; jumping peak power: $r = 0.9997$).

MORPHOLOGY

After all performance trials had been completed at a given site, all frogs were euthanized and preserved in either formalin (Australia, China) or 70% ethanol (Colombia), depending on availability. After fixation, all specimens were later placed in 70% ethanol for long-term storage.

Photos were taken of the hands and feet of each individual to measure the area of inter-digit webbing, toe tips (e.g. enlarged toepads in arboreal frogs or the circular distal end of the toe in species without obvious toepads), and size of the inner metatarsal tubercle (which is often enlarged and used as a spade for digging in burrowing species; Emerson 1976). For each photo either the left hand or left foot was placed against a flat glass plate and photos were taken by either a Canon Powershot A590 IS (China, Colombia) or a Canon Rebel T1i digital SLR camera fitted with a 100mm macro lens (Australia). Areas of inter-digit webbing, tips of digits, and metatarsal tubercle were measured in ImageJ through digitizing the circumference of each structure, and sums of individual webbing or digit tips were taken across the entire foot or hand as an estimate of area for data analysis. Inter-digit webbing of the hands was absent in most species, so we eliminated this variable from further analysis. In most individuals photos of hands and feet were taken immediately after sacrificing them (i.e. before preservation). In a subset of the individuals, doing this procedure immediately after death was not logistically possible (due to mechanical failure of camera equipment), so this procedure was done after preservation. To test for any systematic differences between area estimates from preserved and freshly-euthanized specimens, we took photographs of both states for a subset of frogs from Colombia. A paired t-test showed consistent differences between preserved and freshly-euthanized

frogs in the estimated sizes of toe and finger tips for these frogs, though not for webbing (n = 4 species and 32 individuals; toe tips: t = -4.97, P < 0.001; finger tips: t = -5.29, P < 0.001; foot webbing: t = -1.40, P = 0.172; hand webbing: t = 1.65, P = 0.109). This difference was likely due to the tendency for toe and finger tips to pull back slightly and become concave when they are naturally adhering to the glass plate, particularly in taxa with enlarged discs (i.e., this is how they function to stick to smooth surfaces in live frogs; Emerson and Diehl 1980), resulting in lower estimates of toe tip size in freshly-killed specimens. Nonetheless, because this relationship was consistent within and across species, we corrected for differences between live and preserved specimens (foot toe tips: $A_p = 1.455A_f$, $R^2_{adj} = 0.993$; finger tips: $A_{preserved} = 1.216A_{fresh}$, $R^2_{adj} = 0.990$; where A_p = size of area on preserved specimens, A_f = area on fresh specimens, and equations estimated across all 32 individuals regardless of species).

Next, we measured 10 external variables that are potentially of functional significance: (1) snout-to-urostyle length (SUL; tip of snout to posterior end of urostyle); (2) femur length (tip of urostyle to knee); (3) tibiofibula length (tip of knee to tip of heel / proximal end of the tarsus); (4) tarsus length (tip of heel to proximal edge of inner metatarsal tubercle); (5) foot length (proximal edge of inner metatarsal tubercle to distal end of outstretched fourth toe); (6) head length (posterior corner of jaw to tip of snout); (7) head width (distance between posterior corners of jaw); (8) humerus length (tip of elbow to insertion point at the body wall); (9) radioulnar length (distal edge of outer palmar tubercle to elbow); and (10) hand length (distal edge of outer palmar tubercle to tip of third finger). These variables were chosen so as to reflect variation in overall body size (variable 1), relative hindlimb (vars. 2–5) and forelimb length (vars. 8–10), and

head shape (vars. 6–7). So as to reduce redundancy in our data and because preliminary analyses showed very little variation among species in individual elements of the hindlimbs and forelimbs, we summed those sets of variables (vars. 2–5 and 8–10, respectively) to produce a single measurement for each limb. All external linear measurements were made on preserved specimens.

Finally, the muscle mass of the left hindlimb was quantified in each individual after preservation because of the large role that hindlimb muscle mass plays in performance in frogs (James et al. 2007). The two major muscle groups of the legs (those associated with the femur and the tibiofibula) were dissected out of the left leg via cutting at the origin and insertion points of these muscles. These muscle groups were chosen because they contain the major extensors used in jumping and swimming (primarily the plantaris longus on the lower leg and various muscles on the upper leg; see Marsh 1994; Nauwelaerts et al. 2007; James and Wilson 2008). Muscles were then gently patted dry with tissue paper to absorb surface alcohol and weighed on a mass scale accurate to 0.01g (China) or 0.001g (Colombia, Australia). Finally, the entire frog was blotted dry and weighed, and relative leg muscle mass was calculated simply as the muscle mass from the left leg divided by total frog mass. Species means were calculated for each variable and these were used as data for all subsequent statistical analysis (Appendix Table A4.2).

Some studies have shown changes in measurements done before and after preservation in frogs, thus questioning the utility of preserved specimens (Lee 1982; Deichmann et al. 2009). However, we are interested in relative differences among species and any possible effects of preservation should not introduce systematic error

that would affect interspecific comparisons. This is supported by Deichmann et al. (2009), who showed that the absolute reduction in snout-to-urostyle length (SUL) across 14 species was proportional to SUL itself (i.e., relative differences among species were maintained after preservation).

MICROHABITAT USE

Data on microhabitat use were gathered from the literature. Each species was placed into one of four broad categories: (1) arboreal (typically found above ground level on vegetation), (2) aquatic/semi-aquatic (generally found in or adjacent to water bodies, such as ponds or streams), (3) terrestrial (generally found far from water and on the ground), and (4) burrowing (digs its own burrows with rear feet; note that some frogs burrow head-first [Heyer 1969; Emerson 1976; Ponssa and Barrionuevo 2012], but none were included in this study). Species were categorized based on adult activity outside of the breeding season. Behavior associated with breeding was not considered here because most species in this study associate with water for breeding (yet would not all be considered aquatic or semi-aquatic). We note that many burrowing frogs may not be active in their burrows (and might therefore be considered terrestrial instead), but we nevertheless use this category to include this potentially important behavior, as it involves distinct selection pressures (and hence adaptations) not found in other frogs (Emerson 1976).

In most cases, literature sources categorized a given species using the above category names. For those species whose designations were unclear we placed them within a category based on behavioral descriptions in the literature. Additionally, we

verified these designations during fieldwork. The one exception to this was for burrowing species, which were usually encountered above ground, as encountering such species in burrows or in the act of burrowing is exceptionally rare. Data on microhabitat use are listed in Table 4.1.

PHYLOGENY

We used three approaches to obtain a phylogeny and branch lengths for comparative analyses. First, we used the maximum likelihood phylogeny and branch lengths from Pyron and Wiens (2011), which is the most comprehensive analysis of anuran phylogeny to date. Second, we estimated a time-calibrated phylogeny using the Bayesian uncorrelated lognormal approach (in BEAST; Drummond et al. 2006; Drummond and Rambaut 2007) and using the molecular data of Pyron and Wiens (2011). However, for this analysis, we constrained the topology to that of Pyron and Wiens (2011), to reduce errors in the topology associated with limited taxon sampling. Third, we used the same data and method (BEAST) to simultaneously estimate the phylogeny and divergence times. This latter approach allowed us to incorporate uncertainty in both the phylogeny and branch lengths.

The data set of Pyron and Wiens (2011) consisted of 12 genes (3 mitochondrial and 9 nuclear), including 16S (up to 1,855 bp per species), 12S (1,230 bp), RAG-1 (2,697 bp), cyt-*b* (1,140 bp), TYR (600 bp), RHOD (315 bp), SIA (397 bp), POMC (651 bp), CXCR4 (753 bp), H3A (328 bp), NCX1 (1,335 bp), and SLC8A3 (1,132 bp). These data were compiled from many previous studies of amphibian phylogeny that utilized this partially overlapping set of genes. Not all genes have data for all species, but this

appears to have little impact on the phylogenetic analyses (Pyron and Wiens 2011; see also Wiens and Morrill 2011).

Some of the species used in the performance analyses were not included in the molecular data set of Pyron and Wiens (2011). However, most species could be easily accommodated by utilizing species included in the data matrix that appear to be closely related to the species sampled for performance data. Specifically, we made the following replacements. (1) *Amolops mantzorum* (molecular) for A*. tuberodepressus* (performance), given that some authors consider *A. tuberodepressus* to be a synonym of *A. mantzorum* (Fei et al. 2009). (2) *Calluela guttulata* (molecular) for *Calluela yunnanensis* (performance), the only *Calluela* included in the tree of Pyron and Wiens (2011). (3) *Chiasmocleis shudikarensis* (molecular) for *C. bassleri* (performance), an arbitrary selection between the two *Chiasmocleis* in the tree of Pyron and Wiens (2011). (4) *Hypsiboas sibleszi* (molecular) for *H. hobbsi* (performance), given that both are members of the *Hypsiboas punctatus* group (Frost 2011). (5) *Hypsiboas cinerascens* (molecular) for *H. punctatus* (performance), given that both are in the *H. punctatus* group (Frost 2011) and are very similar morphologically. (6) *Rhinella dapsilis* (molecular) for *Rhinella proboscidea* (performance), given that both belong to the complex of species referred to as *Rhinella margaritifera* (Frost 2011). (7) *Uperoleia laevigata* (molecular) for *U. lithomoda* (performance), given that *U. laevigata* is one of only two *Uperoleia* species in the molecular data set. Finally, although *Limnodynastes convexiusculus* is in the tree, we used *L. salmini* to represent this taxon given its better sampling of genes. Given the broad phylogenetic and temporal scale of this study,

these congeneric replacements should have little impact on the estimated topology and branch lengths.

Analyses with BEAST (v1.5.4) utilized the following settings. Following Pyron and Wiens (2011), we used a separate partition for each gene (with unlinked substitution models but with the clock model and tree model linked across genes). We used the GTR+I+Γ model for each gene (general time reversible with parameters for invariant sites and a gamma distribution of rates among variable sites), with estimated base frequencies and 4 rate categories for variable sites. Protein-coding genes were each partitioned based on codon positions, and ribosomal genes (12S and 16S) were each partitioned based on stems and loops. Substitution and rate heterogeneity parameters were unlinked across these partitions. Dating analyses used an uncorrelated lognormal relaxed clock with an estimated rate. For the unconstrained analysis, a Yule speciation model was used. Given that our sampling of species spanned relatively few of the most relevant fossil taxa for dating, we used previously estimated dates for two important clades as priors (Hyloidea, Ranoidea). We used the estimated ages from Wiens (2011a; penalized likelihood analysis), which utilized an extensive set of fossil calibration points and a slow-evolving nuclear gene. Similar dates were estimated for these two clades using alternate methods and several nuclear and mitochondrial genes (Roelants et al. 2007). Specifically, we used a normal prior on the ages of these clades, with a mean of 73.5 Myr for Hyloidea and 111.9 for Ranoidea. We used an arbitrary standard deviation of 5 Myr, yielding a 95% prior interval of 65.3–81.7 Myr for Hyloidea and 103.7–120.1 Myr for Ranoidea.

For the constrained analyses, we set the monophyly of all clades to match Pyron and Wiens (2011), an analysis based on the same genes but including >2,800 taxa. For the unconstrained analysis, no clades were set to be monophyletic. Each analysis was run for 50 million generations, sampling every 1000 generations. A burn-in of 5 million generations (first 10%) was used. For the unconstrained analysis, we ran two replicate analyses and combined the results, and we ran three replicate analyses for the constrained analysis.

Results were checked using Tracer v1.5.4 (Drummond and Rambaut 2007). For all analyses, the effective sample size (ESS) for estimated dates was >200 in all replicates (although other parameters had ESS < 200). In addition, mean estimates for major clades (e.g. the root, Bufonidae, Dendrobatidae, Hylidae, Microhylidae, Ranidae) for replicate analyses were very similar (e.g., within 1 Myr of each other). This concordance strongly suggested that the estimated dates were stable. For the constrained analyses, the final set of dates was taken from the third replicate (which had the highest mean likelihood). A set of trees with branch lengths was subsampled every 100,000 generations from this analysis for comparative analyses, leaving a set of 450 post-burn-in trees. These trees had identical topologies but somewhat different branch lengths. A consensus tree of these post-burn-in trees is presented in Figure 4.2 and was used for further comparative analyses.

For the unconstrained analyses, the two replicate analyses also gave very similar estimates of topology and clade support (posterior probabilities). We combined the results of the two replicate analyses using LogCombiner v1.5.4 (Drummond and Rambaut 2007). We again subsampled the trees every 100,000 generations, leaving

900 post-burn-in trees for comparative analyses. The majority-rule consensus of the post-burn-in trees showed notable differences with the likelihood tree of Pyron and Wiens (2011) and other studies, including non-monophyly of Hylidae and of the clade of Bufonidae+Dendrobatidae. However, these unusual relationships are only weakly supported. Although these trees may not represent the best possible estimate of topology for these species, the variation in topology allowed us to estimate the robustness of our results to a reasonable alternative topology, as we used the consensus tree for preliminary comparative analyses (see below).

DATA ANALYSIS

Principal components analysis.

We first conducted principal components analysis (PCA) on both the performance and morphological data across all species in the study. We did this for two reasons. First, we wanted to account for redundancy in our data, as we expected most traits to scale with size, as is common for both morphology (e.g. Jolicouer 1963; Moen et al. 2009) and performance (Emerson 1978; Zug 1978; Wilson et al. 2000). Second, we used PCA to isolate this variation in body size from size-independent variation, as we were primarily interested in non-size-related variation among species within locations and across different microhabitats, given that large size variation occurred within all microhabitat categories (see *Relationship of microhabitat use to morphology and performance* below). Morphological data were first ln-transformed to achieve homogeneity of variances and ensure linear relationships among variables. PCAs were conducted on the correlation matrices of traits (instead of covariances; see Manly

1994), given that (1) morphological data consisted of linear, area, and mass measurements, and (2) performance data represented various scales of measurement (e.g. velocity, acceleration, power, and angle).

We carried out the PCA on both raw phenotypic data and phylogenetically-transformed data, the latter following Revell (2009). Both procedures were carried out in R ver. 2.15 (R Development Core Team 2012), and phylogenetic PCA was conducted with the package *phytools* (Revell 2012). Given that both procedures gave similar results (e.g. vector correlation of 0.9996 between the eigenvectors of PC1 from standard PCA and phylogenetic PCA using the BEAST constrained tree; vector correlations among all three trees and standard PCA ranged from 0.9993–0.9999), we used PC scores from the phylogenetic PCA for all subsequent analyses. All PC axes were retained for further analyses instead of using a procedure to drop axes from further consideration (i.e., using a procedure to determine "significant" axes, such as in Franklin et al. 1995). We chose to retain all axes because (1) variation explained by each axis did not decrease drastically as PC dimensions increased (Table 4.2); (2) there was no inherent computational advantage to dropping axes, and (3) given that sample sizes for some microhabitat categories were low relative to others (e.g. 4 semi-aquatic and 5 burrowing species versus 17 terrestrial and 18 arboreal species), ecologically important variation could lie in higher dimensions simply because fewer species contributed to that variation (and thus its low contribution to total variation would push it to higher PC dimensions). In sum, we retained all PC axes so as to fully characterize variation among species and microhabitat categories. However, we note that we obtained qualitatively similar results in all subsequent analyses when using only

principal components 1–4 (in both morphology and performance), retained based on the Parallel Analysis approach of Franklin et al. (1995).

Comparison of morphological and performance diversity of assemblages.

We compared variation in overall disparity (diversity) of the PC spaces in morphology and performance for each of the three geography-based assemblages of species to understand whether assemblages have converged in morphological and/or performance diversity. These analyses were done for each set of variables separately so as to compare whether patterns in morphology matched those for performance.

We used two measures of disparity so as to compare both the the dispersion, or packing, of species in PC space and also the total range of values in that space (Sidlauskas 2007). Dispersion in PC space was calculated as the variance of species around the mean of their respective assemblage, computed as the mean-squared Euclidean distance of species from their respective assemblage mean (Van Valen 1974, Foote 1993). The second measure (range in PC space) was the volume of the convex hull that encloses all data points of an assemblage (Drake and Klingenberg 2010), calculated using the Qhull algorithm (Barber et al. 1996) implemented in the *geometry* package in R. Because this metric only depends on data points at the outer edges of a given distribution, it is a measure of the extreme values of the PC space. Pairwise comparisons among assemblages in values of these two metrics were conducted among the three assemblages, and statistical significance was assessed using both F-tests (variances) and permutation tests (both metrics). Permutation involved randomly resampling deviations from the respective group means (following Drake and

Klingenberg 2010). Statistical tests were two-tailed to evaluate both significant convergence (more similar than expected by chance) and divergence (higher disparity in one group compared to the other).

Phylogenetic transformation of data

We accounted for non-independence due to shared phylogenetic history for all subsequent statistical tests on PC scores. However, even though we used the phylogeny to conduct the PCA, scores from such an analysis are not necessarily phylogenetically independent across species, neither within a given axis nor with respect to other variables (Revell 2009). Thus, we phylogenetically transformed our PC scores by multiplying them by the matrix **D** (as defined by Garland and Ives 2000). Although there are a number of possible ways to produce this matrix such that it has the properties set forth by Garland and Ives (2000) (D. C. Adams and F. J. Rohlf, pers. comm.), we followed the implementation of Blankers et al. (2012). This method rotates the original data into a space that reflects phylogenetic relatedness, scales the observed covariances among species by the expected covariance based on the branch lengths (which in turn reflect the underlying evolutionary model, such as Brownian motion or Ornstein-Uhlenbeck; Martins and Hansen 1997), then rotates the data back into the original data space (Rohlf 2001; D. C. Adams and F. J. Rohlf, pers. comm.). An advantage of using this method to transform data (over, for example, independent contrasts; Felsenstein 1985) is that the transformed data are in the original data space, meaning that it generates values for individual species and thus we can analyze the properties of individual species (e.g. microhabitat use, assemblage membership).

For this transformation, we started with the PC scores from the phylogenetic PC using a given phylogeny, then used the same phylogeny to compute phylogenetically-independent data. While all analyses were done using our three different phylogenies (see *Phylogenetic Methods* above), we almost always found high quantitative similarity in the results from all three trees. Thus, unless otherwise indicated, all quantitative results are from the time-calibrated BEAST tree constrained to fit the maximum-likelihood topology based on including 2800 species (i.e., the phylogeny in our Fig. 4.2). All phylogenetic transformations were performed using the R code written and provided by Blankers et al. (2012).

Relationship between morphology and performance

We initially analyzed a series of simple models between our morphological and performance variables to ensure that our data fit well-established biomechanical relationships, given that many such relationships have been estimated within species (e.g. Nauwelaerts et al. 2007) or within a specific type of microhabitat specialist or clade (e.g. arboreal rhacophorid frogs; Emerson 1991). In other words, we wanted to ensure that a multivariate analysis across all species (see below) was not compromised by pooling species across microhabitat categories, given that such analyses can be challenging to interpret. All analyses were phylogenetic generalized least-squares analyses assuming Brownian motion (Martins and Hansen 1997), and all size-independent variables were estimated using the phylogenetic size-correction procedure of Revell (2009) in the package *phytools* in R (Revell 2012).

We first examined the relationship between body size, the sum of toe- and finger-tip size, and clinging angle in a linear model, with the first two variables as predictors of the third. Biomechanical principles dictate that for a given body size, increased toe-tip size should results in a higher clinging angle due to the increased force of adhesion (Emerson and Diehl 1980; Emerson 1991). Additionally, body size itself should reduce clinging angle because it is mass times the acceleration due to gravity that is the force that causes separation of a frog from its substrate (Emerson 1991). We conducted this analysis on two sets of taxa. The first set was across all species in this study. The second set was composed of just the arboreal taxa with expanded toe pads, as this group most clearly was using only the toe pads for adhesion (i.e., as compared to other taxa with small toe tips that often achieved adhesion via pressing their venter against the substrate; Moen, unpublished results).

Next, we examined the relationship between relative muscle mass in the hindlimb versus acceleration and power in both jumping and swimming. Muscle mass is very important for producing force (and in turn, acceleration and power) during jumping across all animals (James et al. 2007). Hence, we would expect that higher muscle mass leads to greater power and acceleration. We conducted these analyses across all species, given that there is no clear reason why this relationship should be affected by microhabitat use. For this analysis, we conducted four bivariate regressions: (1) peak jumping acceleration; (2) peak jumping power; (3) peak swimming acceleration; and (4) peak swimming power, all regressed on relative muscle mass.

Finally, we examined the relationship between relative muscle mass, relative leg length, and peak jumping velocity. As noted above, acceleration is increased via higher

force output by the legs, and force output is related to muscle mass (Marsh 1994; James et al. 2007; James and Wilson 2008). All things equal, higher acceleration should lead to higher takeoff velocity; thus, higher muscle mass should result in higher takeoff velocity as well. Additionally, relatively longer legs increase the time of the takeoff phase of jumping, and if we assume that acceleration is held constant, a longer takeoff phase will result in a higher peak velocity during takeoff (Marsh 1994; Marsh and John-Adler 1994). Thus, we predicted a positive correlation between relative muscle mass and peak jumping velocity, and likewise a positive correlation between relative leg length and peak jumping velocity. We therefore estimated a single model in which peak jumping velocity was regressed on relative leg muscle mass, relative leg length, and snout-to-urostyle length (SUL). SUL was put into the model to control for variation simply due to overall size, given that the latter is often positively correlated with takeoff velocity (Emerson 1978; Zug 1978; Wilson et al. 2000).

Next, to assess the overall multivariate relationship between morphology and performance, we compared the covariation between morphology and performance across all species by conducting a two-block partial least-squares analysis (2B-PLS; Rohlf and Corti 2000). This is a multivariate approach that constructs linear combinations of the original variables in a way that best describes the covariation among sets of the original variables (in this case, morphological and performance variables). Although the general aim of 2B-PLS is similar to the more familiar canonical correlation analysis (CCA; Manly 1994), we chose to use the former because CCA may not necessarily produce linear combinations of variables that account for the most covariance among datasets (Rohlf and Corti 2000).

Two-block partial least squares takes either a correlation or covariance matrix of the original variables, defines a submatrix of correlations or covariances among variables of different sets (i.e. $\mathbf{R}_{12}$ of Rohlf and Corti 2000), and uses a singular-value decomposition (Jackson 1991) to decompose this submatrix into the product $\mathbf{F}_1\mathbf{D}(\mathbf{F}_2)'$. The matrix **D** is a diagonal matrix of singular values (note that this is distinct from the **D** utilized above for phylogenetic transformation), while $\mathbf{F}_1$ contains the weights for the linear combinations of the original variables of the first set (here, the morphology principal components) and $\mathbf{F}_2$ likewise contains the weights for the second set (here, the performance principal components). These weights can be used to interpret the contribution of the original variables to each of the latent (new) variables of the 2B-PLS, while the singular values indicate the strength of covariance among the latent 2B-PLS variables in each dimension (Rohlf and Corti 2000).

As in other analyses, our variables were phylogenetically-transformed PC scores of both morphology and performance. All 2B-PLS calculations were done directly in R using a singular-value decomposition of the covariance matrix of PC scores, following Rohlf and Corti (2000).

Relationship of microhabitat use with morphology and performance

A statistically significant relationship between microhabitat use and both morphology and performance is necessary in order to ask how ecological diversification (or lack thereof) influences the evolution of morphology and performance (see following sections). Thus, we next conducted one-way MANOVAs on the relationship between microhabitat use and the phylogenetically-transformed PC scores in morphology and

performance. All MANOVA models were estimated in R using the function 'Wilks.test' in the package *rrcov* (Todorov and Filzmoser 2009). Preliminary univariate ANOVAs showed that microhabitat specialists were not distinguishable in terms of size (morphology PC1: $F_{3,40} = 0.068$, $P = 0.977$; performance PC1: $F_{3,40} = 1.402$, $P = 0.256$), so MANOVAs were only conducted on PCs beyond PC1 so as to focus on size-independent variation. Likewise, we only considered these size-independent axes (i.e. PC2–10 for morphology, PC2–8 for performance) in remaining analyses so as to focus on those axes of variation that distinguish microhabitat specialists.

Testing for ecologically conservative dispersal in morphology and performance

To examine whether the phenotypic diversity in a given assemblage is a consequence of in situ evolution or dispersal of ecotypes from other regions, we examined three clades of frogs that are found in both China and Colombia (i.e. they have dispersed around the world) but show similar microhabitat use in both places. These clades are Microhylidae (terrestrial; China: *Microhyla fissipes*, Colombia: *Chiasmocleis bassleri* and *Hamptophryne boliviana*), Bufonidae (terrestrial; China: *Duttaphrynus melanostictus*, Colombia: *Rhinella margaritifera* and *Rhinella proboscidea*), and Hylidae (arboreal; China: *Hyla annectans*, Colombia: genera *Dendropsophus*, *Hypsiboas*, *Osteocephalus*, *Scinax*, and *Sphaenorhynchus*).

For each comparison of Chinese versus Colombian members of the three clades, we calculated the pairwise Euclidean distance in morphology and performance (separately) between the single species that occurs in China and its closest relative in

Colombia (Hylidae, *Osteocephalus planiceps*) or the mean value of its two equally closest relatives (Microhylidae and Bufonidae; see above and Fig. 4.2).

Given that these distances in PC space are only useful relative to similarly-calculated distances among other taxa, we also calculated pairwise distances among all species similar in microhabitat use (136 and153 comparisons among terrestrial and arboreal species, respectively), as well as all 209 comparisons of species from China and Colombia. This allowed us to ask, for example, "How different are the terrestrial microhylid frogs found in China and Colombia compared to differences among all terrestrial frogs or among all pairs of species from China and Colombia?"

How do morphology and performance evolve in association with microhabitat transitions in an in situ radiation?

The Australian hylids have undergone microhabitat diversification in as little as 42 My (their crown age in our phylogeny; Fig. 4.2), whereas their sister group in our phylogeny, the South American hylids, are all arboreal and are dated to be about 58.2 My old (crown age; Fig. 4.2). Using the dates of Wiens et al. (2011), Australian hylid frogs seem to have colonized Australia from South America via an Antarctic land bridge sometime between 72 and 58 My ago (Sanmartín and Ronquist 2004). Given the diversity in microhabitat use within the hylid frogs of Australia (genus *Litoria*; Fig. 4.2), we asked whether this relatively recent diversification in ecology has also resulted in diversification of morphology and performance in manner that fit adaptive expectations, given that frogs in similar microhabitat categories around the world cluster in both morphological and performance space (see Results). Conversely, we might expect to

see that prior evolutionary history may leave a footprint. Specifically, because Australian hylid frogs arrived from South America presumably as arboreal frogs (most *Litoria* are arboreal and the clade is nested within a large, mostly arboreal clade; Duellman and Trueb 1986, Wiens et al. 2006), we might expect that Australian non-arboreal hylids have some aspects of morphology and performance more consistent with the ancestral arboreal microhabitat despite their current microhabitat use.

To assess whether remarkable diversification in morphology or performance has been associated with the diversification of microhabitat use in Australia, we compared the rates of evolution of the hylid frogs of Australia (*Litoria*) to those of their sister clade in our phylogeny, the Colombian hylid frogs (the one exception to this is *Hyla annectans*, which is nested in this group and occurs in China, but from here on we refer to the group as "Colombian" for simplicity). We used the likelihood methods of O'Meara et al. (2006) and Revell and Collar (2009) to estimate rates of evolution for PC axes of morphology and performance (we only examined the first three axes for computational tractability) and to calculate likelihoods of various models (see below). Although in principle one could use these methods to also estimate the evolutionary covariances among traits, we did not do so here because the phylogenetic PCA removed such covariance among PC axes (Revell 2009). Tests for rate variation between Australian and Colombian hylid frogs were carried out separately for morphology and performance. We used a likelihood-ratio test with three degrees of freedom to compare a model with one, global set of rates of evolution (across the three PC axes; 3 rates estimated) with a model in which rates were allowed to differ between the two clades (6 rates estimated).

We utilized the equations of Revell and Collar (2009) to write our own code in R to estimate rates, calculate likelihoods, and compare models.

We next designed three tests to determine whether the amount and direction of evolution in *Litoria* has been consistent with adaptive predictions (i.e., convergence). First, if adaptive evolution has overcome historical constraints, we would expect the distance (in morphology and/or performance) between the *Litoria* using a novel microhabitat (e.g. semi-aquatic) and other frog species using the same microhabitat to be smaller than the distance between these *Litoria* and those in the ancestral microhabitat (arboreal). Distances among these groups in both morphology and performance can easily be calculated and compared.

Second, if divergence in *Litoria* was adaptive, we would expect that the direction of divergence in non-arboreal *Litoria* would be toward the area of phenotype space occupied by other species using similar microhabitats. This leads to two related questions. First, how far along the expected trajectory of evolution have lineages evolved relative to the length of this trajectory? Alternatively, what proportion of a lineage's observed divergence from its ancestor has been in the direction expected? To assess these possibilities, we can calculate an expected direction and amount of evolution based on the vector (in morphology or performance space) between *Litoria* in the ancestral ecological role and other species of frogs in the novel microhabitat role, as we can consider the mean value of all other species of frogs using a given microhabitat, some for a much longer time period than in *Litoria*, as representing an approximate "optimum" (Fig. 4.3). In statistical terms, this vector could be viewed as the maximum-likelihood path of divergence. Likewise, we can calculate a vector of observed change.

This is a vector that begins at the mean phenotype of arboreal *Litoria* and ends at the mean value for *Litoria* in the novel microhabitat (Fig. 4.3). The projection of the latter (observed change) onto the former (expected change) is the amount of divergence between arboreal *Litoria* and a given lineage of non-arboreal *Litoria* along the expected trajectory of evolution. This projection (D_{proj}) is simply the cosine of the angle between the two vectors (observed and expected divergence; D_{obs} and D_{exp}, respectively) multiplied by the observed amount of divergence ($D_{proj} = D_{obs} \cdot \cos \theta$; Fig. 4.3; Hansen and Houle 2008).

We also note here a number of metrics that can be conceptually useful when interpreting these tests. First, the angle between the vectors of expected and observed divergence can itself be heuristically useful. For example, an angle of 0º would indicate evolution in the expected direction, 90º would indicate evolution orthogonal to that expected, and 180º would be completely opposite to the expected direction (Collyer and Adams 2007). Second, in a related sense, an understanding of the covariances within each of these groups can give a sense for strength of selection (see, for example, Estes and Arnold 2007) and evolutionary "path of least resistance" (Schluter 1996). In terms of strength of selection, we can view the mean value and covariances within a given group as a multivariate selection surface (following Estes and Arnold 2007). If there is much variation among non-*Litoria* species in a given microhabitat, then a large difference between the mean value of this group and the *Litoria* species in the same microhabitat would not be as surprising, as weak selection in this microhabitat may permit diverse morphological and performance phenotypes. In the case of the evolutionary line of least resistance, the phenotypic covariance of arboreal *Litoria* (i.e.,

those in the ancestral microhabitat) could be viewed as predicting the likelihood of divergence in the direction of the phenotypic optimum. For example, if variation along the axis of expected divergence is very high, then divergence may be expected to be relatively "easy" and rapid (Schluter 1996). Alternatively, if the variation is very low in this direction, an observation of convergence would seem even more surprising. Though this variation is incorporated in statistical tests, its visualization can be useful and thus we present it graphically in our results.

To address the above two questions of divergence in the expected direction, we divide this projection by the relevant quantity. The projection divided by the total amount of expected change ($p_{exp} = D_{proj} / D_{exp}$) indicates how far along the expected trajectory of evolution non-arboreal *Litoria* have diverged from arboreal *Litoria* relative to the total expected amount of divergence toward non-*Litoria* species that use the same microhabitat. Alternatively, the projection divided by the observed divergence between the two groups of *Litoria* will give the amount of divergence in the expected direction relative to the total observed divergence ($p_{obs} = D_{proj} / D_{obs}$). Note that the latter quantity is mathematically equivalent to the vector correlation between the two divergence vectors, as that correlation is the cosine of the angle between the vectors (i.e. $p_{obs} = D_{proj} / D_{obs} = (D_{obs} \cdot \cos \theta) / D_{obs} = \cos \theta = r_{vec}$).

This framework can allows us to address many questions of convergence and the potential role of history. Of particular interest would be the possibility that the distance between arboreal *Litoria* and those species in the novel microhabitat could be small, reflecting a historical footprint on evolution, but the evolutionary change could still be in the expected direction, reflecting adaptive evolution (Stayton 2006).

To carry out these tests, we first calculated the centroids in morphological and performance space for arboreal *Litoria*, for *Litoria* in each novel microhabitat (i.e. burrowing, semi-aquatic, and terrestrial), and for other species of frogs in our dataset that use the non-arboreal microhabitat types that have evolved within *Litoria*. We then calculated distances between the centroid for arboreal *Litoria* and *Litoria* in each novel microhabitat (D_{obs}), as well as distances between the latter *Litoria* and the centroid of other frog species in a similar microhabitat (D_{micro}; for example, semi-aquatic *Litoria* with other semi-aquatic species around the world; Fig. 4.3). The ratio of these distances (D_{micro} / D_{obs}) was used as a test statistic (see below).

Next, for each novel microhabitat, we calculated the vector correlation (i.e. p_{obs}; following Collyer and Adams 2007) between the vector linking arboreal *Litoria* with *Litoria* in the novel microhabitat (e.g. semi-aquatic) and the vector between arboreal *Litoria* and other species using the same microhabitat as the novel *Litoria* (e.g. semi-aquatic). We then multiplied this vector correlation by the ratio of observed divergence to expected divergence to estimate the relative amount of divergence along the expected divergence vector (as above; (D_{obs} / D_{exp}) r_{vec} = (D_{obs} / D_{exp}) cos θ = D_{proj} / D_{exp} = p_{exp}).

To test the statistical significance of these quantities, we conducted simulations of phenotypic evolution to produce null distributions against which to test our observed distances and relative divergences. For these simulations, we first estimated the Brownian motion evolutionary rate matrix (Revell et al. 2007a) for PC axes across all species in our phylogeny using the "ic.sigma" function in the R package *geiger* (Harmon et al. 2009). We next simulated Brownian motion character evolution along the

phylogeny using this rate matrix (using the “sim.char” function in *geiger*), and then we calculated distances and vector correlations as above. Because these simulations do not incorporate microhabitat use of species, they produce distances and vector correlations among species that are neutral with respect to adaptive expectations. We simulated 9,999 replicates each for morphology and performance.

Statistical significance was assessed with these simulations in two ways. First, we examined each microhabitat transition in *Litoria* individually (i.e. for burrowing, semi-aquatic, and terrestrial *Litoria*) by asking (1) in what proportion of simulation replicates was the ratio of distance among groups (D_{micro} / D_{obs}) smaller than observed, (2) in what proportion of simulations was the vector correlation (i.e., p_{obs}) greater (closer to 1) than the observed correlation, and (3) in what proportion of simulations was p_{exp} closer to 1 than the observed p_{exp}? Second, to assess more generally whether morphological and performance evolution in *Litoria* has been consistent with adaptive predictions across all microhabitat transitions, we also calculated: (1) the proportion of simulation replicates in which all three random distance ratios were smaller than all three observed ratios (i.e. for all three microhabitat categories), (2) the proportion of simulation replicates in which all three vector correlations were larger than all three observed correlations, and (3) the proportion of simulations in which all three p_{exp} were closer to 1 than the three observed p_{exp}. For example, if a given random simulation produced a vector correlation that was larger than observed for burrowing *Litoria* but not for semi-aquatic and terrestrial *Litoria*, this was not considered as extreme as the observed set of correlations that we would expect by chance.

Note that because we are using means of extant species to calculate these distances and vectors, we recognize that we are not comparing actual amounts or directions of evolution. To do so would necessitate comparing ancestors to descendants. Although it might seem intuitively desirable to use ancestral-state estimation to compare estimates of the ancestral and daughter nodes along a branch in which a microhabitat transition has occurred, such a procedure is challenging for two primary reasons. First, uncertainty in ancestral-state estimates of microhabitat use may lead to an inability to confidently locate the branch in which microhabitat transitions occur. Second, estimating values of morphology and performance for parent and daughter nodes along the same branch are non-independent because some subset of taxa is used to estimate values for both nodes. Although some methods have been developed to circumvent the latter problem (McPeek 1995, Revell et al. 2007b), our data do not fit the conditions necessary for such methods to work (e.g. microhabitat transitions occur on neighboring branches).

Results

PRINCIPAL COMPONENTS ANALYSIS

As expected, PC1, which primarily represents a size axis, accounted for a large part of the variation in our data (74.9% in morphology and 56.4% in performance; Table 4.2). The high similarity in magnitude and direction of individual elements of the eigenvectors for PC1 were consistent with this being a representation of overall size variation in morphology (mean ± SE: 0.33 ± 0.01, with the exception of relative leg muscle mass, which by definition was already size-corrected). Likewise, PC1 for performance showed

similar weights across most variables (0.37 ± 0.02, with the exception of clinging angle, which was small and negative [-0.06]) and represented positive scaling with body size (see 2B-PLS results below).

PC2 represented a contrast between relative leg mass and size of toe and finger tips. PC3 showed large positive weights for head size (both length and width) and metatarsal tubercle size, with large negative weights for the area of foot webbing and toe and finger tips (Table 4.2). Finally, PC4 largely represented a contrast between the size of foot webbing versus relative leg muscle mass and size of toe and finger tips (Table 4.2). Interestingly, after accounting for size in PC1, the linear variables snout-to-urostyle length, arm length, and leg length seemed to play very small roles in morphological variation among species. Figure 4.4 shows how species cluster in morphological PC space in PC2–4, chosen for ease of visualization and because these three PC axes represent the largest non-size-based variation. For brevity, we refer readers to Table 4.2 for the interpretation of higher PC axes.

PC axes for performance generally showed strong covariation in sets of the original performance variables. PC2 showed a contrast between the variables peak jumping acceleration, peak jumping power, jumping angle, and clinging angle, and three of the swimming variables (peak velocity, peak acceleration, and peak power; Table 4.2). PC3 largely represented variation in clinging angle, while PC4 represented variation in jumping takeoff angle (Table 4.2). Figure 4.5 shows how species cluster in performance PC space. As in morphology, for brevity we refer readers to Table 4.2 for the relationship between original variables and the higher PC axes.

COMPARISON OF MORPHOLOGICAL AND PERFORMANCE DIVERSITY OF ASSEMBLAGES.

We found that the morphological variance across assemblages was very similar (Table 4.3). This similarity was statistically significant in most *F*-tests, though the permutations were not significant (Table 4.3). In contrast, variance in performance was variable across assemblages, showing its highest values in China and lowest in Australia. Statistical support for these differences, however, was quite variable and depended on the exact comparison and type of test (Table 4.3). In contrast, the volumes of the convex hulls that surrounded PCA morphospace were quite different across assemblages, and performance showed similar diversity in hull volume across assemblages (Table 4.3). Though greatly different in absolute value, only one of the contrasts in hull volume was significantly different (Australia and China in morphology; Table 4.3).

RELATIONSHIP BETWEEN MORPHOLOGY AND PERFORMANCE

As expected, we found that both overall body size (SUL) and relative toe-tip size were both strongly related to maximum clinging angle, with angle negatively related to SUL and positively related to toe-tip size (SUL: $F_{1,41} = 59.66$; $P < 0.001$; relative toe-tip size: $F_{1,41} = 36.03$; $P < 0.001$). When found the same results when we looked only within arboreal taxa (SUL: $F_{1,15} = 47.29$; $P < 0.001$; relative toe-tip size: $F_{1,15} = 11.98$; $P = 0.004$).

Relative muscle mass was strongly positively related to jumping acceleration, as was body size (SUL: $F_{1,41} = 11.77$; $P = 0.001$; relative muscle mass: $F_{1,41} = 19.62$; $P <$

0.001). Jumping power was independent of body size but positively correlated with muscle mass (SUL: $F_{1,41} = 0.42$; $P = 0.522$; relative muscle mass: $F_{1,41} = 15.07$; $P < 0.001$). The same relationships were found in both swimming acceleration (SUL: $F_{1,41} = 5.47$; $P = 0.024$; relative muscle mass: $F_{1,41} = 27.01$; $P < 0.001$) and power (SUL: $F_{1,41} = 0.39$; $P = 0.534$; relative muscle mass: $F_{1,41} = 45.07$; $P < 0.001$).

Body size, relative leg length, and relative muscle mass all were positively correlated with peak jumping velocity, though muscle mass was not quite statistically significant (SUL: $F_{1,40} = 10.86$; $P = 0.002$; relative leg length: $F_{1,40} = 3.16$; $P = 0.083$; relative muscle mass: $F_{1,40} = 21.24$; $P < 0.001$). This indicates that both relative muscle mass and relative leg length each contribute to peak jumping velocity when the other is held constant. Interestingly, the correlation between these two variables was negative ($r = 0.530$; $P < 0.001$), suggesting that across species, jumping velocity can be increased either by increased muscle mass or increased leg length, but usually not via both.

Two-block partial least-square analysis (2B-PLS) showed that covariation in morphology and performance across all species was relatively low, as the analysis accounted for only 11.9% of the maximum potential covariation. However, the first three 2B-PLS axes were significantly greater than expected from random covariation and scores for morphology and performance showed relatively high correlations in these dimensions (Table 4.4). The first dimension reflects an allometric relationship between morphology and performance, showing that large frogs (large values for morphology PC1) tend to have high values for jumping and swimming (performance PC1) and low values for clinging (performance PC3, as maximum clinging angle

negatively loads on this axis; Table 4). Dimension 2 represents a positive relationship between leg muscle mass and overall performance (PC1) and low maximum clinging angle (PC3). Dimension 3 generally shows that large muscle mass, small toe and finger tips, and large webbing in morphology are positively related to high overall performance in swimming relative to overall performance in jumping (PC2). Additionally, in dimension 3 these same morphological variables positively covary with peak acceleration in both jumping and swimming relative to velocity in those same variables (PC5).

RELATIONSHIP OF MICROHABITAT USE WITH MORPHOLOGY AND PERFORMANCE

Species that use different microhabitats show strong differences in both morphology (Wilks's lambda = 0.136, $P < 0.001$) and performance (Wilks's lambda = 0.319, $P = 0.003$). Table 4.5 gives estimated effect sizes for each microhabitat use on PC axes of morphology and performance, which show how species that use different microhabitats are distinct. For example, semi-aquatic species have large leg muscles, large foot webbing, and small toe and finger tips (large, negative values for morphology PC2 and PC4), and their swimming is substantially better than their jumping (large, negative value for performance PC2, which represents a contrast between swimming and jumping performance). Burrowing frogs are distinct from other microhabitat specialists in morphology PC3 and PC5, meaning that they have large heads but small leg muscles, foot webbing, and toe and finger tips (PC3) but have large metatarsal tubercles (PC3, PC5). Arboreal taxa have morphology consistent with having large toe

and finger tips (only group with positive values for PC2 and negative for PC3), and they also are the best at clinging (large, negative value for performance PC3). Terrestrial species seem distinct in neither morphology nor performance.

TESTING FOR ECOLOGICALLY CONSERVATIVE DISPERSAL IN MORPHOLOGY AND PERFORMANCE

Distances in morphology and performance were very low among species within Microhylidae and Bufonidae (Table 4.6), despite the large geographic distances separating them. These distances were approximately 1/3 of the average values of distances among all terrestrial species and also among all pairs of species between China and Colombia. Very few pairs of species show such small distances among them, with the distances among the microhylids and bufonids generally smaller than ≥90% of distances among other species for both performance and morphology (Table 4.6).

However, distances among arboreal frogs in the two locations were not low. In fact, the distance between *Hyla annectans* and *Osteocephalus planiceps* was particularly high in morphology, though differences in performance were somewhat lower than among other arboreal frogs and China-Colombia pairs (Table 4.6).

HOW DO MORPHOLOGY AND PERFORMANCE EVOLVE IN ASSOCIATION WITH MICROHABITAT TRANSITIONS IN AN IN SITU RADIATION?

Rates of evolution of morphology were substantially higher in Australian hylid frogs than in the arboreal Colombian hylids, showing rates that were 1.5, 2.4, and 4.7 times higher

for PC2, PC3, and PC4, respectively. Fitting separate rates to the two clades was statistically supported over a model with a global rate for each PC axis (χ^2 = 8.097, *P* = 0.044). Similarly, performance evolution in Australian hylids occurred at a higher rate than in Colombian hylids, but here differences in rates were even more pronounced, with values 5.4, 2.5, and 2.0 higher across the three PC axes of performance (χ^2 = 10.726, *P* = 0.013).

All novel microhabitat specialists in *Litoria* (i.e. burrowing, semi-aquatic, and terrestrial) were closer in PC space (for both performance and morphology) to other frog species in the same microhabitat than to *Litoria* in the ancestral microhabitat, and values of p_{obs} showed that they have evolved substantially in the expected direction of evolution (all global *P*-values < 0.005; Table 4.7). This was particularly clear in burrowing and semi-aquatic *Litoria*, which showed individually-significant *P*-values for distance (though not for p_{obs}; Table 4.7a,b). Semi-aquatic species have converged (and are most distinct from arboreal *Litoria*) along morphology PC2 (increased muscle mass in the hind limb, smaller toepads) and performance PC2 (good overall swimming relative to clinging and jumping; Fig. 4.6). Burrowing species have converged along morphology PC3 (increased head size and metatarsal tubercle, smaller muscle size, foot webbing, and toe and finger tips; Fig. 4.6) and PC5 (increased metatarsal tubercle; not shown). However, the pattern in performance is less clear. Although closer to other burrowing species than to arboreal *Litoria*, burrowing *Litoria* are relatively far from both other burrowing species and arboreal *Litoria*, which are themselves relatively close in performance PC3 (Fig. 4.6). Terrestrial species, in contrast to the other two novel microhabitat types, show general consistency with adaptive predictions (particularly with

respect to vector correlations), but they are roughly as distant from other terrestrial species as they are from arboreal *Litoria* and do not show statistical significance in any of these metrics (Table 4.7).

When we compare the projection of observed divergence on expected divergence to the total amount of expected divergence (p_{exp}), we see that in terms of morphology, all three lineages of novel microhabitat specialists in *Litoria* have diverged substantially in the predicted direction of divergence from arboreal *Litoria* (Table 4.7c). However, in performance we see that it depends on the lineage. Specifically, terrestrial *Litoria* have only diverged halfway along the predicted trajectory of divergence, whereas semi-aquatic and burrowing *Litoria* have actually "overshot their target," and diverged on these trajectories beyond other frog species in similar microhabitats (i.e., $p_{exp} > 1$; Table 4.7c; Fig. 4.6).

Discussion

In this paper we used three assemblages of frogs to test a series of novel hypotheses about the evolution of morphology and performance. We found that assemblages are very similar in morphological diversity but distinct in performance diversity. Two-block partial least-squares analysis showed that this seems to be related to relatively little correspondence between morphology and performance across species, relative to potential covariation. To understand the ecological and biogeographical drivers of morphological and performance evolution, we next tested whether frogs using similar microhabitats around the world showed similar morphology and performance. We found that indeed there was general correspondence between microhabitat use and

morphology and performance. Next, we showed that some of the phenotypic diversity in the Chinese and Colombian assemblages was a consequence of ecologically conservative dispersal (i.e. biogeographic dispersal with no change in microhabitat use and little change in morphology and performance), though this was not always the case. Specifically, arboreal hylid frogs that are found in the two regions and sister species in our phylogeny were markedly different in morphology and performance. Finally, we showed evidence for adaptive divergence in morphology and performance in Australian hylid frogs (genus *Litoria*), first finding that they exhibit higher rates of evolution in morphology and performance than their sister clade in which microhabitat use has been constant. More detailed comparisons of each transition in microhabitat use (i.e. from the ancestral use [arboreal] to either burrowing, semi-aquatic, or terrestrial) showed that evolution in these novel groups of *Litoria* has resulted in convergence with species of frogs from other clades that use the same microhabitat, instead of some residual similarity to arboreal *Litoria* based on shared evolutionary history. Overall we see that phenotypic diversity in these assemblages may be a consequence of ecologically conservative dispersal, in situ diversification, or both.

ECOLOGICALLY CONSERVATIVE DISPERSAL

We found remarkable similarity in morphology and performance within some clades that are found in both China and Colombia. The distances among microhylids and bufonids in both morphology and performance space were much lower than most distances among all pairs of terrestrial species and also among all pairs of species from China

and Colombia. This remarkable similarity exists despite the long separation between the lineages in these two areas, from 28.1 million years (My) in the bufonid frogs up to 66.9 My in microhylids (Fig. 4.2). The phenotypic similarity maintained over such large expanses of evolutionary time, and despite large biogeographic distances, is even more remarkable given the extensive divergence in morphology in performance that we found among the Australian *Litoria*, a group that we estimated to be just 41.7 million years old.

What might explain such conservatism in morphology and performance despite such large temporal and biogeographic scales of divergence? Much is known about population-level processes that may lead to niche conservatism, including a lack of genetic variation, antagonistic pleiotropy, gene flow, and heterogeneous selection in different parts of a species's range (see review in Wiens 2004; Wiens et al. 2010). In addition, stasis at large time scales may be the result of stabilizing selection coupled with infrequent shifts in adaptive optima throughout the history of a clade (Estes and Arnold 2007; Uyeda et al. 2011). However, much less is known about why species, lineages, or clades are able to spread throughout the world while maintaining their ancestral ecology, morphology, and performance. This pattern of biogeographic dispersal with little ecological or phenotypic change (ecologically conservative dispersal; Stephens and Wiens 2004) has now been documented in body sizes in Middle American treefrogs (Moen et al. 2009), snake-like ecomorphs in lizards (Wiens et al. 2006), and in microhabitat specialists in turtles (Stephens and Wiens 2004). The current study is the first to quantitatively show very little difference in morphology and performance in species from clades that are globally-distributed but ecologically conservative.

Regardless of why we see such conservatism, the implication for studies of the evolution of community structure are clear – without an understanding of how and where phenotypic evolution has proceeded in the constituent species of an assemblage, it may be difficult to understand why we see the current community structure or phenotypic diversity in a given assemblage. This result adds to the mounting number of studies that have shown how the interaction between evolution and biogeography can be crucial to understand the development of community structure (McPeek and Brown 2000; Moen et al. 2009; Wiens 2011b).

DIVERSIFICATION IN MICROHABITAT USE, MORPHOLOGY, AND PERFORMANCE IN AUSTRALIAN FROGS

In contrast to the surprising conservatism in ecology, morphology, and performance in some lineages found in both China and Colombia, we also found that adaptive diversification in Australian *Litoria* has led to equivalent amounts of morphological diversity as those seen in the assemblages of China and Colombia, which show a much more complex history (i.e. ecologically conservative dispersal among these two locations, major clades are much older; see above). Despite the relatively young age of this clade relative to some clades of frogs that show little evolutionary change (see above), we see that it has become as morphologically diverse, and almost as diverse in performance, as other assemblages. We show that this has been achieved via microhabitat diversification and high rates of evolution of morphology and performance in *Litoria*. Furthermore, individual microhabitat transitions seem to have resulted in convergence with other species in similar microhabitats around the world, as shown by

our analyses on expected versus observed evolutionary divergence in *Litoria* found in novel microhabitats (i.e. relative to the ancestral, arboreal role).

We generally found that novel microhabitat specialists in *Litoria* converged with other ecologically equivalent species of frogs. The semi-aquatic *Litoria dahlii* clusters closely in both morphological and performance space with its ecological counterparts (Fig. 4.6), and the divergence from arboreal *Litoria* (representing the ancestral microhabitat use) has largely been in the direction expected – a projection of the observed divergence vector onto the expected divergence vector (i.e. their correlation, p_{obs}) shows that 84.7% of the actual divergence between arboreal *Litoria* and *Litoria dahlii* has been in the direction toward other semi-aquatic frog species. Furthermore, this divergence has been in a direction nearly orthogonal to the primary axis of variation in arboreal Litoria, at least when viewed for PC2 and PC3 (Fig. 4.6). Similarly, burrowing *Litoria* are much closer in morphology and performance space to other burrowing species than to arboreal *Litoria*, and they show a relatively high p_{obs} in morphology, though not for performance. As in the semi-aquatic frogs, divergence in burrowing *Litoria* has been in the direction of least variation in arboreal *Litoria*. Additionally, in this case covariation in performance in other burrowing species suggests that the relatively high values of burrowing *Litoria* on performance PC3 may not be particularly surprising (i.e., along the axis of major variation in other burrowing species, the mean value of burrowing *Litoria* is within 1 standard error of the mean of other burrowing species).

However, terrestrial *Litoria* show a relatively different pattern of evolution – they are roughly equidistant between arboreal *Litoria* and other terrestrial species.

Additionally, they have largely not evolved in the expected direction in morphology, showing the highest amount of divergence from arboreal *Litoria* but with the lowest angle. When we consider covariation in both terrestrial *Litoria* and other terrestrial species (Fig. 4.6), we see that variation is high in the latter group and the mean of terrestrial *Litoria* fits within the 95% confidence bounds of other terrestrial species. This suggests that there is may be lower selection pressure in terrestrial frogs in the variables that we measured than in other microhabitat specialists. Alternatively, and perhaps more likely, is that there is much undescribed ecological diversity within our course characterization of frogs as terrestrial. In other words, a stronger relationship between ecology, morphology, and performance may exist within the species that we have classified as terrestrial, but only after we have made a finer subdivision within terrestrial species.

Overall, there seems to be no little to no effect of history – across all types of novel microhabitat specialists in *Litoria*, the proportion of evolution along the expected vector of divergence (p_{exp}) in morphology is quite high, significantly so in terrestrial and semi-aquatic species. In performance, two lineages (the semi-aquatic *Litoria dahlii* and burrowing *Litoria*) have actually diverged beyond other species in the same microhabitat ($p_{exp} > 1$). Additionally, the time scale over which this divergence has occurred (about 41.7 My; Fig. 4.2) is much smaller than the older assemblages in China and Colombia (approximately 110.3 My in the former [age of common ancestor of primarily Chinese clade] and 74.7 My in the latter [splitting of *Oreobates quixensis* from the rest of a primarily Colombian clade]; Fig. 4.2). Therefore, it seems apparent that lack of time for

adaptation was not a limiting factor in the diversification of morphology and performance in association with microhabitat diversification in *Litoria*.

We note here that we also had three species of myobatrachid frogs in our sample, and these were terrestrial and burrowing. In most of Australia, these two clades (Myobatrachidae and Hylidae) are the only clades represented in a given assemblage. We focused on *Litoria* here because of the great ecological diversity in the genus, and the myobatrachids that we studied fall well within the range of variation in *Litoria* alone (i.e. it is reasonable to discuss the evolution of phenotypic diversity in our Australian assemblage by focusing on the diversification within *Litoria*).

In general, we see that adaptive diversification over a relatively short time scale in Australian hylid frogs has led to similar morphological diversity as in assemblages of species from much older radiations (i.e. in China and Colombia), though this may not be replicated in performance (performance diversity in Australia is the lowest of the three assemblages, though it is not significantly different from Colombia; Table 4.5). Furthermore, detailed examination of individual transitions to terrestrial, burrowing, and semi-aquatic microhabitat use has largely been consistent with adaptive expectations, based on the phenotypes of other frog species around the world that are similar in microhabitat use.

Combined with our results on ecologically conservative dispersal above, we can see that phenotypic diversity in a given assemblage may be a consequence of one of two processes. First, biogeographic dispersal over great distances may be associated with little divergence in microhabitat, morphology, and performance. Thus, at least some phenotypic diversity in assemblages may be the result of evolutionary divergence

that originally occurred outside that assemblage or region. Second, adaptive diversification can also contribute to an assemblage's phenotypic diversity. Here we found that Australian frogs of the genus *Litoria* have done precisely that, filling out the morphospace occupied by older assemblages in China and Colombia in a fraction of the time through in situ diversification. Overall, these results suggest that both adaptive evolution and conservatism have been important in producing the phenotypic diversity seen in frog assemblages, a result that likely applies to most assemblages.

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Table 4.1. Species used in this study and classification of microhabitat use. Definition of microhabitat use categories is listed in the appropriate section in *Material and Methods*. Family names follow assignment by Pyron and Wiens (2011). References are for microhabitat use. In cases where another species was used to determine microhabitat use, that species has at some point in the past been classified as synonymous with the species of this study; hence, we do not expect its microhabitat use to be different (i.e., lack of distinctive morphological and ecological differences was the reason for past synonymy).

Location	Species	Family	Microhabitat use	Reference
Fogg Dam, NT, Australia				
	Cyclorana australis	Hylidae	Burrowing	Tyler et al. 2000
	Cyclorana longipes	Hylidae	Burrowing	Tyler et al. 2000
	Limnodynastes convexiusculus	Myobatrachidae	Terrestrial	Hero et al. 2004a
	Litoria bicolor	Hylidae	Arboreal	Tyler et al. 2000
	Litoria caerulea	Hylidae	Arboreal	Tyler et al. 2000
	Litoria dahlii	Hylidae	Semi-aquatic	Tyler et al. 2000
	Litoria inermis	Hylidae	Terrestrial	Tyler et al. 2000
	Litoria nasuta	Hylidae	Terrestrial	Tyler et al. 2000
	Litoria pallida	Hylidae	Terrestrial	Tyler et al. 2000
	Litoria rothii	Hylidae	Arboreal	Tyler et al. 2000
	Litoria rubella	Hylidae	Arboreal	Tyler et al. 2000
	Litoria tornieri	Hylidae	Terrestrial	Tyler et al. 2000
	Platyplectrum ornatum	Myobatrachidae	Burrowing	Hero et al. 2004b
	Uperoleia lithomoda	Myobatrachidae	Burrowing	Tyler et al. 1981
Baoshan, Yunnan, China				
	Amolops tuberodepressus	Ranidae	Torrent	Liu and Yang 2000
	Babina pleuraden	Ranidae	Semi-aquatic	Yang and Rao 2008
	Bufo melanostictus	Bufonidae	Terrestrial	Chanda 2002
	Calluella yunnanensis	Microhylidae	Burrowing	IUCN 2011*
	Chiromantis doriae	Rhacophoridae	Arboreal	Chanda 2002
	Hyla annectans	Hylidae	Arboreal	Ahmed et al. 2009

Microhyla fissipes	Microhylidae	Terrestrial	Chanda 2002 (as *M. ornata*)
Nanorana yunnanensis	Dicroglossidae	Semi-aquatic	Inger et al. 1990
Odorrana grahami	Ranidae	Torrent	Yang et al. 2004
Rhacophorus dugritei	Rhacophoridae	Terrestrial	Inger et al. 1990
Rhacophorus rhodopus	Rhacophoridae	Arboreal	Inger et al. 1999 (as *R. bipunctatus*)
Leticia, Amazonas, Colombia			
Adenomera hylaedactyla	Leptodactylidae	Terrestrial	Duellman 2005
Allobates femoralis	Dendrobatidae	Terrestrial	Duellman 2005
Ameerega trivittata	Dendrobatidae	Terrestrial	Rodríguez and Duellman 1994
Chiasmocleis bassleri	Microhylidae	Terrestrial	Duellman 1978
Dendropsophus rhodopeplus	Hylidae	Arboreal	Duellman 2005
Dendropsophus sarayacuensis	Hylidae	Arboreal	Duellman 1978
Dendropsophus triangulum	Hylidae	Arboreal	Duellman 1978
Hamptophyrne boliviana	Microhylidae	Terrestrial	Duellman 2005
Hypsiboas hobbsi	Hylidae	Arboreal	Cochran and Goin 1970
Hypsiboas lanciformis	Hylidae	Arboreal	Duellman 1978
Hypsiboas punctatus	Hylidae	Arboreal	Duellman 2005
Leptodactylus leptodactyloides	Leptodactylidae	Semi-aquatic	Duellman 2005
Leptodactylus rhodomystax	Leptodactylidae	Terrestrial	Rodríguez and Duellman 1994
Oreobates quixensis	Craugastoridae	Terrestrial	Duellman 1978
Osteocephalus planiceps	Hylidae	Arboreal	Duellman 2005
Rhinella margaritifera	Bufonidae	Terrestrial	Duellman 2005 (as *Bufo typhonius*)
Rhinella proboscidea	Bufonidae	Terrestrial	Duellman 2005 (as *Bufo typhonius*)
Scinax ruber	Hylidae	Arboreal	Duellman 2005
Sphaenorhynchus lacteus	Hylidae	Arboreal	Duellman 2005

[a]Sources for both these species only indicate that they are found near fast-flowing streams. When collecting these two species in the field, we always found them perched on vegetation above the streams and thus we classify them as arboreal.
[b]Information on microhabitat use is largely absent for *Calluella yunnanensis*. However, IUCN (2011) indicates burrowing as characteristic for almost all other members of the genus, so we extend that characterization to *C. yunnanensis*.

Table 4.2. Results of phylogenetic principal components analysis, using the BEAST phylogeny in which the topology was constrained to match the ML topology of Pyron and Wiens (2011). Simulation eigenvalues refer to those obtained via the simulation procedure we used to choose axes for further analysis (we retained all axes whose variation was higher than in the random simulations, in this case 2–4 for both performance and morphology).

(a) Morphology

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalues	7.486	1.051	0.766	0.426	0.136	0.053	0.037	0.019	0.015	0.012
Percent of total variation	74.86	10.51	7.66	4.26	1.36	0.53	0.37	0.19	0.15	0.12

Eigenvectors

Original variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Snout-to-urostyle length	0.358	-0.009	0.159	0.015	-0.126	0.248	-0.238	-0.761	0.258	0.258
Leg length	0.356	-0.117	0.058	0.001	-0.342	0.449	0.149	0.004	-0.366	-0.617
Head length	0.344	-0.124	0.265	0.052	-0.461	-0.439	0.157	0.126	-0.383	0.449
Head width	0.347	-0.046	0.319	-0.002	0.021	-0.497	-0.153	0.126	0.513	-0.475
Arm length	0.359	0.012	0.100	0.060	0.102	0.457	0.362	0.466	0.430	0.325
Relative leg mass	0.105	-0.841	-0.426	0.279	0.108	-0.069	-0.021	-0.025	0.071	0.024
Tubercle area	0.335	-0.087	0.273	-0.172	0.760	0.004	-0.119	-0.006	-0.427	0.041
Foot webbing area	0.266	0.016	-0.491	-0.814	-0.083	-0.105	0.030	0.013	0.067	0.040
Toe tip area	0.315	0.309	-0.361	0.301	-0.072	0.065	-0.680	0.311	-0.103	0.075
Finger tip area	0.290	0.398	-0.403	0.365	0.206	-0.261	0.514	-0.274	-0.043	-0.100

(b) Performance

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Eigenvalues	4.509	1.282	1.111	0.579	0.322	0.151	0.036	0.010
Percent of total variation	36.07	10.26	8.89	4.63	2.58	1.21	0.29	0.08

Eigenvectors

Original variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Jump - peak velocity	0.410	0.133	0.291	-0.192	0.308	-0.686	0.118	0.335
Jump - peak acceleration	0.386	0.336	-0.191	-0.259	-0.520	0.226	0.535	0.164
Jump - peak power	0.417	0.318	0.088	-0.297	-0.155	0.046	-0.655	-0.417
Jump - takeoff angle	0.271	0.423	0.147	0.846	0.049	0.088	0.017	-0.014
Swim - peak velocity	0.419	-0.281	0.004	-0.068	0.511	0.263	0.385	-0.511
Swim - peak acceleration	0.291	-0.498	-0.380	0.291	-0.418	-0.464	-0.037	-0.214
Swim - peak power	0.414	-0.357	-0.142	0.038	0.131	0.408	-0.340	0.616
Maximum clinging angle	-0.055	0.367	-0.827	-0.030	0.393	-0.129	-0.071	0.023

Table 4.3. Comparison of disparity in morphology and performance across assemblages. (a) Variances: actual variances for each locality are listed on the diagonal of each matrix, while *P*-values estimated by permutation and *F*-tests are listed below and above the diagonal, respectively. Note that for morphology, *P*-values represent the probability that each pair of variances is different, whereas for performance it is the probability that the variance is the same (two-tailed tests). (b) Hull volume: estimated hull volumes are listed on the diagonal of each matrix, while *P*-values estimated by permutation are found below the diagonal for each comparison (all *P*-values here represent the probability that any two assemblages are different). Note that neither variances nor hull volumes have units, as principal components were calculated from correlations.

(a) Variances

Morphology

	Australia	China	Colombia
Australia	152.98	0.019	0.042
China	0.117	154.92	0.059
Colombia	0.305	0.313	146.89

Performance

	Australia	China	Colombia
Australia	164.33	0.161	0.054
China	0.014	207.97	0.125
Colombia	0.283	0.180	178.95

(b) Hull Volume

Morphology

	Australia	China	Colombia
Australia	54.55		
China	0.003	12.95	
Colombia	0.874	0.194	1307.66

Performance

	Australia	China	Colombia
Australia	6984.35		
China	0.535	1401.70	
Colombia	0.252	0.303	20787.61

Table 4.4. Results of the two-block partial least-squares (2B-PLS) analysis on phylogenetically-transformed morphological and performance data across all species. Values below each column of "Dim1–3" represent weights of the linear combinations of original variables; higher absolute values indicate a stronger contribution to the covariation between 2B-PLS scores in that dimension. Particularly high weights in a given dimension are in bold. "Singular values" represent the amount of covariance explained by a given dimension, and "Correlation" is the correlation among 2B-PLS scores in that dimension. Only statistically-significant dimensions are shown (see Results).

		Dimensions		
Matrix	Variable	1	2	3
$\mathbf{F}_1$	Morphology PC1	**0.941**	0.314	-0.117
	Morphology PC2	-0.310	**0.675**	**-0.593**
	Morphology PC3	-0.120	**0.651**	**0.634**
	Morphology PC4	-0.006	-0.038	**-0.465**
	Morphology PC5	-0.050	0.132	0.010
	Morphology PC6	0.015	0.017	0.088
	Morphology PC7	0.031	-0.046	-0.028
	Morphology PC8	0.002	-0.007	-0.044
	Morphology PC9	-0.009	0.030	0.073
	Morphology PC10	-0.007	0.032	-0.003
$\mathbf{F}_2$	Performance PC1	**0.606**	**-0.768**	-0.130
	Performance PC2	-0.285	0.031	**-0.675**
	Performance PC3	**0.697**	**0.611**	0.077
	Performance PC4	0.007	-0.007	0.283
	Performance PC5	0.252	0.183	**-0.659**
	Performance PC6	-0.045	-0.041	0.068
	Performance PC7	-0.006	-0.010	0.049
	Performance PC8	-0.013	-0.003	0.031
Singular value		2.631	1.381	0.544
Correlation		0.666	0.633	0.631

Table 4.5. Effect sizes of phylogenetic MANOVA relating morphology and performance to microhabitat use (two models run separately).

Morphology

	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
arboreal	0.577	-0.652	0.007	-0.113	-0.029	0.011	-0.010	0.029	-0.015
burrowing	-0.081	0.703	-0.552	0.462	-0.119	0.018	0.026	-0.052	0.019
semi-aquati	-1.040	0.031	-0.596	-0.204	-0.004	-0.056	-0.119	-0.021	-0.008
terrestrial	-0.284	0.353	0.275	-0.049	0.041	0.012	0.035	0.003	0.020

Performance

	PC2	PC3	PC4	PC5	PC6	PC7	PC8
arboreal	0.083	-0.425	-0.175	0.384	-0.152	-0.014	-0.010
burrowing	0.301	0.778	-0.005	-0.339	0.090	0.059	-0.021
semi-aquati	-1.060	0.303	0.718	-0.319	0.201	0.068	0.022
terrestrial	0.037	0.137	-0.017	-0.180	0.060	-0.030	0.004

Table 4.6. Comparison of distances among members of clades found in both China and Colombia. "Within" indicates the pairwise distance among sister species/lineages in both China and Colombia, "Same micro" indicates average pairwise distance among all species (across all three assemblages of this study) using the same microhabitat as that of the focal clade, and "China-Colombia" indicates average pairwise distance among all pairs of species in which one species is from China and the other from Colombia. "Prop. less" indicates the proportion of distances within a given category (same microhabitat or China-Colombia) that are smaller than those observed in the focal clade.

Morphology

	Within	Same micro	Prop. less	China-Colombia	Prop. less
Microhylidae	5.32	15.25	0.029	17.22	0.014
Bufonidae	6.19	15.25	0.059	17.22	0.029
Hylidae	21.12	12.14	0.908	17.22	0.794

Performance

	Within	Same micro	Prop. less	China-Colombia	Prop. less
Microhylidae	9.60	17.76	0.103	19.07	0.062
Bufonidae	9.10	17.76	0.081	19.07	0.048
Hylidae	12.02	16.49	0.261	19.07	0.177

Table 4.7. Comparison of *Litoria* in novel microhabitats to other species of frogs using similar microhabitats and to other *Litoria* in the ancestral microhabitat (arboreal). (a) Calculations of distance between *Litoria* in the novel microhabitat and other species in that microhabitat (D_{micro}), the former with *Litoria* in the ancestral, arboreal microhabitat (D_{obs}), and P_{sim} estimated via simulation. "Global P_{sim}" represents whether *Litoria* in novel microhabitats as a whole are closer in PC space to other ecologically similar species than to arboreal *Litoria*. (b) Angles (θ, in degrees) between vectors of expected and observed divergence from arboreal *Litoria*, proportion of total divergence from arboreal *Litoria* that is along the expected trajectory of divergence (p_{obs}), and P_{sim} calculated via simulation. (c) Same as in (b), but p_{exp} reflects the actual divergence along the expected trajectory of evolution relative to expected amount of evolution along this axis (see Methods for details). Global P_{sim} in (b) and (c) are as in (a).

(a) Distances

	Morphology			Performance		
	D_{micro}	D_{obs}	P_{sim}	D_{micro}	D_{obs}	P_{sim}
burrowing	12.246	18.49	0.020	12.819	18.78	0.023
semi-aquatic	9.314	16.85	0.013	12.166	25.37	0.007
terrestrial	16.061	19.04	0.098	11.131	11.21	0.160
	Global P_{sim} = 0.0004			Global P_{sim} = 0.0008		

(b) Divergence along expected trajectory relative to total observed divergence

	Morphology			Performance		
	θ	p_{obs}	P_{sim}	θ	p_{obs}	P_{sim}
burrowing	37.22	0.796	0.253	57.96	0.530	0.224
semi-aquatic	32.03	0.848	0.152	25.53	0.902	0.073
terrestrial	54.16	0.586	0.195	42.40	0.738	0.313
	Global P_{sim} = 0.0049			Global P_{sim} = 0.0029		

(c) Divergence along expected trajectory relative to total expected divergence

	Morphology			Performance		
	θ	p_{exp}	P_{sim}	θ	p_{exp}	P_{sim}
burrowing	37.22	0.747	0.228	57.96	1.170	0.164
semi-aquatic	32.03	0.845	0.031	25.53	1.303	0.060
terrestrial	54.16	0.715	0.031	42.40	0.506	0.085
	Global P_{sim} = 0.0010			Global P_{sim} = 0.0019		

Figure 4.1. Example of velocity and acceleration profiles used in this study, as obtained by two smoothing procedures done in QuickSAND (Walker 1998) for an individual of *Leptodactylus leptodactyloides*. (a) and (b) show velocity and acceleration profiles, respectively, obtained using the GCV algorithm of Woltring (1985). Walker (1998) notes conditions under which this algorithm can be unstable (high camera speed, low magnification) and examination of these two traces clearly show this to be the case – for example, velocity increases after takeoff and acceleration fluctuates wildly between extremely large positive and negative values, both before and after takeoff. (c) and (d) show traces obtained using manual adjustment of the smoothing parameter of the quintic spline, done until biologically reasonable features are obtained in the traces. These include a monotonic increase in both velocity and acceleration until acceleration peaks during takeoff, then a peak in velocity and acceleration becoming negative at takeoff (due to gravity once the frog's legs have left the ground and thus have ceased applying force). [Note that the vertical scales of (c) and (d) are different so as to more clearly illustrate the features of each curve.] In some cases, both manual smoothing and GCV gave almost identical results. To maintain consistency, however, all data presented in this paper were obtained via the manual smoothing procedure.

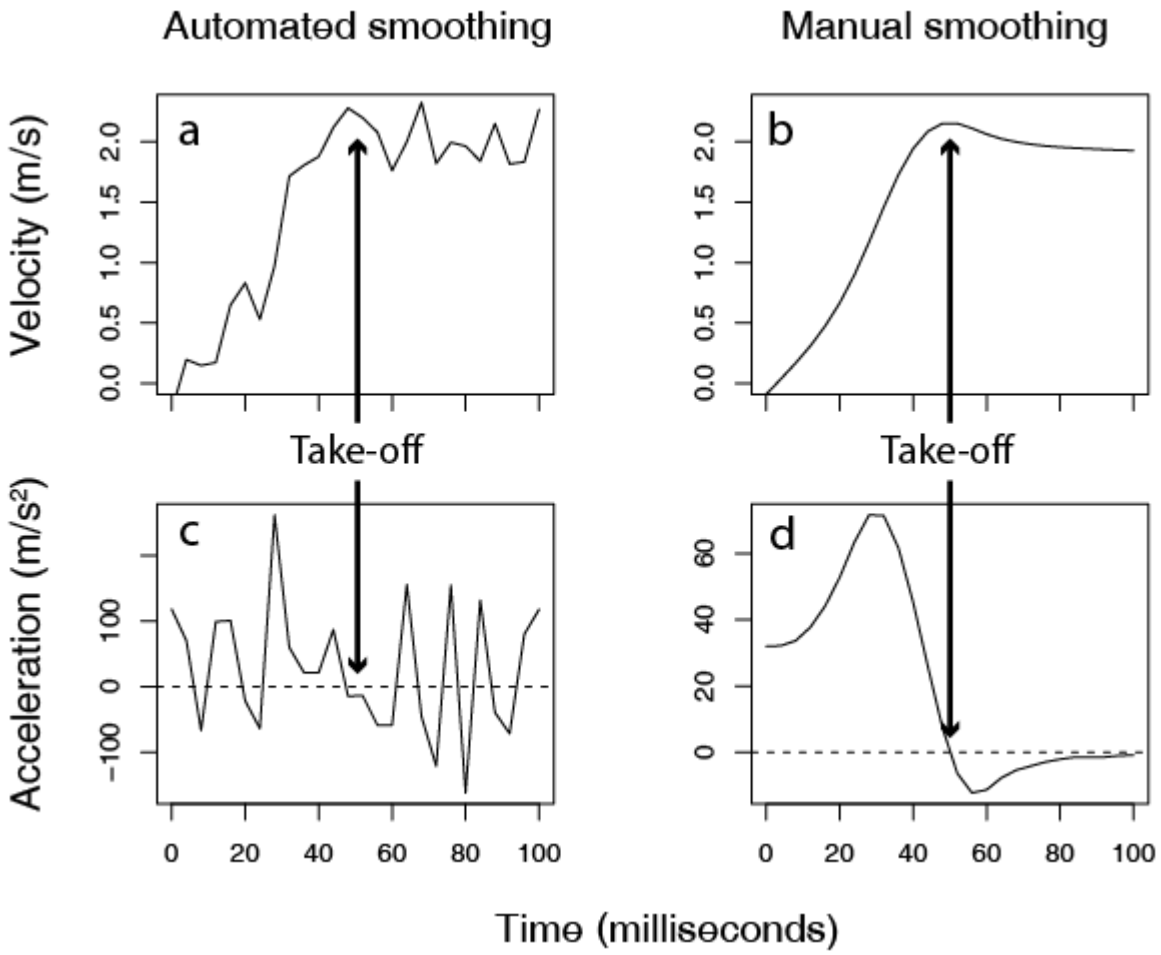


Figure 4.2. Phylogeny of the species in the current study (BEAST phylogeny with topology constrained to mirror the phylogeny of Pyron and Wiens [2011]; see Methods). Microhabitat use of species is indicated at the tips, and branch lengths are in units of millions of years (My). Node labels indicate major clades: (1) Ranoidea, (2) Hyloidea, (3) Myobatrachidae, (4) Microhylidae, (5) Ranidae, (6) Rhacophoridae, (7) Leptodactylidae, (8) Dendrobatidae, (9) Bufonidae, and (10) Hylidae.

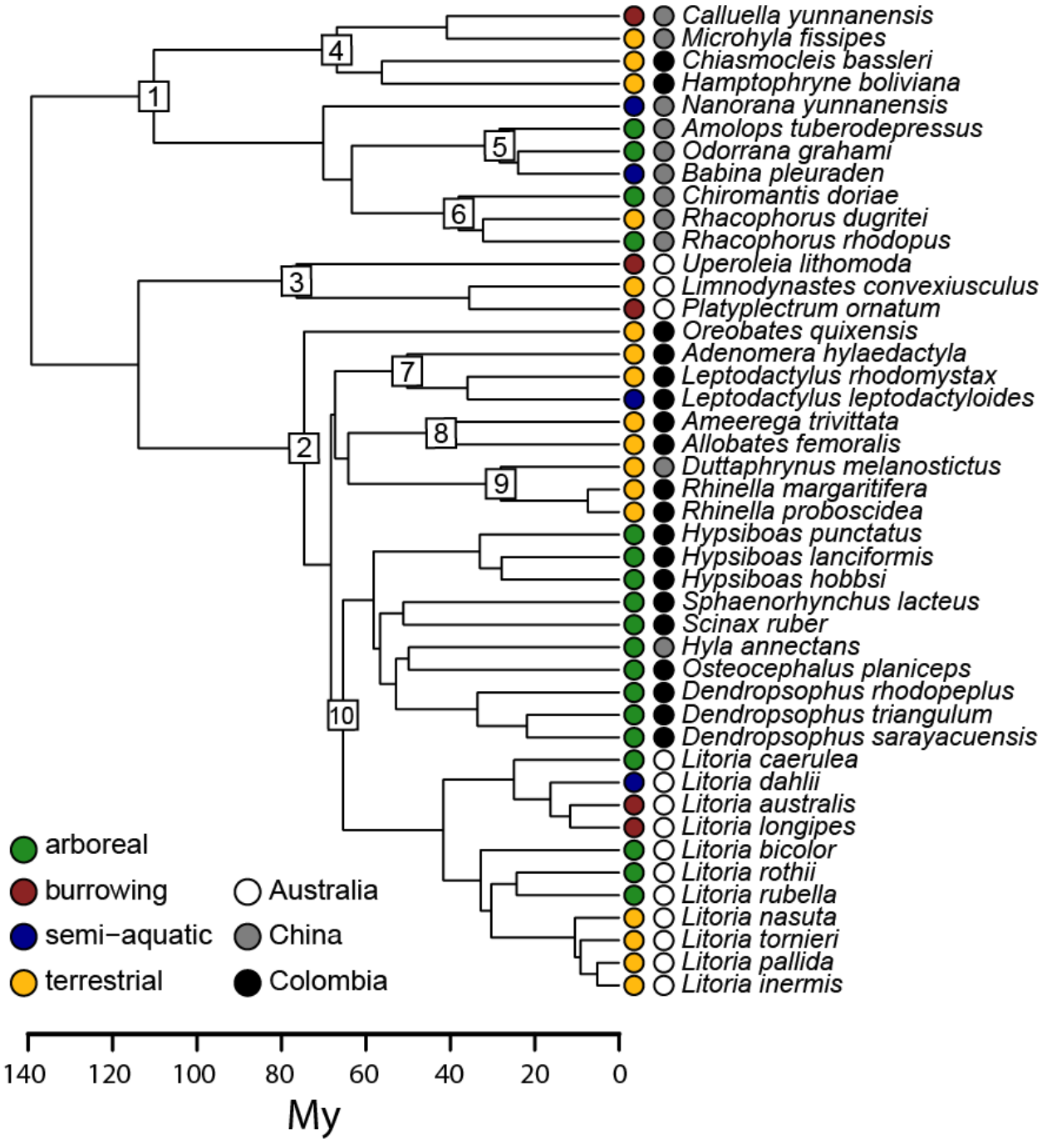


Figure 4.3. Hypothetical example of our approach that looks at vectors of expected and observed divergence among various groups. Black square represents the centroid of arboreal *Litoria* (ancestral microhabitat use). White square represents the centroid of *Litoria* that are in the novel microhabitat category, and the while circle is the centroid of non-*Litoria* frogs species that use the same microhabitat as the latter *Litoria*. D_{obs}, D_{micro}, D_{proj}, D_{exp}, and θ are as described in the text. Note that only two dimensions are shown in this example for visual clarity, but this approach can be done in any n-dimensional trait space.

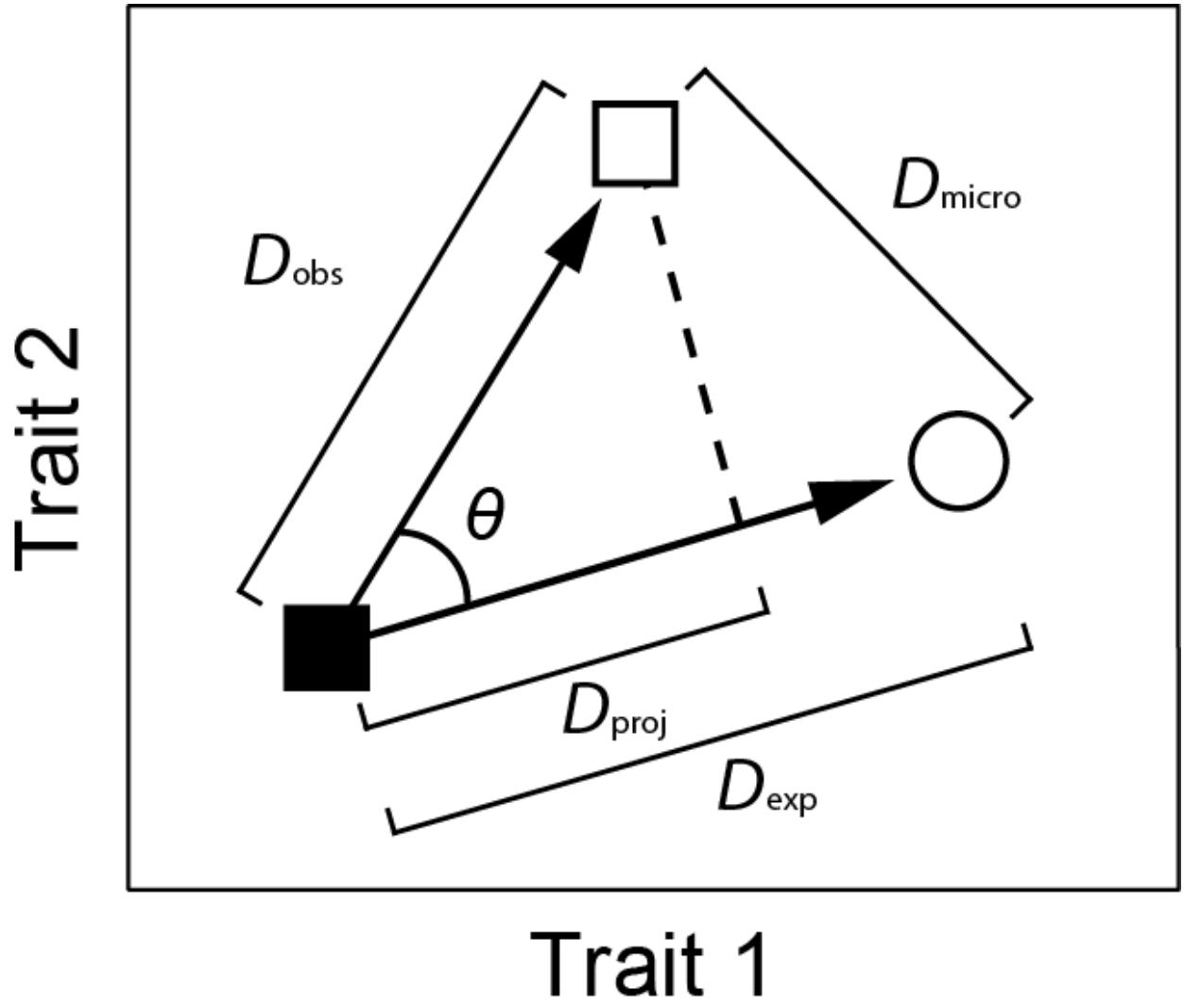


Figure 4.4. Principal components scores for morphology, plotted for PC2–4, which show the greatest amount of non-size-related variation among species. Colors indicate microhabitat use of each species, while symbol shape indicates from which assemblage it comes.

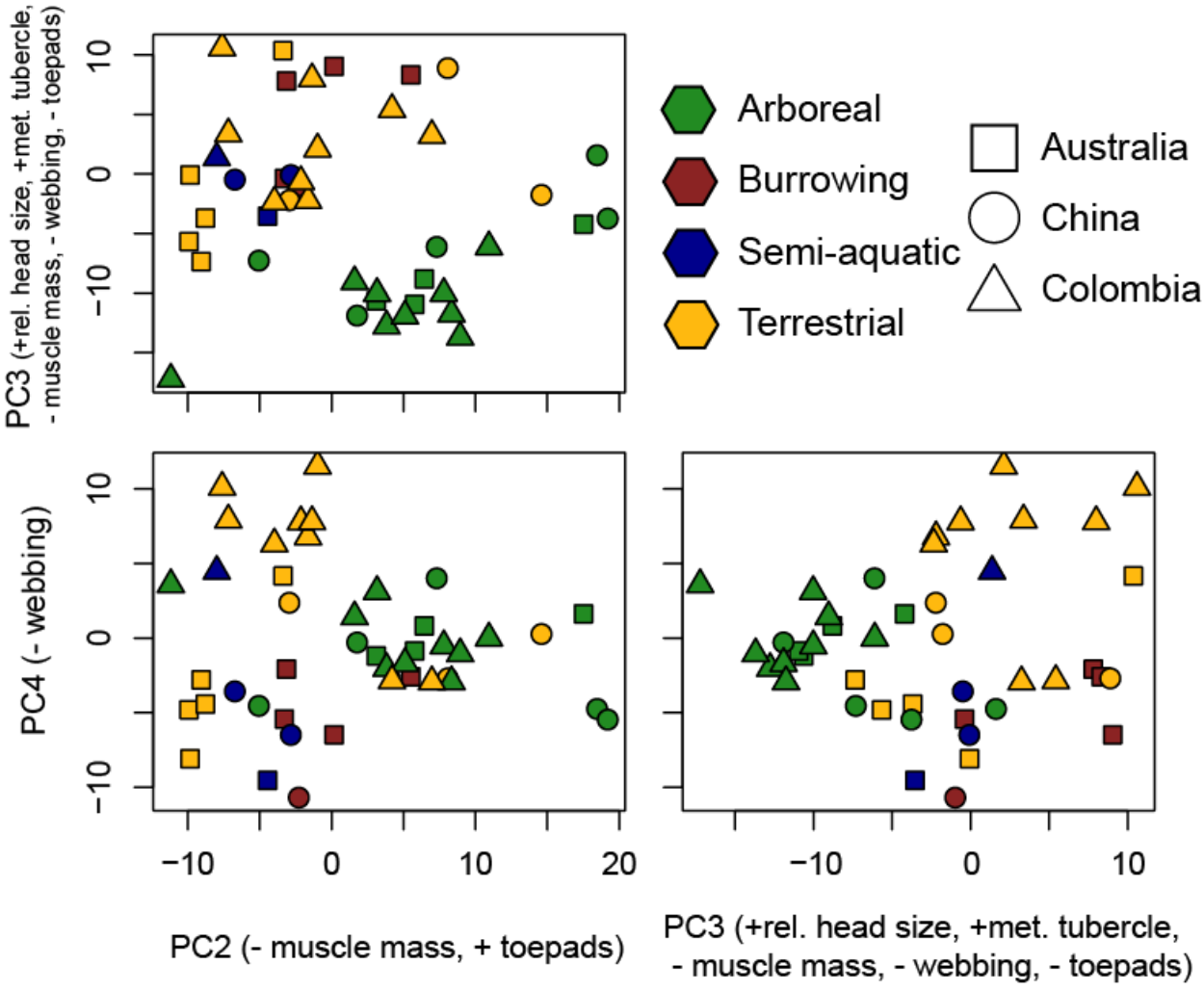


Figure 4.5. Principal components scores for performance, plotted for PC2–4, which show the greatest amount of non-size-related variation among species. Colors indicate microhabitat use of each species, while symbol shape indicates from which assemblage it comes.

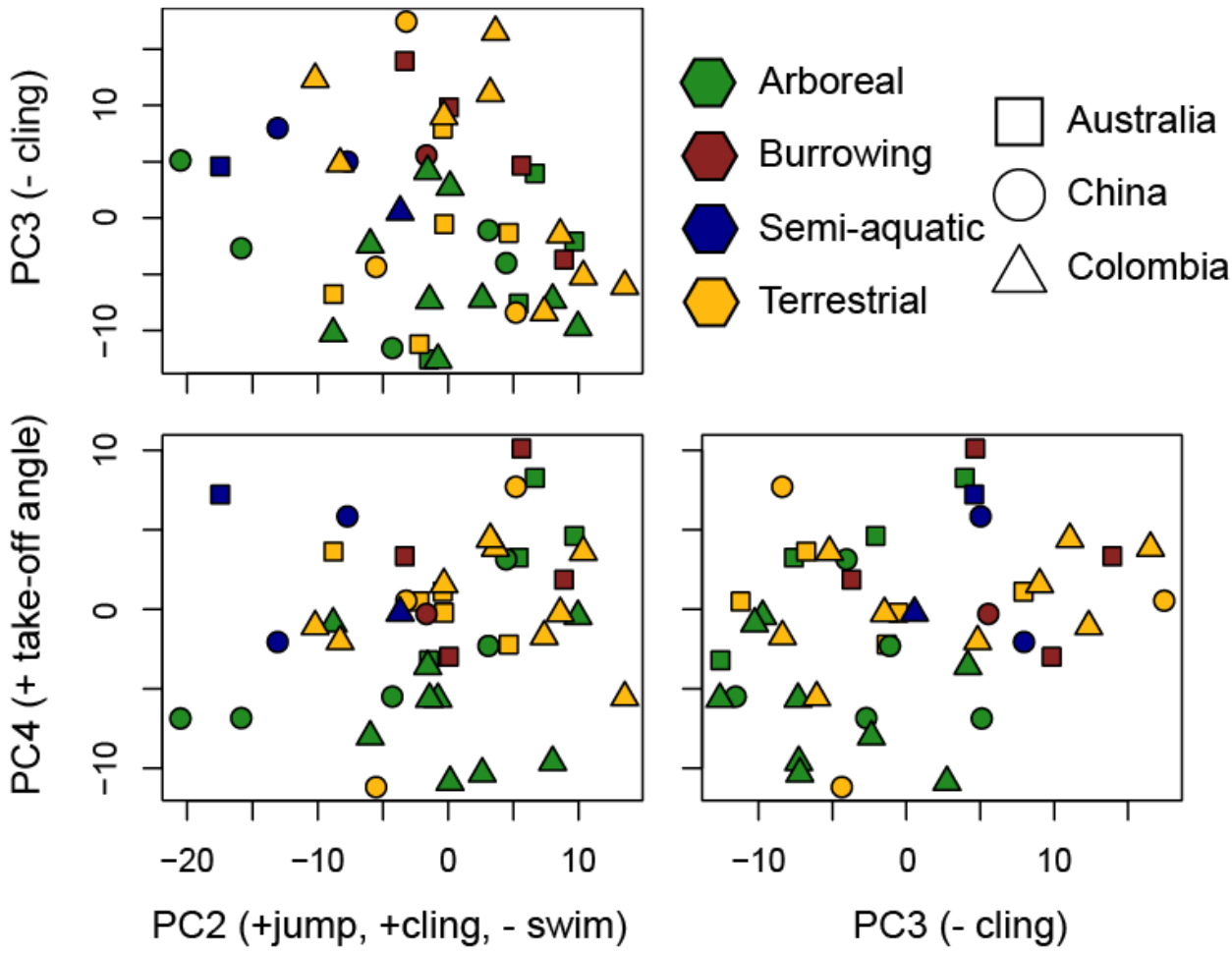
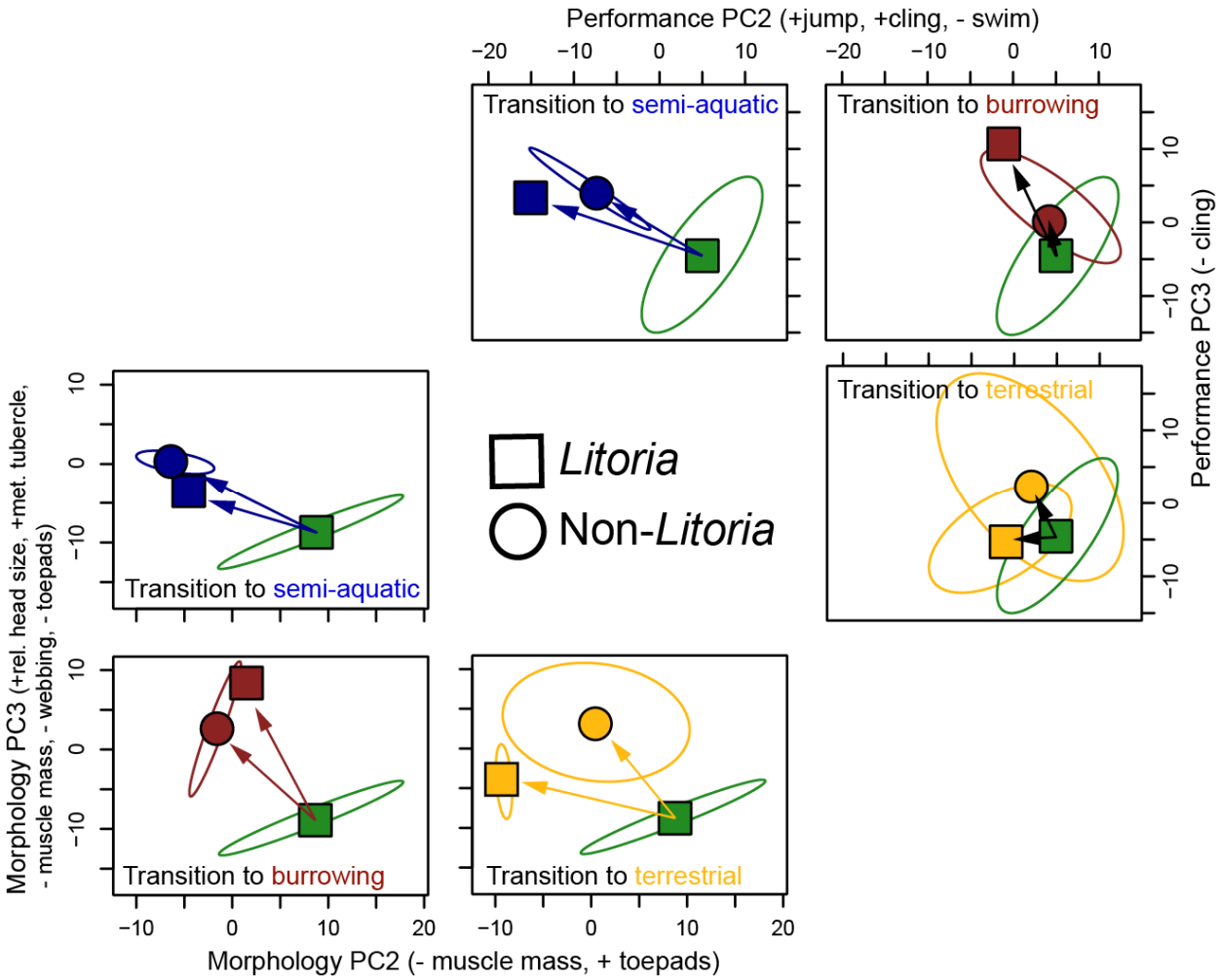


Figure 4.6. Plots of distances and angles of *Litoria* in novel microhabitats (non-green squares) compared to other species in same microhabitat (circles) and to *Litoria* in ancestral habitat (arboreal; green squares). Plots of morphology are on the bottom left and performance plots are on upper right. Only PC2 and PC3 are shown for ease of visualization, but note that they do not represent the complexity of the data found in statistical analysis (i.e., beyond PC3). All datapoints reflect the centroid (mean) for each group they represent. Ellipses represent variation within each group along their principle axes of variation for PC2 and PC3 (for groups in which the number of species was greater than 2), and radii are 1 standard error along each principle axis of variation.



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Appendix 1

Specimens measured for the morphometric analysis of *Osteopilus*. All specimens were from the Smithsonian Museum of Natural History (USNM); species names are followed by the USNM specimen number.

O. brunneus. − 251411–251412, 251415, 251419, 251477, 251490–251491, 251495, 251498, 251543–251544, 251549–251551, 251582, 251584, 251596, 251612–251614. *O. crucialis*. − 167627, 251619, 252456, 327244. *O. dominicensis*. − 224937, 259578, 259589–259591, 259593, 259595, 259599, 259606–259610, 259613. *O. marianae*. − 139250, 251620–251629, 266469–266471, 327177. *O. pulchrilineatus*. − 65730, 74560, 74566, 140234, 140236, 329642–329656. *O. septentrionalis*. − 137858–137860, 137868, 137890, 137892, 137895, 137899, 137901–137903, 137886, 236538–236539, 311987, 315785, 315797, 335668, 335670, 497935. *O. vastus*. − 55301, 65753–65759, 66984, 66986, 74512, 74514–74516, 74519, 118837–118838. *O. wilderi.* − 251194–251195, 251218, 251220–251223, 251225–251226, 251258, 251265, 251279, 251282, 251290, 251340, 251368–251370, 251373, 251993.

Appendix 2: Chapter 2 expanded materials and methods

Body size ranges in treefrog assemblages

To assess the similarity of body size ranges found across treefrog assemblages, we compiled body size data and species lists from regional assemblages throughout the world and local sites within regions. We use the term "treefrog" in a general sense, indicating the treefrog ecomorph rather than a specific clade of frogs (i.e., arboreal frogs with enlarged toe pads; Pough et al. 2002). It should be noted that we excluded some potential "treefrogs" and focus only on the most species-rich treefrog clade within each region. Although we expect that there will be evolution of body-size extremes in many regions, we do not necessarily expect this pattern in every clade in every region. More specifically, we did not deal with frogs of the family Centrolenidae (mostly small bodied) and Hemiphractidae (mostly large bodied; sensu Wiens et al. 2005), which occur primarily in montane regions of South America but are less species-rich than South American hylids and have specialized life histories (IUCN et al. 2006). These two clades are not closely related to hylid treefrogs or each other (Wiens et al. 2006b). We note that both centrolenids and hemiphractids have each evolved a broad range of body sizes, but not necessarily at every location, and their body size evolution may be constrained by interactions with each other and with sympatric hylids. Furthermore, around the world there are various lineages that are at least semi-arboreal that show seemingly continuous variation from no toepads to toepads, including *Eleutherodactylus* and some frogs of the families Microhylidae and Ranidae (Duellman and Trueb 1986). Because it would be difficult to identify all species within these groups that would be considered "treefrogs," we only included the major treefrog clades within each region. Regions were delineated with respect to geographic areas of independent treefrog evolutionary history, determined by examining species composition and using the phylogenies of Bossuyt et al. (2006) for ranoid frogs, Wiens et al. (2006b) for hylid treefrogs, and Roelants et al. (2007) and Wiens (2007) for overall frog phylogeny. Each region was considered to be largely independent because nearly its entire treefrog fauna arose from either (1) a single treefrog colonization within the region (regions 3, 5, 6, and 8 below), or (2) an independent origin of the treefrog ecomorph (regions 1, 2, 4, and 7 below). For the four regions that slightly deviated from our criteria for independence, we present the body size range of only the descendents of the primary colonization (regions 3 and 6) or independent evolution of the treefrog ecomorph (regions 1 and 2), such that the ranges presented are independent. These regions are (1) Africa (sub-Saharan only), (2) Madagascar, (3) Holarctic (North Africa, Europe, temperate northern Asia, and North America), (4) Southeast Asia and India, (5) Australasia (Australia and New Guinea), (6) Middle America (Mexico to Panama), (7) South America (the Amazon Basin and Brazilian Atlantic forest), and (8) the Caribbean (without Trinidad and Tobago). Literature data on local sites indicated that most local sites within these regions had body size ranges similar to those for the entire region. However, a formal comparison of local sites surveyed to date within all regions was problematic for two reasons. First, difficulties existed in comparing different sites across different regions due to differences in sampling intensities at different sites. Second, at the local scale, the occurrence of widespread taxa that occurred in many local assemblages posed problems for comparisons within a region, since such local

assemblages were not independent in their taxonomic composition. Thus, we present two examples of well-sampled local sites within each region to document that local assemblages may also exhibit the size ranges typical of the regional fauna. Because high-elevation treefrogs can have substantial variation in body size at different altitudes (e.g. Amezquita 1999), we chose only low-elevation communities. Note that although species lists may not necessarily indicate syntopic species that are currently interacting per se, such lists were the finest resolution we could obtain, particularly for tropical areas.

We used snout-to-vent length (SVL) as a metric of body size (see next section). Because most sources of local species composition did not list the SVL data for local populations, we used maximum reported SVL for all species to maintain consistency. This also helped avoid sampling artifacts, in which a species is known or expected to be present but has not been sampled enough to get an accurate estimate of the maximum SVL within that local site. Although the mean SVL may be preferable to maximum SVL, data for the mean of most species were not available. Similarly, we use maximum SVL to maximize the amount of body size data, but results were similar using only male maximum SVL. Maximum SVL data were gathered primarily from field guides or surveys that covered broad regions, as follows: Africa (Schiøtz 1999; Channing 2001), Madagascar (Glaw and Vences 1994), Holarctic (Conant and Collins 1998; Fei et al. 1999; Arnold 2003; Stebbins 2003; Goris and Maeda 2004; Lannoo 2005), Southeast Asia and India (Berry 1975; Manthey and Grossman 1997; Daniel 2002), Australasia (Menzies 1977; Barker et al. 1995), Middle America (Duellman 2001), South America (many sources; see Table A2.1), and the Caribbean (Trueb and Tyler 1974; Schwartz and Henderson 1991). We recognize that this literature does not include all species from some regions (e.g., India, Australasia). However, the sources do cover a sufficiently large number of species to document the occurrence of the body size range characteristic of treefrog assemblages (see RESULTS).

Morphometrics

To ascertain whether body size is the major axis of morphological differentiation among Caribbean treefrog species (compared to a trait like gape width, for example), we examined morphometric variation in the group. Museum specimens were measured at the U.S. National Museum of Natural History (see Appendix 1). With one exception, between four and ten individuals of each sex of each species were measured, depending on specimen availability. We attempted to measure only sexually mature individuals (estimated by nuptial pad presence in males and size in females; Duellman and Trueb 1986, p. 56). If more than 10 individuals were available for a given sex-species combination, the largest 10 individuals were sampled to ensure sampling of sexually mature individuals at the large end of the body size distribution for each species (given that we use maximum SVL in subsequent analyses).

Morphometric data consisted of 12 linear measurements typically used to quantify body shape and size in treefrogs (e.g., Duellman 2001). These included: (1) snout-to-vent length (SVL; tip of snout to anterior margin of cloaca), (2) tibia length (tip of knee to tip of heel), (3) foot length (proximal edge of inner metatarsal tubercle to tip of fourth toe), (4) head length (posterior corner of jaw to tip of snout), (5) head width (distance between posterior corners of jaw), (6) interorbital distance (width of bone

between two orbits), (7) internarial distance, (8) eye-to-nostril distance (posterior tip of nostril to anterior corner of eye), (9) eye diameter (distance between anterior and posterior corners of eye), (10) hand length (proximal edge of outer palmar tubercle to tip of third finger), (11) thumb length (insertion point of thumb into hand to tip of thumb), and (12) radioulnar length (elbow to distal edge of outer palmar tubercle). All measurements were ln-transformed before analysis.

Because these measurements were highly correlated with one another, we partitioned them into orthogonal axes of variation by performing principal components analysis (PCA; Manly 1994) on the correlation matrix. We examined the proportion of variation explained by each component and examined the loadings for each variable to interpret each component in terms of the original variables. The PCA was conducted in JMP IN (Version 4.0.4, SAS Institute, Inc., Cary, NC, 2001).

Sexual size dimorphism (SSD) is widespread among *Osteopilus* species, with females larger than males (results not shown). Thus, sexual selection could be responsible for some of the variation in size. However, we expect that sexual selection has played a small role at most in the overall diversification of body sizes within *Osteopilus*, because female-biased SSD in frogs has been typically ascribed to fecundity selection (i.e., unidirectional toward larger female size; Shine 1979; Woolbright 1983). In contrast, we see evidence for either diversification into all sizes or into predominantly smaller sizes within *Osteopilus* (see *Results*). Additionally, all subsequent analyses were also conducted using only males, but the results were qualitatively identical when the maximum size of either sex was used.

Community Analyses

A simple test to investigate whether the body sizes of treefrog species on Jamaica and Hispaniola may be structured non-randomly is to compare two models of community assembly. Our approach is similar to those of Fox and Brown (1993) and Gillespie (2004), but instead of simulating community assembly under a null model (as in the former) or calculating probabilities based on random assembly only (as in the latter), we compare the direct probability of a given community structure under two different models of assembly. First, in a random assembly model, the probability of occurrence of a certain body size in a local community (here, Jamaica and Hispaniola) is directly proportional to the frequency of that body size within the source pool [here, the mainland (South American) treefrog species pool]. In an alternative model, underrepresented body sizes in the source pool have a greater chance of arriving in a community, perhaps due to competition among species of similar body sizes (e.g., although very large species of treefrogs are relatively rare, they may have greater odds than a medium-sized species of invading a community in which a medium-sized species already exists). This latter model will be called the “biased assembly” model for convenience. [Note that one could also view this as a test of random versus biased body size evolution, in which the Caribbean species are assumed to form a star phylogeny (cf. Schluter 1990). However, for brevity we will use the “assembly” terminology throughout.]

One criticism of this approach would be that previous phylogenetic analyses indicated that most of the Caribbean species form a clade (Faivovich et al. 2005; Wiens et al. 2006b), and thus an assembly model of multiple invasions from South America is

not realistic (see Losos 1990 for a similar example). Although we concur with this criticism, we emphasize that this test is only documenting the low probability of seeing the even body size spacing in Caribbean communities, given the frequencies of possible body sizes hylids could be; it is not meant to realistically model the actual assembly or evolution of Caribbean communities. We use this test as part of many tests (see below) that each lend support to the idea that Caribbean communities are highly structured with respect to body size.

The model of random community assembly was based on the hypergeometric probability model, a simple model of sampling from a population without replacement (Sokal and Rohlf 1995). Here, the "population" is the pool of South American and Caribbean treefrogs, and the "samples" are the treefrog communities on Jamaica and Hispaniola (see below). The hypergeometric model is appropriate for sampling from a population that is divided up into discrete categories, in this case body size classes. With two categories (e.g., 0 and 1), the probability of obtaining d_0 species of body size type 0 in a sample of size n (Sokal and Rohlf 1995) is

$$P(x = d_0 \mid n, D_0, D_1) = \frac{\binom{D_0}{d_0}\binom{D_1}{n - d_0}}{\binom{D_0 + D_1}{n}}$$

where D_0 and D_1 are the total number of species of type 0 and 1, respectively, within the sampled population (e.g., source pool).

This can easily be extended to additional discrete categories. In this analysis, we use four categories, one each for small, medium, large, and very large body size (based on Duellman 2001; see Table A2.3 for corresponding variable definitions). Thus, the probability of the body size distribution within a community (d_0 small, d_1 medium, d_2 large, and $n - d_0 - d_1 - d_2$ very large), given random sampling, the sampling distribution of body sizes (i.e., the source pool of tropical South American and Caribbean treefrogs), and sample size (n = total species within the community) is

$$P(\mathbf{x} = \mathbf{d} \mid n, \mathbf{D}) = \frac{\binom{D_0}{d_0}\binom{D_1}{d_1}\binom{D_2}{d_2}\binom{D_3}{n - d_0 - d_1 - d_2}}{\binom{D_0 + D_1 + D_2 + D_3}{n}}$$

where $\mathbf{d} = (d_0, d_1, d_2)$ and $\mathbf{D} = (D_0, D_1, D_2, D_3)$.

For the source pool, we used maximum reported SVL of the Caribbean species as well as South American hylids, since Caribbean treefrogs (both *Osteopilus* and *Hypsiboas*) are deeply nested within South American clades (Faivovich et al. 2005; Wiens et al. 2005, 2006b), suggesting that Caribbean treefrogs initially dispersed from northern South America. Additionally, using only Caribbean species, for example, may make our analyses susceptible to the "Narcissus effect" of community assembly analyses (Colwell and Winkler 1984). This effect results in an underestimation of the

effect of competition, due to sampling from a post-competition source pool in which body sizes that have been excluded from the observed communities or never evolved due to competition aren't included. Maximum SVL was obtained from literature sources for all nine Caribbean species as well as for 445 of the 453 South American species of the family Hylidae listed in Frost (2007). SVL data and references are presented in Table A2.1. (Note that we also conducted analyses using only maximum male SVL, but this gave qualitatively similar results). Here, we calculated the probability of seeing one small, one medium, one large, and one very large species in Jamaica, and one medium, one large, and two very large species in Hispaniola given 47 small, 86 medium, 52 large, and 15 very large species in mainland South America and the Caribbean [Table A2.3; note that the total number of species in our "species pool" was only 200, because we experienced computational difficulties using the full species pool of 454 (e.g., the normalization constant Q for the biased model was as high as 10^{763} during parameter estimation). Instead, we used 200 species, with the proportion of species in each body size category determined from all 454 species. Although this reduction of the species pool may influence our results, it probably does so only slightly and should not qualitatively alter them, as further drastic reductions in the size of the assumed species pool (to 100 and 50 species) gave quantitatively similar results as using 200 species (results not shown)]. Hypergeometric probabilities of body size distributions for Jamaica and Hispaniola were calculated by hand.

The hypergeometric distribution is appropriate for obtaining the probability of the body size distribution within a community if no sampling bias exists (i.e., "random" assembly). However, if community assembly is influenced by processes that prevent certain types from entering, such as competition preventing similarly sized species from coexisting within a community, then a sampling bias would exist. To incorporate this bias, it is appropriate to use the non-central hypergeometric distribution (McCullagh and Nelder 1989). This distribution incorporates additional parameters to estimate the bias in sampling from the different categories. The sampling biases for sizes small, medium, large, and very large frogs are ω_0, ω_1, ω_2, and ω_3, respectively. Thus, the probability of a particular community body size distribution conditioned on the sampling biases [$\boldsymbol{\omega} = (\omega_0, \omega_1, \omega_2, \omega_3)$], sampling distribution (**D**), and number of species within the community (n) is

$$P(\mathbf{x}=\mathbf{d}\mid n,\mathbf{D},\boldsymbol{\omega}) = \omega_0^{\,d_0}\omega_1^{\,d_1}\omega_2^{\,d_2}\omega_3^{\,n-d_0-d_1-d_2}\frac{\binom{D_0}{d_0}\binom{D_1}{d_1}\binom{D_2}{d_2}\binom{D_3}{n-d_0-d_1-d_2}}{\binom{D_0+D_1+D_2+D_3}{n}}Q^{-1}$$

where Q is a normalization constant. This equation can be reparameterized in terms of ratios (following Munch and Conover 2003; see also McCullagh and Nelder 1989) comparing the bias parameters of classes 0-2 to class 3, as in $\psi_0 = \omega_0/\omega_3$. Additionally, the terms that do not depend on d_0, d_1, and d_2 can be taken out of the equation because those constant terms will also be in the normalization constant and thus will cancel out. Doing this, we arrive at

$$P(\mathbf{x}=\mathbf{d}\mid n,\mathbf{D},\text{¿}) = Q^{-1}\left(\frac{\psi_0^{\,d_0}\psi_1^{\,d_1}\psi_2^{\,d_2}}{d_0!\,d_1!\,d_2!(n-d_0-d_1-d_2)!(D_0-d_0)!(D_1-d_1)!(D_2-d_2)!(D_3-n+d_0+d_1+d_2)!}\right)$$

where the normalization constant, Q, is equal to

$$Q = \sum_{i=0}^{4} \sum_{j=0}^{4-i} \sum_{k=0}^{4-i-j} \left(\frac{\psi_0^i \psi_1^j \psi_2^k}{i!\, j!\, k!\, (n-i-j-k)!\, (D_0-i)!\, (D_1-j)!\, (D_2-k)!\, (D_3-n+i+j+k)!} \right).$$

Note that the probabilities derived above are for a single community only. If we assume that the communities of Hispaniola and Jamaica were assembled independently (see Results), their probabilities can be multiplied for a combined likelihood of the body size distributions occurring on both islands. Unique bias parameters for each island (total of six free parameters) or a single parameter for each size category across the two islands (three free parameters) can be estimated. Here, we use the latter strategy because we expect that the same processes are driving the similar body size distributions on the two islands. Maximum-likelihood estimates (MLEs) and confidence intervals of the bias parameters were calculated in MatLab (ver. 6.5, The MathWorks Inc., Natick, MA). MatLab code is available from the authors upon request.

The two models were compared via a likelihood ratio (*LR*) test, which can be used to compare nested models (Edwards 1972). Here, the random assembly model is a special case of (i.e., nested within) the biased assembly model when all $\psi_i = 1$. The *LR*-test statistic is

$$LR = 2 \ln \left(\frac{\lambda_{Hisp}\left(\hat{\psi}_0, \hat{\psi}_1, \hat{\psi}_2\right) * \lambda_{Jam}\left(\hat{\psi}_0, \hat{\psi}_1, \hat{\psi}_2\right)}{\lambda_{Hisp}\left(\text{all } \psi_i = 1\right) * \lambda_{Jam}\left(\text{all } \psi_i = 1\right)} \right)$$

where $\hat{\psi}_i =$ maximum likelihood estimate of bias parameter *i*. Given the random assembly model, this *LR* is expected to be asymptotically distributed as $\chi^2_{p,\alpha}$, where p = the number of free parameters differing between the two models and α = the desired level of statistical significance. In this case, $p = 3$ and we set $\alpha = 0.05$.

A limitation to this approach exists in that the body size categories are somewhat arbitrary. Although we used those of Duellman (2001), which best captured the even spacing of body sizes among Caribbean species, we could have used the categories of Savage (2002) or any other arbitrary distinction. Indeed, despite the similar body size ratios among species on Jamaica and Hispaniola (results not shown), the body sizes of Hispaniolan species are shifted higher than Jamaican species, resulting in zero “small” but two “very large” species on Hispaniola (Table A2.3). One could alter the model for use of continuous body size distributions, with probabilities of biased assembly related to amount of distributional overlap. However, this also is problematic, because one must specify a function relating the amount of overlap in intraspecific body size distributions and the probability of biased assembly, which we see as equally arbitrary as discrete categories (see also Dayan and Simberloff 2005).

Phylogenetic analyses

TAXON SAMPLING

A previous analysis (Wiens et al. 2006b) showed that eight of the nine species of Caribbean treefrogs form a monophyletic group (*Osteopilus*) within the hylid clade

Lophiohylini (sensu Faivovich et al. 2005), but provided only weak support for relationships within *Osteopilus* and among genera within Lophiohylini. To better estimate relationships within *Osteopilus*, we obtained new molecular data for Lophiohylini. We sampled all nine treefrog species from the Greater Antilles, including all *Osteopilus* and *Hypsiboas heilprini*. In addition, we included 14 other species of Lophiohylini, with at least one representative of each currently recognized genus (Table A2.4). Finally, for outgroups to Lophiohylini, we sampled multiple species of each of the other major clades of Hylinae (Table A2.4; Faivovich et al. 2005; Wiens et al. 2006b).

Because we needed phylogenies with branch lengths to estimate the rate of body size evolution in non-*Osteopilus* neotropical treefrogs, we also conducted Bayesian analyses (see below) to estimate phylogenies of Cophomantini, the *Dendropsophus* clade (sensu Wiens et al. 2006b), Phyllomedusinae, and the *Scinax* clade (sensu Wiens et al. 2006b). We used data from the 325-taxon data set for hylid frogs and outgroups assembled by Wiens et al. (2006b), which had been analyzed using only parsimony. We analyzed these four clades separately to reduce the number of taxa and thus make the analyses more tractable for Bayesian methods.

MOLECULAR DATA

For our analysis within Lophiohylini, molecular data were sequenced from five mitochondrial and four nuclear gene regions. The mitochondrial data included the ribosomal small subunit [12S; 1016 base pairs (bp); also including adjacent tRNA-Phe and tRNAVal], cytochrome oxidase I (COI; 584 bp), cytochrome *b* (385 bp), NADH dehydrogenase subunit 1 (ND1; 1242 bp; including adjacent tRNA genes), and NADH dehydrogenase subunit 2 (ND2; 580 bp). The nuclear genes included proopiomelanocortin A (POMC; 601 bp), proto-oncogene cellular myelocytomatosis exon 2 (*c-myc*; 417 bp), recombinase activating protein 1 (RAG-1; 1399 bp), and tensin 3 (TNS3; 512 bp). Additional molecular data were obtained from Faivovich et al. (2005) for 13 taxa for which we lacked tissue samples (some non-*Osteopilus* Lophiohylini) for three genes (12S, cytochrome *b*, RAG-1). In addition, their data for four additional genes were added, both for those 13 species and for the 10 species included in both our sampling and theirs. These additional genes included both mitochondrial [ribosomal large subunit (16S; 1646 bp)] and nuclear [tyrosinase (530 bp), sevenin-absentia (SIA; 307 bp), rhodopsin (316 bp)] markers. All sequences for the Cophomantini, *Dendropsophus* clade, *Scinax* clade, and Phyllomedusinae were obtained from Darst and Cannatella (2004), Faivovich et al. (2004, 2005), and Wiens et al. (2005, 2006b). Because our taxon and gene sampling for these clades was identical to that within the 325-taxon dataset of Wiens et al. (2006b), Genbank numbers for these analyses can be found within the online appendix of Wiens et al. (2006b).

DNA was extracted from ethanol preserved tissues using standard methods and was amplified using the polymerase chain reaction (PCR); specific protocols are available from the authors upon request. Primer sequences are listed in Table A2.5. PCR products were purified and sequenced directly using an ABI 3100 automated sequencer. Sequences were edited using SeqEd 1.0.3 (Applied Biosystems, Foster City, CA). GenBank numbers are given in Table A2.4, and voucher specimen numbers can be found within each sequence's GenBank entry.

Sequence data from the current study and previous studies were combined into a single matrix. Preliminary analyses of genes sequenced both for this study and by Faivovich et al. (2005) (i.e., 12S, cytochrome *b*, RAG-1) supported the monophyly of different individuals within species of *Osteopilus* species for which multiple individuals were sampled across studies (*O. crucialis*, *O. dominicensis*, *O. septentrionalis*, and *O. vastus*). Therefore, we combined data across studies for individual taxa so as to minimize the amount of missing data for any given taxon. Nevertheless, our combination of data from different studies still resulted in missing data for some taxa. Our analyses should be largely insensitive to this issue for a number of reasons. First, within the group of interest (*Osteopilus*), little missing data existed for the nine genes for which we generated DNA sequences. Secondly, both simulation (reviewed by Wiens 2006) and empirical (Driskell et al. 2004, Wiens et al. 2005) studies indicate that even highly incomplete taxa can be accurately placed within a phylogeny if the overall number of characters is large (i.e., thousands of characters, as is the case here), and in many cases the addition of taxa with incomplete data can increase phylogenetic accuracy relative to excluding those taxa entirely (Wiens 1998b, 2005).

DNA SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS

Alignment of protein-coding genes was straightforward. Sequence data were converted into amino acid residues (for alignment only) and aligned by eye using Se-Al 1.d1 (Rambaut 1995). Ribosomal DNA and tRNA sequences were aligned first by Clustal X version 1.8.1 (Thompson et al. 1994). Adjustments were made by eye in PAUP* (ver. 4.0b10, Swofford 2002) to conform to proposed secondary structure (see below). Clustal X alignments were conducted using default settings (gap opening = 15; gap extension = 6.666; delay divergent sequences = 30%; transition:transversion = 50%), and regions that differed under different gap-opening penalties (12.5, 15, and 17.5) were excluded from analyses. Secondary structure for ribosomal DNA was inferred by comparing our sequences to the proposed structure for the hylid *Pseudacris regilla* (12S; Graybeal 1997) and the ranid *Rana catesbeiana* (16S; Nagae 1988), as listed on the European ribosomal RNA database (http://www.psb.ugent.be/rRNA/). Minor adjustments were made to conform to nucleotide complementarity within stems, as well as to avoid placing insertions and deletions within stems. Wiens et al. (2005) found that the secondary structure model of 12S for *P. regilla* was very similar to those proposed for all non-hylid frog taxa. Thus, we expect that these models should be accurate for our analyses within hylids.

Our primary estimate of phylogeny was based on a partitioned Bayesian analysis of all the genes combined. However, both parsimony and Bayesian analyses of the separate and combined genes were conducted. In order to test among genes for strongly supported incongruence that might be indicative of incongruent gene histories (Wiens 1998a), we analyzed the data from each gene separately, the mitochondrial data alone, and then the nuclear data alone. Strong statistical support was considered to be a bootstrap value of ≥ 70% (Hillis and Bull 1993) or Bayesian posterior probability (Pp) of ≥ 0.95 (Wilcox et al. 2002; Alfaro et al. 2003; Huelsenbeck and Rannala 2004). We found no strongly supported incongruence among genes or sets of genes (see *Results*). As a result, we combined data from all 13 genes into one combined analysis, because we consider the best estimate of phylogeny to come from a combined analysis

of all data (de Queiroz and Gatesy 2007). The combined data matrix, as well as our best estimate of the topology of Lophiohylini (see *Results*), has been archived within TreeBASE (www.treebase.org) under study accession number S2202.

Parsimony analyses were conducted in PAUP*. We used a heuristic search with random-taxon-addition and tree bisection-reconnection (TBR) branch swapping. To foster a thorough search of tree space, we conducted 1,000 replicate searches and retained a single tree per replicate. Statistical support for individual branches was assessed by non-parametric bootstrap (Felsenstein 1985a). We performed 500 pseudoreplicate searches, using 10 random-taxon-addition sequence replicates per pseudoreplicate, TBR branch swapping, and saving a single tree per replicate.

Bayesian analyses were performed in MrBayes 3.1 (Huelsenbeck and Ronquist 2001). All analyses consisted of two replicate Monte-Carlo Markov chains, each run for 6 million generations total, with trees sampled every 1,000 generations. Visual observation of the log-likelihood and parameter traces indicated that all analyses converged on the posterior distribution before 200,000 generations in both replicates. Comparison of the log-likelihoods, parameter means, and topology for each replicate and of the branch lengths and posterior probabilities for each branch suggested that in all searches, both replicates reached the same posterior distribution. Thus, after conservatively eliminating the trees produced from the first million generations of each replicate as burn-in, the sampled trees from both replicates in each analysis were pooled to estimate the phylogeny. Default priors were used, except that the gamma distribution shape parameter prior was set to exponential (as suggested by Zwickl and Holder 2004) with a mean (0.75) derived from maximum-likelihood or Bayesian posterior estimates from previous studies of the same genes in other frogs (e.g., Symula et al. 2003; Fromhage et al. 2004; Crawford and Smith 2005; van der Meijden et al. 2006). Our prior mean (0.75) is intermediate to those estimates and is close to the estimated value for a combined analysis of nuclear and mitochondrial data (van der Meijden et al. 2006).

Models for Bayesian analyses were chosen using a two-step process. First, models for each gene were chosen with MrModeltest 2.2 (Nylander 2004), a modification of Modeltest (Posada and Crandall 1998). The Akaike Information Criterion (AIC) was used to select the best fitting model for each gene (Pol 2004; Posada and Buckley 2004). Stem and loop regions of the 12S and 16S genes were assigned their own model, as we expected stems and loops to evolve under substantially different substitution models. Additionally, a separate model was assigned to the tRNA preceding ND1. Models for protein-coding genes were assigned for the entire gene; when within-gene partitions were specified (see below for partitioning strategy), each codon partition was assigned the model of its gene but with its own codon-specific rate parameters (i.e., we did not test among classes of models due to the small size of some codon-specific partitions).

Secondly, we decided upon an optimal gene-partitioning strategy by conducting successive analyses, with a different partitioning strategy for each analysis, and comparing the model fit of each partitioning strategy by using the Bayes factor (Nylander et al. 2004). The four partitioning strategies included, in increasing order of complexity: (1) one partition each for all structural (ribosomal and tRNA) mitochondrial genes, all protein-coding mitochondrial genes, and all nuclear genes, (2) a different

partition for each gene, (3) separate partitions within mitochondrial genes (stems and loops for 12S and 16S; codon positions for protein-coding genes) but only a single partition for each nuclear gene, and (4) a separate partition for each codon position within all protein-coding genes, as well as stems and loops for 12S and 16S. After each analysis, model parameter traces were inspected to identify potential cases of overpartitioning (diffuse, undersampled posterior distributions; Nylander et al. 2004) and/or non-identifiability of parameters (Rannala 2002; Castoe et al. 2004). Finally, the harmonic mean of the ln-likelihoods of the trees from the pooled posterior sample (i.e., post-burn-in trees) was calculated to compare partitioning strategies using the Bayes factor (Nylander et al. 2004). As in previous papers (e.g., Nylander et al. 2004), we considered a Bayes factor of > 10 to be very strong evidence in favor of a higher-partitioned model.

The procedure of substitution model choice for each gene was conducted separately for all clades analyzed separately in this paper (i.e., Cophomantini, *Dendropsophus* clade, Lophioylini, Phyllomedusinae, *Scinax* clade). However, because of the prohibitive computational time of choosing the optimal partitioning strategy, this latter test was only conducted for Lophiohylini (clade containing *Osteopilus*). For Lophiohylini, the most partitioned model (number 4 above) received the most support (strategy 4 vs. 3: Bayes factor = 1230.94). Additionally, all recent Bayesian analyses of hylid frogs have found the most partitioned model to be the optimal model (Wiens et al. 2005, 2006b). Thus, we applied the fourth partitioning strategy to the four additional hylid clades analyzed in this paper.

Rate of Body-Size Evolution

Diversifying selection, coupled with ecological opportunity, can result in a high rate of character evolution (Schluter 2000). Thus, we suggest that a high rate of body-size evolution within *Osteopilus* may be further evidence of adaptive processes driving the diversification of body sizes within this genus. We predict that the absence of other treefrog clades in the Caribbean might lead to an accelerated rate of body-size evolution among *Osteopilus* species, allowing them to rapidly occupy the ecological niches filled by small-, medium-, large-, and very large-bodied treefrog species in mainland tropical South America (and in other communities around the world). Alternatively, the absence of such an increase in *Osteopilus* might suggest that the ranges of body sizes on Hispaniola and Jamaica evolved (or were otherwise assembled) randomly rather than deterministically.

To evaluate the significance of the rate of body size evolution in *Osteopilus*, we estimated the rate of body size evolution within this clade and then compared it to tropical South American species. We compared *Osteopilus* to South American species because the former are derived from an otherwise predominantly South American clade (Lophiohylini) and in particular, *Osteopilus* community evolution may represent the early stages of older treefrog assemblages, which are represented by South American communities (see *Discussion*).

Comparing rates of evolution requires trees with comparable branch lengths (i.e., in the same units) for all the relevant clades. Because somewhat different molecular data sets were available for different clades (e.g., Lophiohylini vs. other clades), we obtained comparable branch lengths across all clades by estimating a chronogram

separately for each clade and then combining branch lengths across the tree by using time as a common currency (see Wiens et al. 2006a). We converted the molecular branch lengths from the Bayesian analysis of the combined data into units of time using a penalized likelihood method (PL; Sanderson 2002) in the program *r8s* (version 1.6 for Unix; Sanderson 2003). PL "smooths" out the rate heterogeneity in molecular branch lengths, producing an ultrametric tree. When combined with dates for one or more nodes, the procedure can produce branch lengths in units of time.

For this analysis, we used the "allcompat" command when summarizing trees from the posterior distribution for each Bayesian phylogenetic analysis. This command produces a fully-bifurcating tree, but one which includes some clades with Pp < 0.50. We did this to eliminate polytomies, which are potentially problematic for PL analyses. Although some nodes were therefore resolved but poorly supported, we do not expect this to be a problem for two reasons. First, most trees (4 of 5) had few nodes with Pp < 0.50. Second, the group with the most poorly resolved clades, the *Dendropsophus* clade, had very low variability in SVL among species, such that alternative resolutions of weakly resolved nodes should not greatly affect the inferred rate of body size evolution.

We used branch lengths from the Bayesian analysis of the combined data. To determine the optimal level of rate smoothing, we used the Truncated-Newton (TN) algorithm in *r8s*, with cross-validation assessment of potential smoothing parameters ranging from 10^{-1} to $10^{4.5}$, evaluated at each exponential increment of 0.5.

For each of our clades we used the age of each clade estimated by Wiens et al. (2006b) to calibrate the ultrametric trees produced by *r8s.* The chronogram of Wiens et al. (2006b) was based on 9 fossil calibration points, including all relevant hylid fossils. Wiens et al. (2006b) presented two sets of dates (age of Neobatrachia of 100 or 160 million years), and we used both to estimate two sets of divergence times for each clade.

To calculate rates of body-size evolution, we used the likelihood method of O'Meara et al. (2006) in the program *Brownie*. The parameter calculated by this method (σ^2) is the variance of character change that accumulates at each step of a Brownian motion random-walk model of trait evolution (Felsenstein 1985b). Because this parameter influences the rate at which the overall character variance in a clade accumulates, it can be thought of as the rate of morphological evolution (Martins 1994; Collar et al. 2005). Rates were calculated for (1) *Osteopilus*, (2) Lophiohylini exclusive of *Osteopilus*, (3) Cophomantini, (4) the genus *Dendropsophus*, (5) the *Scinax* clade, (6) Phyllomedusinae, and (7) all major South American clades combined exclusive of *Osteopilus* (i.e., groups 2-6 above). The phylogeny for the last group was constructed with a "supertree" approach (Sanderson et al. 1998). Individually-estimated Bayesian phylogenies and chronograms (see above) for groups 2-6 were manually added to a dated "backbone" chronogram from Wiens et al. (2006b). Estimating a phylogeny, branch lengths, and chronogram for all taxa simultaneously would have been difficult given the large number of taxa, large number of diverse genes, and complex models of character evolution (i.e., Bayesian analysis of the entire tree was not possible due to the prohibitive computational time; see Wiens et al. 2006b for an explanation).

To test for a significantly higher rate of body-size evolution in *Osteopilus*, we conducted a censored test (O'Meara et al. 2006) between *Osteopilus* and other South American hylids, from which *Osteopilus* is derived and in which relative conservatism in

body size within clades seems to occur. Censored tests prune the clade of interest (here, *Osteopilus*) from the tree, estimate rates for the pruned subtree and for the larger tree without the subtree, and then compare the likelihoods of the one-rate (for the entire tree) and two-rate (as above) models. To compare the likelihoods, we used a likelihood ratio (*LR*) test. O'Meara et al. (2006) noted that the *LR* can be biased when comparing groups of different sample size (numbers of species), as we have here. However, they stated that the bias would tend to underestimate the rate for the smaller group. In our case, underestimating the rate in *Osteopilus* would make our results more conservative.

For body size we used the maximum reported SVL for each species, irrespective of sex (to maximize the amount of data available). However, we do not expect this to systematically bias our results, as sexual dimorphism occurs to some extent in all major hylid clades and the absence of sex-specific size data was dependent on literature sources, rather than clade-specific. An analysis using maximum male size gave qualitatively identical results (not shown). Maximum SVL was ln-transformed before analysis to model rate of proportional change, rather than absolute change (i.e., additive changes in a ln-transformed variable are equivalent to multiplicative changes in the original variable) (O'Meara et al. 2006). We obtained SVL data from the literature for 171 of the 175 species that were included in our phylogeny. Our phylogenetic sampling from all clades except *Osteopilus* was not complete; thus, a concern exists that our results are not representative of body size evolution in the undersampled clades. However, we expect our results to be conservative for two reasons. First, we sampled some of the largest and smallest known species from each clade. When coupled with incomplete taxon sampling, we expect that our inclusion of the full range of body sizes within these clades will inflate the rate for the non-*Osteopilus* clades, thus reducing the potential significance of a high rate of body size evolution in *Osteopilus*. Secondly, common distributional statistics (mean, median, and variance) from our samples approximate those for all members of each clade, for which body sizes were obtained for the community assembly analyses (see above). Thus, we suggest that our incomplete taxon sampling did not influence our results in any predictable manner, except perhaps to make them more conservative.

A significantly higher rate of body-size evolution in *Osteopilus* would imply a higher probability of seeing the observed body-size extremes than if body size evolved in *Osteopilus* under the lower rate for all South American and Caribbean hylids. However, we note that this, by itself, is not a direct test of how unlikely it is that we see such extremes. Thus, we calculated a simple odds ratio of the probability of seeing such extremes given the rate of body-size evolution from the two-rate model (a separate rate is estimated for *Osteopilus*) versus the one-rate model (one rate for all South American and Caribbean hylids). To do this, we calculated the probability of obtaining body sizes equal to or more extreme than the smallest and largest species on Jamaica and Hispaniola (four total) by sampling from a normal distribution with mean equal to the mean of all *Osteopilus* and variance obtained in one of two ways. In both cases, the variance was calculated as the product of the root-to-tip distance on the ultrametric *Osteopilus* phylogeny and the rate of evolution. In the first case, we used the rate estimated for *Osteopilus* in the above two-rate model of evolution. In the second, we used the rate estimated from the one-rate model. We then calculated an odds ratio

(simply the ratio of the two probabilities) to compare the probability of seeing the observed body size extremes within the Caribbean based on the two rates.

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Table A2.1. Maximum snout-to-vent length (SVL) data used to determine the species pool of the community analyses. SVL_{max} in millimeters (mm).

Species	SVL_{max}	Reference
"Hyla" alboguttata	46	Duellman 1978
"Hyla" warreni	36.2	Duellman and Hoogmoed 1992
Agalychnis litodryas	70.2	Duellman 2001
Agalychnis spurrelli	92.8	Cochran and Goin 1970
Aparasphenodon bokermanni	71.1	Pombal 1993
Aparasphenodon brunoi	75	Cochran 1955
Aparasphenodon venezolanus	58	Rivero 1961
Aplastodiscus albofrenatus	40	Lutz 1973
Aplastodiscus albosignatus	52	Lutz 1973
Aplastodiscus arildae	41.6	Heyer et al. 1990
Aplastodiscus callipygius	50.7	Cruz and Peixoto "1984" [1985]
Aplastodiscus cavicola	37.3	Cruz and Peixoto "1984" [1985]
Aplastodiscus cochranae	50.3	Garcia et al. 2001
Aplastodiscus ehrhardti	39.1	Cruz and Peixoto "1985" [1987]
Aplastodiscus eugenioi	39	Carvalho-e-Silva and Carvalho-e-Silva 2005
Aplastodiscus flumineus	50.4	Cruz and Peixoto "1984" [1985]
Aplastodiscus ibirapitanga	43.4	Cruz Pimenta and Silvano 2003
Aplastodiscus leucopygius	45.1	Cruz and Peixoto "1984" [1985]
Aplastodiscus musicus	50	Cochran 1955
Aplastodiscus perviridis	46.1	Garcia et al. 2001
Aplastodiscus sibilatus	*33.6*	Cruz et al. 2003
Aplastodiscus weygoldti	41.7	Cruz and Peixoto "1985" [1987]
Argenteohyla siemersi	70	Cei 1980
Bokermannohyla ahenea	56.7	Napoli and Caramaschi 2004
Bokermannohyla alvarengai	80	Lutz 1973
Bokermannohyla astartea	44.1	Heyer et al. 1990
Bokermannohyla caramaschii	70	Napoli 2005
Bokermannohyla carvalhoi	67	Peixoto 1981
Bokermannohyla circumdata	71	Lutz 1973
Bokermannohyla claresignata	61	Lutz 1973
Bokermannohyla clepsydra	39	Cochran 1955
Bokermannohyla diamantina	51.7	Napoli and Juncá 2006
Bokermannohyla feioi	40.3	Napoli and Caramaschi 2004
Bokermannohyla gouveai	69	Pombal and Haddad 1993
Bokermannohyla hylax	63.4	Heyer et al. 1990
Bokermannohyla ibitiguara	44.1	Cardoso 1983
Bokermannohyla ibitipoca	42.7	Caramaschi and Feio 1990

Bokermannohyla izecksohni	50.8	Jim and Caramaschi 1979
Bokermannohyla langei	66	Lutz 1973
Bokermannohyla lucianae	49.2	Napoli and Silva-Pimenta 2003
Bokermannohyla luctuosa	60.6	Pombal and Haddad 1993
Bokermannohyla martinsi	64	Lutz 1973
Bokermannohyla nanuzae	42	Bokermann and Sazima 1973b
Bokermannohyla pseudopseudis	44	Lutz 1973
Bokermannohyla ravida	47.6	Caramaschi et al. 2001
Bokermannohyla saxicola	45	Lutz 1973
Bokermannohyla sazimai	36.4	Caramaschi and Feio 1990
Bokermannohyla vulcaniae	53.3	de Vasconcelos and Giaretta 2003
Corythomantis greeningi	86.5	Jared et al. 1999
Cruziohyla calcarifer	78.5	Duellman 2001
Cruziohyla craspedopus	73	Hoogmoed and Cadle 1990
Dendropsophus acreanus	35	Lutz 1973
Dendropsophus allenorum	26.2	Duellman 2005
Dendropsophus amicorum	22.6	Mijares-Urrutia 1998
Dendropsophus anataliasiasi	21.8	Napoli and Caramaschi 1999a
Dendropsophus anceps	42	Lutz 1973
Dendropsophus aperomeus	25	Duellman 1982
Dendropsophus araguaya	20.5	Napoli and Caramaschi 1998
Dendropsophus baileyi	23	Cochran 1952
Dendropsophus battersbyi	33	Rivero 1961
Dendropsophus berthaLutzae	24	Lutz 1973
Dendropsophus bifurcus	35	Duellman 1978
Dendropsophus bipunctatus	28	Lutz 1973
Dendropsophus bogerti	33.3	Cochran and Goin 1970
Dendropsophus bokermanni	28	Duellman 1978
Dendropsophus branneri	21	Lutz 1973
Dendropsophus brevifrons	25	Duellman 1978
Dendropsophus cachimbo	24.2	Napoli and Caramaschi 1999a
Dendropsophus carnifex	32.5	Duellman 1969
Dendropsophus cerradensis	19.3	Napoli and Caramaschi 1998
Dendropsophus coffeus	26	Köhler et al. 2005
Dendropsophus columbianus	35.4	Duellman and Trueb 1983
Dendropsophus cruzi	25	Pombal and Bastos 1998
Dendropsophus decipiens	21	Lutz 1973
Dendropsophus delarivai	26.6	Köhler and Lötters 2001b
Dendropsophus dutrai	38.1	Gomes and Peixoto 1996
Dendropsophus ebraccatus	36.8	Cochran and Goin 1970
Dendropsophus elegans	35.7	Bastos and Haddad 1996

Dendropsophus elianeae	26	Napoli and Caramaschi 2000
Dendropsophus gaucheri	19.2	Lescure and Marty 2000 Guyane
Dendropsophus giesleri	31.5	Weygoldt and Peixoto 1987
Dendropsophus grandisonae	20.8	*Goin 1966*
Dendropsophus gryllatus	30.6	Duellman 1973
Dendropsophus haddadi	24	Bastos and Pombal 1996
Dendropsophus haraldschultzi	25	Rodríguez and Duellman 1994
Dendropsophus jimi	22.3	Napoli and Caramaschi 1999b
Dendropsophus joannae	20.6	Köhler and Lötters 2001a
Dendropsophus koechlini	29	Duellman 2005
Dendropsophus labialis	56	Amezquita 1999
Dendropsophus leali	28	Duellman 2005
Dendropsophus leucophyllatus	50	Lescure and Marty 2000
Dendropsophus limai	19	Bokermann 1962a
Dendropsophus luteoocellatus	31	Rivero 1961
Dendropsophus marmoratus	56	Rodríguez and Duellman 1994
Dendropsophus mathiassoni	21.4	Cochran and Goin 1970
Dendropsophus melanargyreus	50	Lescure and Marty 2000
Dendropsophus meridensis	42	Rivero 1961
Dendropsophus meridianus	23	Lutz 1973
Dendropsophus microcephalus	30.9	Duellman 2001
Dendropsophus microps	33	Lutz 1973
Dendropsophus minusculus	24	Duellman 1997
Dendropsophus minutus	25.9	Duellman 1997
Dendropsophus miyatai	20.4	Vigle and Goberdhan-Vigle 1990
Dendropsophus nahdereri	49	Lutz 1973
Dendropsophus nanus	23.8	Prado and Haddad 2005
Dendropsophus novaisi	32	Lutz 1973
Dendropsophus oliveirai	20	Carvalho-e-Silva et al. 2003
Dendropsophus padreluna	34.4	Kaplan and Ruiz 1997
Dendropsophus parviceps	27	Duellman 1978
Dendropsophus pauiniensis	24	Heyer 1977
Dendropsophus pelidna	38.5	Duellman 1989
Dendropsophus phlebodes	27.8	Duellman 2001
Dendropsophus praestans	31.5	Duellman and Trueb 1983
Dendropsophus pseudomeridianus	22.7	Cruz et al. 2000
Dendropsophus rhea	20.7	Napoli and Caramaschi 1999b
Dendropsophus rhodopeplus	29	Duellman 1978
Dendropsophus riveroi	23	Rodríguez and Duellman 1994
Dendropsophus rossalleni	23	Rodríguez and Duellman 1994
Dendropsophus rubicundulus	25.4	Napoli and Caramaschi 1999a

Dendropsophus ruschii	29	Weygoldt and Peixoto 1987
Dendropsophus sanborni	20	Lutz 1973
Dendropsophus sarayacuensis	37	Rodríguez and Duellman 1994
Dendropsophus schubarti	25.5	Duellman 2005
Dendropsophus seniculus	43	Lutz 1973
Dendropsophus soaresi	31.7	Caramaschi and Jim 1983
Dendropsophus stingi	26.2	Kaplan 1994
Dendropsophus studerae	29.6	Carvalho-e-Silva et al. 2003
Dendropsophus subocularis	26.1	Duellman and Crump 1974
Dendropsophus timbeba	22.5	Martins and Cardoso 1987
Dendropsophus tintinnabulum	20	Lutz 1973
Dendropsophus triangulum	42	Rodríguez and Duellman 1994
Dendropsophus tritaeniatus	22	Bokermann 1965
Dendropsophus virolinensis	32.2	Kaplan and Ruiz 1997
Dendropsophus walfordi	19.5	Bokermann 1962b
Dendropsophus werneri	23	Lutz 1973
Dendropsophus xapuriensis	18.4	Martins and Cardoso 1987
Dendropsophus yaracuyanus	36.6	Mijares-Urrutia and Rivero 2000
Ecnomiohyla phantasmagoria	109.7	Cochran and Goin 1970
Ecnomiohyla tuberculosa	90	Rodríguez and Duellman 1994
Hylomantis aspera	41.7	Cruz 1988
Hylomantis buckleyi	54.7	Cannatella 1980
Hylomantis danieli	80.8	Ruiz-Carranza et al. 1988
Hylomantis granulosa	38.7	Cruz 1988
Hylomantis hulli	37.1	Duellman and Mendelson 1995
Hylomantis medinai	49	Funkhouser 1962
Hylomantis psilopygion	47.3	Cannatella 1980
Hyloscirtus albopunctulatus	41.5	Cochran and Goin 1970
Hyloscirtus alytolylax	43.9	Duellman 1972
Hyloscirtus armatus	74.5	Duellman et al. 1997
Hyloscirtus bogotensis	57.8	Ruiz-Carranza and Lynch 1982
Hyloscirtus callipeza	33	Duellman 1989
Hyloscirtus caucanus	63.3	Ardila-Robayo et al. 1993
Hyloscirtus charazani	55	Vellard 1970
Hyloscirtus denticulentus	52.2	Duellman 1972
Hyloscirtus estevesi	22	Rivero 1968
Hyloscirtus jahni	34.5	Rivero 1961
Hyloscirtus larinopygion	55.6	Duellman and Berger 1982
Hyloscirtus lascinius	47	Rivero 1969
Hyloscirtus lindae	68.1	Duellman and Altig 1978
Hyloscirtus lynchi	46.4	Ruiz-Carranza and Ardila-Robayo 1991

Hyloscirtus pacha	66.5	Duellman and Hillis 1990
Hyloscirtus palmeri	50	Duellman 2001
Hyloscirtus pantostictus	64.1	Duellman and Berger 1982
Hyloscirtus phyllognathus	39.3	Duellman 1972
Hyloscirtus piceigularis	41	Ruiz-Carranza and Lynch 1982
Hyloscirtus platydactylus	42.3	Duellman 1972
Hyloscirtus psarolaimus	63.4	Duellman and Hillis 1990
Hyloscirtus ptychodactylus	77.3	Duellman and Hillis 1990
Hyloscirtus sarampiona	68.8	Ruiz-Carranza and Lynch 1982
Hyloscirtus simmonsi	44.3	Duellman 1989
Hyloscirtus staufferorum	59.7	Duellman and Coloma 1993
Hyloscirtus tapichalaca	66.5	Kizirian et al. 2003
Hyloscirtus torrenticola	35.5	Duellman and Altig 1978
Hypsiboas albomarginatus	62	Lutz 1973
Hypsiboas alboniger	64.7	Duellman et al. 1997
Hypsiboas albopunctatus	75	Lutz 1973
Hypsiboas alemani	30.5	Rivero 1964
Hypsiboas andinus	62.7	Duellman et al. 1997
Hypsiboas atlanticus	40.2	Caramaschi and Velosa 1996
Hypsiboas balzani	52.3	Duellman et al. 1997
Hypsiboas beckeri	33.9	Caramaschi and Cruz 2004
Hypsiboas benitezi	37	Rivero 1961
Hypsiboas bischoffi	69	Lutz 1973
Hypsiboas boans	132	Duellman 2001
Hypsiboas buriti	31.9	Caramaschi and Cruz 1999
Hypsiboas caingua	33.1	Lavilla and Cei 2001
Hypsiboas calcaratus	61	Rodríguez and Duellman 1994
Hypsiboas callipleura	45	Boulenger 1902
Hypsiboas cinerascens	54	Rodríguez and Duellman 1994
Hypsiboas cipoensis	37.5	Cruz and Caramaschi 1998
Hypsiboas cordobae	50	Lutz 1973
Hypsiboas crepitans	75	Lutz 1973
Hypsiboas cymbalum	49	Lutz 1973
Hypsiboas dentei	54	Lescure and Marty 2000
Hypsiboas ericae	36.9	Caramaschi and Cruz 2000
Hypsiboas exastis	99	Caramaschi and Rodrigues 2003
Hypsiboas faber	104	Heyer et al. 1990
Hypsiboas fasciatus	51	Rodríguez and Duellman 1994
Hypsiboas freicanecae	42.2	Carnaval and Peixoto 2004
Hypsiboas fuentei	57	Goin and Goin 1968
Hypsiboas geographicus	85	Lescure and Marty 2000

Hypsiboas goianus	37.6	Cruz and Caramaschi 1998
Hypsiboas guentheri	47	Lutz 1973
Hypsiboas heilprini	54.3	Trueb and Tyler 1974
Hypsiboas hobbsi	42.5	Cochran and Goin 1970
Hypsiboas hutchinsi	56	Pyburn and Hall 1984
Hypsiboas joaquini	51.5	Lutz 1973
Hypsiboas lanciformis	94	Rodríguez and Duellman 1994
Hypsiboas latistriatus	51.6	Caramaschi and Cruz 2004
Hypsiboas lemai	35.4	Duellman 1997
Hypsiboas leptolineatus	32.2	Cruz and Caramaschi 1998
Hypsiboas leucocheilus	81.2	Caramaschi and Niemeyer 2003
Hypsiboas lundii	76	Bokermann and Sazima 1973b
Hypsiboas marginatus	51.1	Caramaschi and Cruz 2000
Hypsiboas marianitae	56.8	Duellman et al. 1997
Hypsiboas melanopleura	47.7	Duellman et al. 1997
Hypsiboas microderma	34	Rodríguez and Duellman 1994
Hypsiboas multifasciatus	75	Lescure and Marty 2000
Hypsiboas nympha	36	Faivovich et al. 2006
Hypsiboas ornatissimus	42	Lescure and Marty 2000
Hypsiboas palaestes	50.9	Duellman et al. 1997
Hypsiboas pardalis	75	Lutz 1973
Hypsiboas pellucens	61.6	Cochran and Goin 1970
Hypsiboas phaeopleura	36.9	Caramaschi and Cruz 2000
Hypsiboas polytaenius	41.5	Cruz and Caramaschi 1998
Hypsiboas pombali	65.7	Caramaschi et al. 2004b
Hypsiboas prasinus	55	Cochran 1955
Hypsiboas pugnax	80	Duellman 2001
Hypsiboas pulchellus	50	Lutz 1973
Hypsiboas pulidoi	23.2	Rivero 1968
Hypsiboas punctatus	41.7	Duellman 1974a
Hypsiboas raniceps	82	Caramaschi and Niemeyer 2003
Hypsiboas rhythmicus	34.2	Señaris and Ayarzagüena 2002
Hypsiboas riojanus	56	Cei 1980
Hypsiboas roraima	45.5	Duellman and Hoogmoed 1992
Hypsiboas rosenbergi	93.2	Duellman 2001
Hypsiboas rubracylus	50.4	Cochran and Goin 1970
Hypsiboas secedens	57	Lutz 1973
Hypsiboas semiguttatus	41.6	Caramaschi and Cruz 2000
Hypsiboas sibleszi	35.7	Duellman 1997
Hypsiboas stenocephalus	30.4	Caramaschi and Cruz 1999
Hypsiboas varelae	52.9	Lavilla and Cei 2001

Hypsiboas wavrini	113	Hoogmoed 1990
Itapotihyla langsdorffii	99	Lutz 1973
Lysapsus caraya	16.5	Gallardo 1964
Lysapsus laevis	21	Parker 1935
Lysapsus limellum	23	Prado and Haddad 2005
Myersiohyla aromatica	46.6	Ayarzagüena and Señaris 1993
Myersiohyla inparquesi	50.4	Ayarzagüena and Señaris 1993
Myersiohyla kanaima	49.1	Duellman and Hoogmoed 1992
Myersiohyla loveridgei	42	Rivero 1961
Nyctimantis rugiceps	67.5	Duellman and Trueb 1976
Osteocephalus buckleyi	64.1	Cochran and Goin 1970
Osteocephalus cabrerai	62.4	Duellman and Mendelson 1995
Osteocephalus carri	64.1	Cochran and Goin 1970
Osteocephalus deridens	50.6	Jungfer et al. 2000
Osteocephalus elkejungingerae	22	Henle 1981
Osteocephalus exophthalmus	32.7	Smith and Noonan 2001
Osteocephalus fuscifacies	53.2	Jungfer et al. 2000
Osteocephalus heyeri	47.7	Lynch 2002
Osteocephalus leoniae	40.1	Faivovich et al. 2006
Osteocephalus leprieurii	62	Rodríguez and Duellman 1994
Osteocephalus mutabor	75.7	Jungfer and Hodl 2002
Osteocephalus oophagus	62.7	Lescure and Marty 2000
Osteocephalus pearsoni	54.7	Trueb and Duellman 1971
Osteocephalus planiceps	89.2	Ron and Pramuk 1999
Osteocephalus subtilis	38.8	Martins and Cardoso 1987
Osteocephalus taurinus	103.9	Ron and Pramuk 1999
Osteocephalus verruciger	73	D. S. Moen unpublished
Osteocephalus yasuni	61.9	Ron and Pramuk 1999
Osteopilus brunneus	76	Schwartz and Henderson 1991
Osteopilus crucialis	122	Schwartz and Henderson 1991
Osteopilus dominicensis	98.7	Trueb and Tyler 1974
Osteopilus marianae	40	Schwartz and Henderson 1991
Osteopilus pulchrilineatus	42.8	Trueb and Tyler 1974
Osteopilus septentrionalis	140	Schwartz and Henderson 1991
Osteopilus vastus	141.9	Trueb and Tyler 1974
Osteopilus wilderi	28.7	Trueb and Tyler 1974
Phasmahyla cochranae	33.9	Heyer et al. 1990
Phasmahyla exilis	34.5	Cruz 1980
Phasmahyla guttata	35	Cochran 1955
Phasmahyla jandaia	32	Bokermann and Sazima 1978
Phrynohyas coriacea	67.6	Lescure and Marty 2000

Phrynohyas hadroceps	60	Lescure and Marty 2000
Phrynohyas imitatrix	70.1	Lutz 1973
Phrynohyas lepida	58.7	Pombal et al. 2003
Phrynohyas mesophaea	100	Lutz 1973
Phrynohyas resinifictrix	100	Lescure and Marty 2000
Phrynohyas venulosa	113.7	Duellman 2001
Phrynomedusa appendiculata	37.4	Heyer et al. 1990
Phrynomedusa bokermanni	46	Cruz 1991
Phrynomedusa fimbriata	45.6	Cruz 1985
Phrynomedusa marginata	31	Izecksohn and Cruz 1976
Phrynomedusa vanzolinii	36.5	Cruz 1991
Phyllodytes acuminatus	24.5	Bokermann 1966b
Phyllodytes auratus	35	Murphy 1997
Phyllodytes brevirostris	24	Peixoto and Cruz 1988
Phyllodytes edelmoi	28.7	Peixoto et al. 2003
Phyllodytes gyrinaethes	27.9	Peixoto et al. 2003
Phyllodytes kautskyi	38	Peixoto and Cruz 1988
Phyllodytes luteolus	23	Bokermann 1966b
Phyllodytes melanomystax	26.6	Caramaschi et al. 1992
Phyllodytes punctatus	22.8	Caramaschi and Peixoto 2004
Phyllodytes tuberculosus	26	Bokermann 1966b
Phyllodytes wuchereri	27.1	Caramaschi et al. 2004a
Phyllomedusa atelopoides	45	Duellman 2005
Phyllomedusa azurea	44.4	Caramaschi 2006
Phyllomedusa bahiana	74.5	Pombal and Haddad 1992
Phyllomedusa baltea	63.5	Cannatella 1982
Phyllomedusa bicolor	135	Lescure et Marty 2000
Phyllomedusa boliviana	76.4	Vaira 2001
Phyllomedusa burmeisteri	79	Cochran 1955
Phyllomedusa camba	84	de la Riva 1999
Phyllomedusa centralis	42	Bokermann 1965
Phyllomedusa coelestis	64.8	Duellman and Mendelson 1995
Phyllomedusa distincta	66	Pombal and Haddad 1992
Phyllomedusa duellmani	54.2	Cannatella 1982
Phyllomedusa ecuatoriana	55.4	Cannatella 1982
Phyllomedusa hypochondrialis	46	Prado and Haddad 2005
Phyllomedusa iheringii	75	Cei 1980
Phyllomedusa itacolomi	46.1	Caramaschi et al. 2006
Phyllomedusa megacephala	49.1	Caramaschi 2006
Phyllomedusa neildi	76	Barrio-Amorós 2006
Phyllomedusa nordestina	43.7	Caramaschi 2006

Phyllomedusa oreades	42.6	Brandão 2002
Phyllomedusa palliata	62.3	Duellman 2005
Phyllomedusa perinesos	65.2	Cannatella 1982
Phyllomedusa rohdei	36	Cochran 1955
Phyllomedusa sauvagii	70	Cei 1980
Phyllomedusa tarsius	111.8	Duellman 1974b
Phyllomedusa tetraploidea	69.4	Pombal and Haddad 1992
Phyllomedusa tomopterna	59	Rodríguez and Duellman 1994
Phyllomedusa trinitatis	95.5	Barrio-Amorós 2006
Phyllomedusa vaillantii	84	Rodríguez and Duellman 1994
Phyllomedusa venusta	97.7	Duellman 2001
Pseudis bolbodactyla	51.4	Caramaschi and Cruz 1998
Pseudis cardosoi	55.9	Kwet 2000
Pseudis fusca	51	Caramaschi and Cruz 1998
Pseudis minuta	50.5	Kwet 2000
Pseudis paradoxa	75	Lescure and Marty 2000
Pseudis tocantins	37.7	Caramaschi and Cruz 1998
Scarthyla goinorum	23	Duellman 2005
Scarthyla vigilans	20.8	Solano 1971
Scinax acuminatus	48	Prado and Haddad 2005
Scinax agilis	19.5	Faivovich 2005
Scinax albicans	44	Lutz 1973
Scinax alcatraz	32	Lutz 1973
Scinax altae	25	Dunn 1933
Scinax alter	32	Lutz 1973
Scinax angrensis	32	Lutz 1973
Scinax arduous	19.5	Peixoto 2002
Scinax argyreornatus	15.8	Faivovich 2005
Scinax ariadne	46.5	Lutz 1973
Scinax aromothyella	31.8	Faivovich 2005
Scinax atratus	20	Peixoto 1988a
Scinax auratus	23	Lutz 1973
Scinax baumgardneri	29	Rivero 1961
Scinax berthae	25	Faivovich 2005
Scinax blairi	32.5	Fouquette and Pyburn 1972
Scinax boesemani	33	Lescure et Marty 2000
Scinax brieni	40	Lutz 1973
Scinax caldarum	35	Lutz 1973
Scinax camposseabrai	35.9	Caramaschi and Cardoso 2006
Scinax canastrensis	38	Cardoso and Haddad 1982
Scinax carnevallii	32	Caramaschi and Kisteumacher 1989

Scinax castroviejoi	48.7	de la Riva 1993
Scinax catharinae	45	Lutz 1973
Scinax centralis	21.2	Pombal and Bastos 1996
Scinax chiquitanus	36.2	Duellman 2005
Scinax constrictus	35.6	Lima et al. 2004
Scinax crospedospilus	37.6	Heyer et al. 1990
Scinax cruentommus	32	Duellman 1978
Scinax curicica	31.5	Pugliese et al. 2004
Scinax cuspidatus	29	Lutz 1973
Scinax danae	29.5	Duellman 1986
Scinax duartei	37	Lutz 1973
Scinax elaeochrous	40.3	Duellman 2001
Scinax eurydice	42	Lutz 1973
Scinax exiguus	24.5	Duellman 1986
Scinax flavidus	30.5	La Marca 2004
Scinax flavoguttatus	43.1	Lutz 1973
Scinax funereus	43	Duellman 1978
Scinax fuscomarginatus	24	Cochran 1955
Scinax fuscovarius	48	Lutz 1973
Scinax garbei	49.1	Duellman and Mendelson 1995
Scinax granulatus	40	Lutz 1973
Scinax hayii	53	Lutz 1973
Scinax heyeri	35.6	Peixoto and Weygoldt 1987
Scinax hiemalis	33	Haddad and Pombal 1987
Scinax humilis	34	Lutz 1973
Scinax ictericus	33.5	Duellman 2005
Scinax jolyi	43.7	Lescure and Marty 2000
Scinax jureia	33.6	Pombal and Gordo 1991
Scinax karenanneae	30.5	Pyburn 1993
Scinax kennedyi	37.3	Pyburn 1973
Scinax lindsayi	25.4	Pyburn 1992
Scinax littoralis	39.9	Pombal and Gordo 1991
Scinax littoreus	25.5	Peixoto 1988b
Scinax longilineus	48	Lutz 1973
Scinax luizotavioi	27.5	Caramaschi and Kisteumacher 1989
Scinax machadoi	26	Bokermann and Sazima 1973a
Scinax manriquei	32.5	Barrio-Amoros et al. 2004
Scinax maracaya	28	Cardoso and Sazima 1980
Scinax melloi	18.7	Peixoto 1988a
Scinax nasicus	39	Lutz 1973
Scinax nebulosus	40	Lutz 1973

Scinax obtriangulatus	39	Lutz 1973
Scinax oreites	39.3	Duellman and Wiens 1993
Scinax pachycrus	33	Lutz 1973
Scinax parkeri	23.9	Duellman 1986
Scinax pedromedinae	31.5	Duellman 2005
Scinax peixotoi	25.1	Brasileiro et al. 2007
Scinax perereca	42.2	Pombal et al. 1995
Scinax perpusillus	25	Lutz 1973
Scinax pinima	29	Bokermann and Sazima 1973a
Scinax proboscideus	46	Lescure and Marty 2000
Scinax quinquefasciatus	30	Fowler 1913
Scinax ranki	28.7	Andrade and Cardoso 1987
Scinax rizibilis	34	Lutz 1973
Scinax rostratus	45.7	Duellman 2001
Scinax ruber	45	Rivero 1961
Scinax similis	41	Lutz 1973
Scinax squalirostris	29	Lutz 1973
Scinax strigilatus	28	Cochran 1955
Scinax sugillatus	45.4	Duellman 1973
Scinax trapicheiroi	40	Lutz 1973
Scinax trilineatus	22.5	Hoogmoed and Gorzula 1979
Scinax uruguayus	25.8	Langone 1990
Scinax v-signatus	27	Lutz 1973
Scinax wandae	26.9	Pyburn and Fouquette 1971
Scinax x-signatus	42.5	Heyer et al. 1990
Sphaenorhynchus bromelicola	30	Bokermann 1966a
Sphaenorhynchus carneus	23	Rodríguez and Duellman 1994
Sphaenorhynchus dorisae	40	Rodríguez and Duellman 1994
Sphaenorhynchus lacteus	48	Duellman 1978
Sphaenorhynchus orophilus	32	Heyer et al. 1990
Sphaenorhynchus palustris	36	Bokermann 1966a
Sphaenorhynchus pauloalvini	24	Bokermann 1973
Sphaenorhynchus planicola	24	Cochran 1955
Sphaenorhynchus platycephalus	33	Harding 1991
Sphaenorhynchus prasinus	31	Bokermann 1973
Sphaenorhynchus surdus	28	Cochran 1952
Tepuihyla aecii	36.8	Mijares-Urrutia et al. 1999
Tepuihyla celsae	56.2	Mijares-Urrutia et al. 1999
Tepuihyla edelcae	45.7	Mijares-Urrutia et al. 1999
Tepuihyla galani	49.5	Mijares-Urrutia et al. 1999
Tepuihyla luteolabris	59.2	Ayarzagüena et al. 1992

Tepuihyla rimarum	44.6	Mijares-Urrutia et al. 1999
Tepuihyla rodriguezi	38.1	Duellman and Hoogmoed 1992
Tepuihyla talbergae	32.7	Duellman and Yoshpa 1996
Trachycephalus atlas	98	Bokermann 1966c
Trachycephalus jordani	75.4	Cochran and Goin 1970
Trachycephalus nigromaculatus	86	Cochran 1955
Xenohyla eugenioi	45.5	Caramaschi 1998
Xenohyla truncata	42	Lutz 1973

Table A2.2. Proportion of diet overlap, as assessed by Schoener's (1970) index of proportional overlap (see METHODS).

	O. brunneus	*O. dominicensis*	*O. marianae*	*O. pulchrilineatus*	*O. septentrionalis*	*O. vastus*	*O. wilderi*
O. brunneus	1	0.5773	0.65	0.2	0.55	0.4	0.2703
O. dominicensis	0.5773	1	0.5955	0.4	0.5379	0.6182	0.2526
O. marianae	0.65	0.5955	1	0.25	0.5	0.3833	0.1351
O. pulchrilineatus	0.2	0.4	0.25	1	0.0833	0.4	0.0541
O. septentrionalis	0.55	0.5379	0.5	0.0833	1	0.2167	0.2455
O. vastus	0.4	0.6182	0.3833	0.4	0.2167	1	0.2559
O. wilderi	0.2703	0.2526	0.1351	0.0541	0.2455	0.2559	1

Table A2.3. Setup of community assembly analyses. Species were placed into categories based on the maximum recorded snout-to-vent length (SVL). For each size category, D_i and d_i represent the number of species in the total species pool and Caribbean communities, respectively. For each Di, larger numbers indicate the total number of species that fit in that size category, whereas the smaller numbers in parentheses indicate the reduced number used for analysis (see Materials and Methods). All size categories are based on Duellman (2001). Jamaican and Hispaniolan species are listed in their respective categories, followed by their maximum SVL in parentheses. All Caribbean species are of the genus Osteopilus unless otherwise noted.

Size categories

	Small (X < 30mm)	Medium (30 ≤ X < 50mm)	Large (50 ≤ X < 80mm)	Very Large (X ≥ 80mm)
South American + Caribbean treefrogs	D_0 = 107 (47)	D_1 = 195 (86)	D_2 = 117 (52)	D_3 = 35 (15)
Jamaica	d_0 = 1 *O. wilderi* (29)	d_1 = 1 *O. marianae* (40)	d_2 = 1 *O. brunneus* (76)	d_3 = 1 *O. crucialis* (122)
Hispaniola	d_0 = 0	d_1 = 1 *O. pulchrilineatus* (43)	d_2 = 1 *Hypsiboas heilprini* (54)	d_3 = 2 *O. dominicensis* (99) *O. vastus* (142)

Table A2.4. Genbank accession numbers for DNA sequences analyzed in the analysis of Lophiohylini. Genbank numbers for Cophomantini, the *Dendropsophus* clade, Phyllomedusinae, and the *Scinax* clade can be found in Wiens et al. 2006. The first part of the table reflects data for mitochondrial genes, while the second part reflects nuclear data.

	Mitchondrial gene					
Taxon	12S	16S	ND1	ND2	COI	cytochrome *b*
Outgroups						
Acris crepitans	AY819360[b]	AY843559[c]	AY819491[b]	...	...	AY843782[c]
Aplastodiscus leucopygius	AY819430[b]	AY843638[c]	AY819544[b]	...	...	AY843873[c]
Dendropsophus ebraccatus	AY819367[b]	AY843624[c]	AY819499[b]	EU034096[g]	...	EU034061[g]
Dendropsophus koechlini	AY819369[b]	...	AY819501[b]	...	...	...
Dendropsophus microcephalus	AY819371[b]	AY843643[c]	AY819503[b]	...	...	AY843880[c]
Dendropsophus nanus	AY819373[b]	AY549346[c]	AY819505[b]	...	...	AY843888[c]
Duellmanohyla soralia	AY819362[b]	AY843584[c]	AY819493[b]	...	...	AY843806[c]
Hyla cinerea	AY819366[b]	AY549327[c]	AY819498[b]	...	...	AY549380[c]
Hyloscirtus colymba	DQ380353[e]	AY843620[c]	AY819553[b]	EU034095[g]	...	AY843848[c]
Hyloscirtus polytaenius	AY819374[b]	AY843655[c]	AY819506[b]	...	...	AY843895[c]
Hypsiboas boans	AY819364[b]	AY843610[c]	AY819496[b]	...	...	AY843835[c]
Hypsiboas heilprini	DQ380357[e]	AY843632[c]	EU034080[g]	...	...	EU034062[g]
Hypsiboas raniceps	AY819375[b]	AY843657[c]	AY819507[b]	...	...	AY843900[c]
Plectrohyla guatemalensis	AY819444[b]	AY843731[c]	DQ055833[d]	...	...	AY843976[c]
Pseudacris regilla	AY819376[b]	AY843737[c]	AY819508[b]	...	...	
Pseudis paradoxus	AY819353[b]	AY843730[c]	AY819483[b]	...	...	AY843985[c]
Scinax catharinae	AY819390[b]	AY843756[c]	AY819522[b]	...	...	AY844001[c]
Scinax crospedospilus	AY819391[b]	...	AY819523[b]	...	...	...
Smilisca cyanosticta	AY819393[b]	AY843763[c]	AY819525[b]	...	...	AY844008[c]
Sphaenorhynchus lacteus	AY819394[b]	AY549367[c]	AY819526[b]	...	...	AY844012[c]
Lophiohylini						
Aparasphenodon brunoi	AY843567[c]	AY843567[c]	...	...	...	AY843789[c]
Argenteohyla siemersi	AY843570[c]	AY843570[c]	...	...	...	AY843792[c]
Corythomantis greeningi	AY843578[c]	AY843578[c]	...	...	...	AY843800[c]

"Hyla" alboguttata	DQ380347[e]	...	EU034081[g]	EU034097[g]	...	EU034063[g]
Itapotihyla langsdorfii	AY819379[b]	AY843706[c]	AY819511[b]	...	...	AY843951[c]
Nyctimantis rugiceps	EU034032[g]	AY843780[c]	...	EU034098[g]	...	AY843945[c]
Osteocephalus buckleyi	DQ380378[e]	...	EU034082[g]	...	...	EU034064[g]
Osteocephalus cabrerai	AY843705[c]	AY843705[c]	...	...	...	AY843950[c]
Osteocephalus leprieurii	AY549361[a]	AY549361[a]	...	...	...	AY843952[c]
Osteocephalus mutabor	DQ380379[e]	...	...	...	...	...
Osteocephalus oophagus	AY843708[c]	AY843708[c]	...	...	...	AY843953[c]
Osteocephalus planiceps	DQ380380[e]	...	...	EU034099[g]	EU034049[g]	...
Osteocephalus taurinus	AY819380[b]	AY843709[c]	AY819512[b]	EU034100[g]	EU034050[g]	EU034065[g]
Osteocephalus verruciger	DQ380381[e]	...	...	EU034101[g]	...	EU034066[g]
Osteopilus brunneus	DQ380382[e]	...	EU034083[g]	EU034102[g]	EU034051[g]	EU034067[g]
Osteopilus crucialis	AY819419[e]	AY843710[c]	EU034084[g]	EU034103[g]	EU034052[g]	AY843955[c]
Osteopilus dominicensis	AY819443[b]	AY843711[c]	EU034085[g]	EU034104[g]	EU034053[g]	EU034068[g]
Osteopilus marianae	DQ380383[e]	...	EU034086[g]	...	EU034054[g]	EU034069[g]
Osteopilus pulchrilineatus	AY819436[b]	...	EU034087[g]	EU034105[g]	EU034055[g]	EU034070[g]
Osteopilus septentrionalis	AY819381[b]	AY843712[c]	AY819513[b]	EU034106[g]	EU034056[g]	EU034071[g]
Osteopilus vastus	DQ380384[e]	AY843713[c]	EU034091[g]	...	EU034057[g]	EU034075[g]
Osteopilus wilderi	DQ380385[e]	...	EU034092[g]	EU034110[g]	EU034058[g]	...
Phrynohyas coriacea	DQ380386[e]	...	EU034093[g]	EU034111[g]	...	EU034076[g]
Phrynohyas hadroceps	AY843717[c]	AY843717[c]	...	...	...	AY843962[c]
Phrynohyas imitatrix	EU034036[g]	...	...	EU034112[g]	...	...
Phrynohyas mesophaea	AY843718[c]	AY843718[c]	...	...	...	AY843963[c]
Phrynohyas resinifictrix	AY843719[c]	AY843719[c]	...	...	...	AY843964[c]
Phrynohyas venulosa	AY819382[b]	AY549362[c]	AY819514[b]	...	...	EU034077[g]
Phyllodytes auratus	AY819383[b]	...	AY819515[b]	...	...	EU034078[g]
Phyllodytes luteolus	AY843721[c]	AY843721[c]	...	...	...	AY843965[c]
Phyllodytes sp.	AY843722[c]	AY843722[c]	...	...	...	AY843966[c]
Tepuihyla edelcae	AY843770[c]	AY843770[c]	...	...	...	...
Tepuihyla sp.	DQ380389[e]	...	EU034094[g]	...	EU034059[g]	...

Trachycephalus jordani	AY819395[b]	AY843771[c]	AY819527[b]	EU034113[g]	EU034060[g]	EU034079[g]	
Trachycephalus nigromaculatus	AY843772[c]	AY843772[c]	...	...	...	AY844016[c]	
Osteopilus septentrionalis individuals used in preliminary analyses							
USNM 315332	AY819381[b]	...	AY819513[b]	EU034106[g]	EU034056[g]	EU034071[g]	
USNM 317832	EU034033[g]	...	EU034088[g]	EU034107[g]	...	EU034072[g]	
USNM 497935	EU034034[g]	...	EU034089[g]	EU034108[g]	...	EU034073[g]	
USNM 317831	EU034035[g]	...	EU034090[g]	EU034109[g]	...	EU034074[g]	

Taxon	Nuclear gene						
	POMC	*cmyc* exon 2	Rhodopsin	RAG-1	Tyrosinase	SIA	TNS3
Outgroups							
Acris crepitans	AY819109[b]	AY819194[b]	AY844533[c]	AY844358[c]	AY844019[c]	AY844762[c]	...
Aplastodiscus leucopygius	...	...	AY844622[c]	AY844425[c]	AY844084[c]	AY844840[c]	...
Dendropsophus ebraccatus	AY819117[b]	AY819202[b]	AY844604[c]	AY844415[c]	AY844070[c]	AY844822[c]	...
Dendropsophus koechlini	AY819119[b]	AY819204[b]	...	...	...	...	...
Dendropsophus microcephalus	AY819121[b]	AY819206[b]	AY844628[c]	AY844430[c]	...	AY844846[c]	...
Dendropsophus nanus	AY819123[b]	AY819208[b]	AY844634[c]	AY844437[c]	...	AY844852[c]	...
Duellmanohyla soralia	AY819111[b]	AY819196[b]	AY844557[c]	AY844378[c]	AY844034[c]	AY844783[c]	...
Hyla cinerea	AY819116[b]	AY819201[b]	AY844597[c]	AY844408[c]	AY844063[c]	AY844816[c]	DQ830949[f]
Hyloscirtus colymba	AY819157[b]	AY819323[b]	AY844599[c]	AY844410[c]	AY844065[c]	AY844818[c]	...
Hyloscirtus polytaenius	AY819124[b]	AY819209[b]	AY844641[c]	AY844443[c]	...	AY844859[c]	...
Hypsiboas boans	AY819114[b]	AY819199[b]	AY844588[c]	...	AY844055[c]	AY844809[c]	...
Hypsiboas heilprini	EU034114[g]	EU034037[g]	AY844613[c]	...	...	AY844831[c]	...
Hypsiboas raniceps	AY819125[b]	AY819210[b]	AY844646[c]	...	AY844103[c]	AY844863[c]	...
Plectrohyla guatemalensis	DQ055807[d]	DQ055780[d]	AY844719[c]	AY844501[c]	AY844160[c]	AY844924[c]	...
Pseudacris regilla	AY819126[b]	AY819211[b]	AY844725[c]		AY844165[c]	...	...
Pseudis paradoxus	AY819102[b]	AY819187[b]	AY844727[c]	AY844506[c]	AY844167[c]	...	...
Scinax catharinae	AY819140[b]	AY819225[b]	AY844742[c]	AY844517[c]	...	AY844941[c]	...

Scinax crospedospilus	AY819141[b]	AY819226[b]	...	...	...	...	...
Smilisca cyanosticta	AY819143[b]	AY819228[b]	AY844750[c]	AY844524[c]	AY844184[c]	AY844947[c]	DQ830957[f]
Sphaenorhynchus lacteus	AY819144[b]	AY819229[b]	AY844754[c]	AY844527[c]	AY844188[C]	...	...
Lophiohylini							
Aparasphenodon brunoi	...	...	AY844541[c]	AY844364[c]	AY844023[c]	AY844769[c]	...
Argenteohyla siemersi	...	...	AY844544[c]	AY844367[c]	AY844026[c]	AY844772[c]	...
Corythomantis greeningi	...	...	AY844551[c]	AY844374[c]	AY844030[c]	AY844779[c]	...
"Hyla" alboguttata	EU034115[g]	...	...	EU034132[g]	...	...	EU034151[g]
Itapotihyla langsdorfii	AY819129[b]	AY819214[b]	AY844697[c]	AY844482[c]	AY844137[c]	AY844903[c]	...
Nyctimantis rugiceps	...	...	...	...	...	...	...
Osteocephalus buckleyi	EU034116[g]	EU034038[g]	...	EU034133[g]	...	...	EU034152[g]
Osteocephalus cabrerai	...	...	AY844696[c]	AY844481[c]	AY844136[c]	AY844902[c]	...
Osteocephalus leprieurii	...	...	AY844698[c]	AY844483[c]	AY844138[c]	AY844904[c]	...
Osteocephalus mutabor	EU034117[g]	EU034039[g]	...	...	...	...	...
Osteocephalus oophagus	...	...	AY844699[c]	AY844484[c]	AY844139[c]	...	...
Osteocephalus planiceps	EU034118[g]	EU034040[g]	...	EU034134[g]	...	...	EU034153[g]
Osteocephalus taurinus	AY819130[b]	AY819215[b]	AY844700[c]	EU034135[g]	AY844140[c]	AY844905[c]	EU034154[g]
Osteocephalus verruciger	EU034119[g]	EU034041[g]	...	...	...	...	EU034155[g]
Osteopilus brunneus	EU034120[g]	EU034042[g]	...	EU034136[g]	...	...	EU034156[g]
Osteopilus crucialis	EU034121[g]	...	...	...	...	...	EU034157[g]
Osteopilus dominicensis	EU034122[g]	...	AY844701[c]	EU034137[g]	AY844141[c]	...	EU034158[g]
Osteopilus marianae	EU034123[g]	EU034043[g]	...	EU034138[g]	...	...	EU034159[g]
Osteopilus pulchrilineatus	EU034124[g]	EU034044[g]	...	EU034139[g]	...	...	EU034160[g]
Osteopilus septentrionalis	AY819131[b]	AY819216[b]	...	EU034140[g]	AY844142[c]	AY844906[c]	EU034161[g]
Osteopilus vastus	EU034128[g]	EU034046[g]	...	EU034144[g]	AY844143[c]	AY844907[c]	EU034162[g]
Osteopilus wilderi	EU034129[g]	EU034047[g]	...	EU034145[g]	...	...	EU034163[g]
Phrynohyas coriacea	EU034130[g]	EU034048[g]	...	EU034146[g]	...	...	EU034164[g]
Phrynohyas hadroceps	...	...	AY844704[c]	AY844490[c]	AY844146[c]	...	...
Phrynohyas imitatrix	...	...	...	...	...	...	...
Phrynohyas mesophaea	...	...	AY844705[c]	AY844491[c]	AY844147[c]	AY844910[c]	...

Phrynohyas resinifictrix	...	...	AY844706[c]	AY844492[c]	AY844148[c]	AY844911[c]	...
Phrynohyas venulosa	AY819132[b]	AY819217[b]	AY844707[c]	EU034147[g]	AY844149[c]	AY844912[c]	EU034165[g]
Phyllodytes auratus	AY819133[b]	AY819218[b]	...	EU034148[g]	...	...	EU034166[g]
Phyllodytes luteolus	...	...	AY844708[c]	AY844494[c]	AY844150[c]	AY844913[c]	...
Phyllodytes sp.	...	...	AY844709[c]	...	AY844151[c]	AY844914[c]	...
Tepuihyla edelcae	...	...	...	AY844530[c]	...	...	...
Tepuihyla sp.	EU034131[g]	...	...	EU034149[g]	...	...	...
Trachycephalus jordani	AY819145[b]	AY819230[b]	AY844758[c]	EU034150[g]	AY844190[c]	AY844953[c]	EU034167[g]
Trachycephalus nigromaculatus	...	...	AY844759[c]	...	AY844191[c]	...	...
Osteopilus septentrionalis individuals used in preliminary analyses							
USNM 315332	AY819131[b]	AY819216[b]	...	EU034140[g]	...	...	...
USNM 317832	EU034125[g]	EU034045[g]	...	EU034141[g]	...	...	...
USNM 497935	EU034126[g]	...	...	EU034142[g]	...	...	...
USNM 317831	EU034127[g]	...	...	EU034143[g]	...	...	EU034161[g]

[a] = Faivovich et al. 2004
[b] = Wiens et al. 2005
[c] = Faivovich et al. 2005
[d] = Smith et al. 2005
[e] = Wiens et al. 2006
[f] = Smith et al. 2007
[g] = this study

Table A2.5. Primers used to amplify and sequence DNA sequence data. Primers are listed in the order in which they occur on each gene.

Primer	Direction[a]	Sequence (5'-3')	Source
12S			
MVZ59	F	ATAGCACTGAAAAYGCTDAGATG	Graybeal 1997
t-Phe-frog	F	ATAGCRCTGAARAYGCTRAGATG	Modified ‘‘MVZ 59’’ (Graybeal 1997)
t-Phe3-frog	F	TTGGTCCTAACCTTGTAATC	this study
t-Val3-frog	R	CCATGTTACGACTTGCCTCT	this study
t-Val-frog	R	TGTAAGCGARAGGCTTTKGTTAAGCT	Wiens et al. (2005)
MVZ50	R	TYTCGGTGTAAGYGARAKGCTT	Graybeal 1997
COI			
COX	F	TGATTCTTTGGGCATCCTGAAG	Schneider et al. 1998
COY	R	GGGGTAGTCAGAATAGCGTCG	Schneider et al. 1998
cytochrome *b*			
MVZ15	F	GAACTAATGGCCCACAWWTACGNAA	Moritz et al. 1992
H15149	R	AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA	Kocher et al. 1989
ND1			
16S-frog	F	TTACCCTRGGGATAACAGCGCAA	Wiens et al. 2005
ND1 F1	F	AGCCATAATCATCTGAACC	Smith et al. 2005
ND1 F2	F	GCMATAATYATYTGAACCC	Smith et al. 2005
WL379	F	GCAATAATYATYTGAACMCC	this study
WL384	R	GAGATWGTTTGWGCAACTGCTCG	this study
ND1 R1	R	TCCTCCCTATCAAGGAGGTCC	Smith et al. 2005
tMet-frog	R	TTGGGGTATGGGCCCAAAAGCT	Wiens et al. 2005
ND2			
L4437b	F	CAGCTAAAAAAGCTATCGGGCCCATACC	Macey et al 1997
ND2r102	R	CAGCCTAGGTGGGCGATTG	Sarah Smith, pers. com.

cmyc exon 2			
cmyc1U	F	GAGGACATCTGGAARAARTT	Crawford 2003
cmyc-ex2d R	R	TCATTCAATGGGTAAGGGAAGACGACC	Wiens et al. 2005
POMC			
POMC-1	F	GAATGTATYAAAGMMTGCAAGATGGWCCT	Wiens et al. 2005
POMC-6	F	TCTGCMGAGTCACCRGTGTTTC	Smith et al. 2005
WL382	R	ATTCATTTTGTACTTCCG	this study
POMC-7	R	TGGCATTTTTGAAAAGAGTCAT	Smith et al. 2005
POMC-2	R	TAYTGRCCCTTYTTGTGGGCRTT	Wiens et al. 2005
RAG-1			
RS1F	F	TGCAGTCAGTAYCAYAARATGTAC	Paul Chippindale pers. com.
WL385	F	AGAAGAACGAAAGAAATGGCAGGC	this study
R1-GFF	F	GAGAAGTCTACAAAAAVGGCAAAG	Faivovich et al. 2005
WL386	R	GTTTCCTTGGACATGAGTTTTC	this study
R1-GFR	R	GAAGCGCCTGAACAGTTTATTAC	Faivovich et al. 2005
TNS3			
WL423	F	CAGCATAGGTACTTTATCATCATCAG	Smith et al. 2007
WL421	R	CAGTGTTGGAGAAGATGGTATGTC	Smith et al. 2007

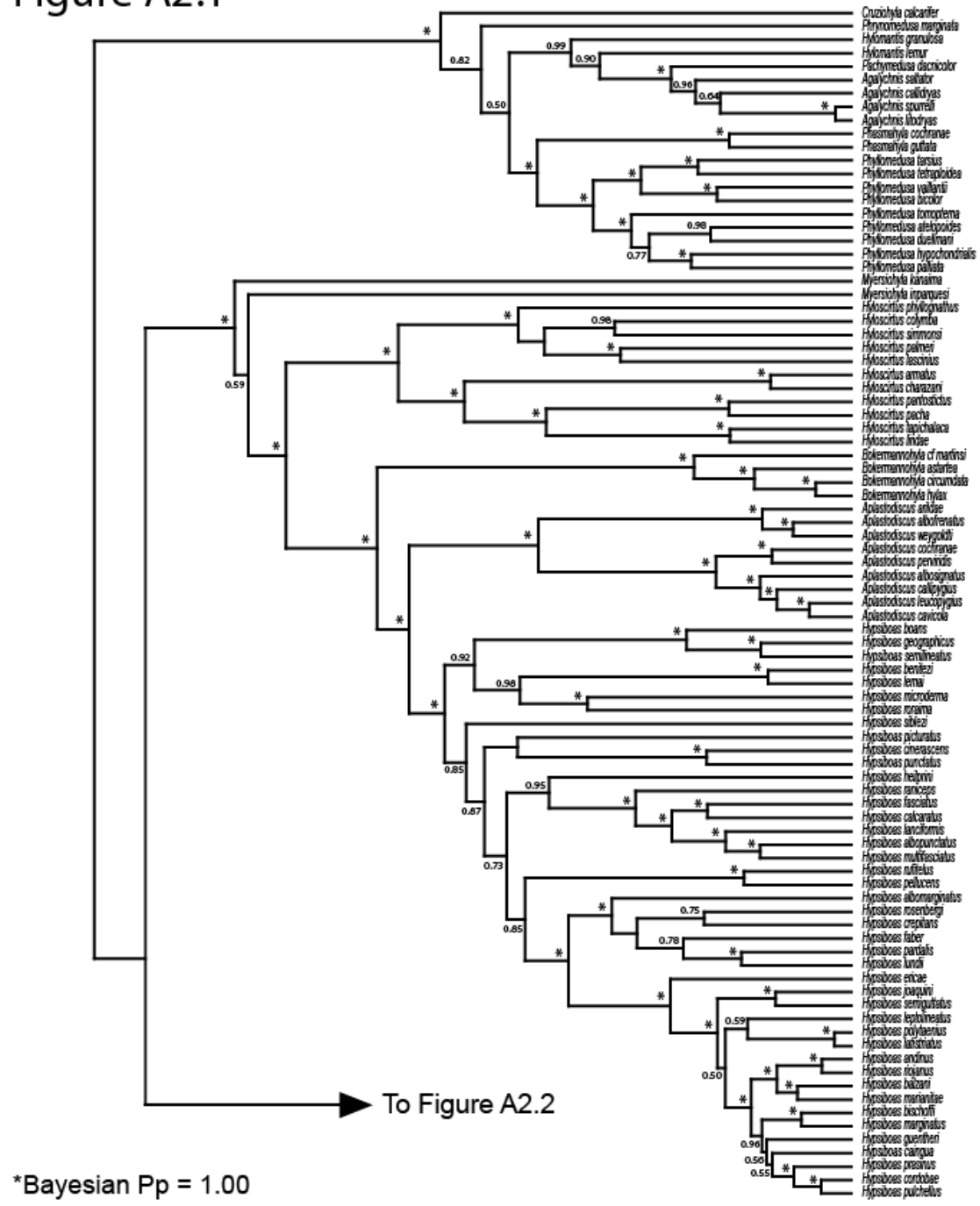
[a]F indicates “forward;” primers amplify the gene from the 5’ end of the published DNA sequence. R primers amplify DNA in the opposite direction on the complimentary strand (“reverse”).

Table A2.6. Ratios of body sizes of Jamaican and Hispaniolan treefrogs. Ratios are calculated as the maximum snout-to-vent length (SVL) of row species divided by maximum SVL of column species. The maximum reported SVL is in parentheses behind each species's name.

Jamaica	*O. wilderi*	*O. marianae*	*O. brunneus*	*O. crucialis*
Osteopilus wilderi (29 mm)	1.00			
Osteopilus marianae (40 mm)	1.38	1.00		
Osteopilus brunneus (76 mm)	2.62	1.90	1.00	
Osteopilus crucialis (122 mm)	4.21	3.05	1.61	1.00
Hispaniola	*O. pulchrilineatus*	*H. heilprini*	*O. dominicensis*	*O. vastus*
Osteopilus pulchrilineatus (43mm)	1.00			
Hypsiboas heilprini (54 mm)	1.26	1.00		
Osteopilus dominicensis (99 mm)	2.30	1.83	1.00	
Osteopilus vastus (142 mm)	3.30	2.63	1.43	1.00

Figures A2.1 and A2.2. Phylogeny of South American Hylidae, estimated by (1) separate Bayesian analyses of each major South American clade, (2) converting branch lengths into units of time using the program r8s, and (3) connecting these clades together by placing on an ultrametric phylogeny (with branch lengths in units of time) of the Hylidae, as estimated by Wiens et al. (2006b). See methods for further details. Branch lengths are in units of time, with the upper and lower scale bars reflecting divergence times estimated using the younger and older (respectively) sets of calibration dates. Nodal values indicate Bayesian posterior probabilities (Pp). Nodal asterisks indicate Pp = 1.0. Note that (1) deep nodes do not show nodal support values because we did not estimate relationships among the major clades in this study, and (2) two major hylid clades, the Pelodryadinae (Australian treefrogs) and the Middle American clade, are not included on this phylogeny, as they were not appropriate for our rate of body size evolution analyses.

Figure A2.1


Cruziohyla calcarifer
Phrynomedusa marginata
Hylomantis granulosa
Hylomantis lemur
Plectromedusa dacnicolor
Agalychnis saltator
Agalychnis callidryas
Agalychnis spurrelli
Agalychnis litodryas
Phasmahyla cochranae
Phasmahyla guttata
Phyllomedusa tarsius
Phyllomedusa tetraploidea
Phyllomedusa vaillantii
Phyllomedusa bicolor
Phyllomedusa tomopterna
Phyllomedusa atelopoides
Phyllomedusa duellmani
Phyllomedusa hypochondrialis
Phyllomedusa palliata
Myersiohyla kanaima
Myersiohyla inparquesi
Hyloscirtus phyllognathus
Hyloscirtus colymba
Hyloscirtus simmonsi
Hyloscirtus palmeri
Hyloscirtus lascinius
Hyloscirtus armatus
Hyloscirtus charazani
Hyloscirtus pantostictus
Hyloscirtus pacha
Hyloscirtus lapichalaca
Hyloscirtus lindae
Bokermannohyla cf martinsi
Bokermannohyla astartea
Bokermannohyla circumdata
Bokermannohyla hylax
Aplastodiscus ehrhardti
Aplastodiscus albofrenatus
Aplastodiscus weygoldti
Aplastodiscus cochranae
Aplastodiscus perviridis
Aplastodiscus albosignatus
Aplastodiscus callipygius
Aplastodiscus leucopygius
Aplastodiscus cavicola
Hypsiboas boans
Hypsiboas geographicus
Hypsiboas semilineatus
Hypsiboas benitezi
Hypsiboas lemai
Hypsiboas microderma
Hypsiboas ronaima
Hypsiboas sibleszi
Hypsiboas picturatus
Hypsiboas cinerascens
Hypsiboas punctatus
Hypsiboas heilprini
Hypsiboas raniceps
Hypsiboas fasciatus
Hypsiboas calcaratus
Hypsiboas lanciformis
Hypsiboas albopunctatus
Hypsiboas multifasciatus
Hypsiboas nufitelus
Hypsiboas pellucens
Hypsiboas albomarginatus
Hypsiboas rosenbergi
Hypsiboas crepitans
Hypsiboas faber
Hypsiboas pardalis
Hypsiboas lundii
Hypsiboas ericae
Hypsiboas joaquini
Hypsiboas semiguttatus
Hypsiboas leptolineatus
Hypsiboas polytaenius
Hypsiboas latistriatus
Hypsiboas andinus
Hypsiboas rosinus
Hypsiboas balzani
Hypsiboas marianitae
Hypsiboas bischoffi
Hypsiboas marginatus
Hypsiboas quentheri
Hypsiboas caingua
Hypsiboas prasinus
Hypsiboas cordobae
Hypsiboas pulchellus
0.82
0.99
0.90
0.96
0.04
0.50
0.98
0.77
0.59
0.98
0.92
0.98
0.85
0.87
0.95
0.73
0.85
0.75
0.78
0.59
0.50
0.96
0.56
0.55
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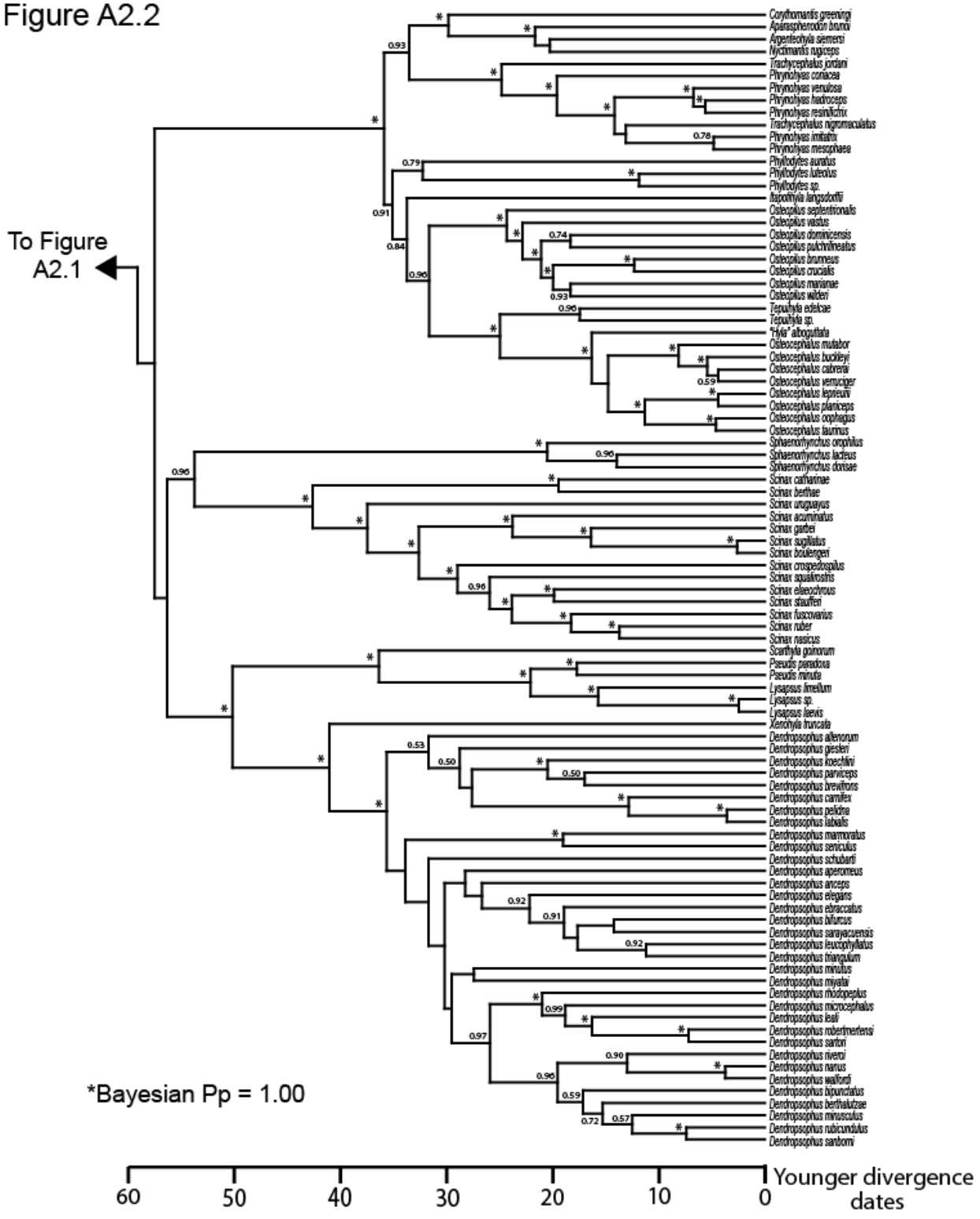
*Bayesian Pp = 1.00
70
60
50
40
30
20
10
0
Younger divergence dates

Figure A2.2


To Figure A2.1
Corythomantis greeningi
Aparasphenodon brunoi
Argenteohyla siemersi
Nyctimantis rugiceps
Trachycephalus jordani
Phrynohyas coriacea
Phrynohyas venulosa
Phrynohyas hadroceps
Phrynohyas resinifictrix
Trachycephalus nigromaculatus
Phrynohyas imitatrix
Phrynohyas mesophaea
Phyllodytes auratus
Phyllodytes luteolus
Phyllodytes sp.
Itapotihyla langsdorffii
Osteopilus septentrionalis
Osteopilus vastus
Osteopilus dominicensis
Osteopilus pulchrilineatus
Osteopilus brunneus
Osteopilus crucialis
Osteopilus marianae
Osteopilus wilderi
Tepuihyla edelcae
Tepuihyla sp.
"Hyla" albopunctata
Osteocephalus mutabor
Osteocephalus buckleyi
Osteocephalus cabrerai
Osteocephalus verruciger
Osteocephalus leprieurii
Osteocephalus planiceps
Osteocephalus oophagus
Osteocephalus taurinus
Sphaenorhynchus orophilus
Sphaenorhynchus lacteus
Sphaenorhynchus dorsae
Scinax carnavinae
Scinax berthae
Scinax uruguayus
Scinax acuminatus
Scinax garbei
Scinax sugillatus
Scinax boulengeri
Scinax crospedospilus
Scinax squalirostris
Scinax elaeochrous
Scinax stauffer
Scinax fuscovarius
Scinax ruber
Scinax nasicus
Scarthyla goinorum
Pseudis paradoxa
Pseudis minuta
Lysapsus limellum
Lysapsus sp.
Lysapsus laevis
Xenohyla truncata
Dendropsophus allenorum
Dendropsophus giesleri
Dendropsophus koechlini
Dendropsophus parviceps
Dendropsophus brevifrons
Dendropsophus carnifex
Dendropsophus pelidna
Dendropsophus labialis
Dendropsophus marmoratus
Dendropsophus seniculus
Dendropsophus schubarti
Dendropsophus aperomeus
Dendropsophus anceps
Dendropsophus elegans
Dendropsophus ebraccatus
Dendropsophus bifurcus
Dendropsophus sarayacuensis
Dendropsophus leucophyllatus
Dendropsophus triangulum
Dendropsophus minutus
Dendropsophus miyatai
Dendropsophus rhodopeplus
Dendropsophus microcephalus
Dendropsophus leali
Dendropsophus robertmertensi
Dendropsophus sartori
Dendropsophus riveroi
Dendropsophus nanus
Dendropsophus walfordi
Dendropsophus bipunctatus
Dendropsophus berthalutzae
Dendropsophus minusculus
Dendropsophus rubicundulus
Dendropsophus sanborni
*Bayesian Pp = 1.00
60
50
40
30
20
10
0
Younger divergence dates

Appendix 3: Chapter 3 null models and supplementary data

Null models

In this section, we develop null models for testing whether the value of a given index for a given community differs significantly from expectations based on chance. We focus on the ROTI (Regional Origin Trait Index), which is the major emphasis of our paper. For the CTDI (Community Trait Dispersal Index), development of a null model is very difficult because one cannot simply shuffle species among communities (the basis for most null models in community ecology). Shuffling species among communities would change the number of communities in which each trait origin is represented, a value upon which this index is calculated. Determining null values for the CTDI seems impossible without an extensive simulation study with a very large parameter space.

Below we create a null model for the ROTI using the hypergeometric distribution, which relates the fraction of species with character-state origins due to ISE vs. ECD (i.e., the ROTI) in a given community with that expected based on a random sampling of species from a regional species pool. We then discuss and illustrate how changes in the regional species pool and number of species in communities influence the ROTI, and we present results from these null models for Middle American hylid communities. Finally, we conclude with a brief discussion on the realism of these null models and how these considerations affect the interpretation of one's results.

THE BASIC MODEL

We examine the significance of a given value of ROTI for a community, given the overall frequency of ISE and ECD events among species within the region as a whole. Thus, we ask how deviant a given community's ROTI is when considered in light of the overall number of species whose character states were the consequence of ISE and ECD events within the region as a whole. As a simple example, we might see a high ROTI in communities composed of species derived from a within-region radiation in which many character states originated in the region by in-situ evolution. Conversely, communities composed of many recent colonists from outside the region may have a significantly low ROTI.

Values for a null model can be generated in at least three different ways. First, one could conduct a simulation, in which one simulates the details of a system but without the process of interest. Second, one could reshuffle the data in a way that creates a null distribution that does not reflect the process of interest (e.g., shuffle species among communities to assume ecological equivalence). Third, if a reasonable probability distribution can be specified for the process of interest, one can model the process and calculate probabilities directly. We take this third approach here.

We test for the statistical significance of the ROTI by considering community assembly as a process of sampling species without replacement from a larger regional pool, using the hypergeometric probability distribution (Sokal and Rohlf 1995). Using this distribution, one can calculate the probability of observing the number of species with a character state derived from ISE as a consequence of random assembly versus assembly in which one type of regional origin (ISE or ECD) might be favored.

The hypergeometric probability distribution is a model of sampling from a population without replacement, where the "population" here is the regional pool of all

Middle American hylid species (see below for variations), and the "sample" is a community. This distribution is appropriate when sampling units can be classified into discrete categories; in this case, a sampled species has a character state (body-size class or larval habitat type) that can be classified as having originated in the region by an ISE or ECD event. We can model the statistical significance of the ROTI in this way because it is calculated as the number of species with a character-state that originated through ISE in the region (d_I) divided by the total number of species in the community (n). Thus, under the null model of random assembly, the probability that, for a given character, a community of size n has d_I species with ISE is

$$P(x = d_I \mid n, D_I, D_E) = \frac{\binom{D_I}{d_I}\binom{D_E}{n - d_I}}{\binom{D_I + D_E}{n}} \quad (1)$$

where D_I and D_E are the total number of species with character-state origins by ISE and ECD, respectively, within the sampled population (i.e., the regional source pool; Sokal and Rohlf 1995). Note that the term "$n - d_I$" could also be represented by d_E, the number of species whose character state originated by ECD.

The hypergeometric distribution as described above is appropriate for obtaining the probability under "random" assembly of a given number of species in a community with their character states from ISE. However, various processes may lead to a predominance of species that trace their traits to ISE or ECD (e.g., a community that is more isolated from dispersal from other regions, due to geographic or ecological barriers, may have less species with traits derived through ECD). In other words, if more species with character states that originated in a region through ISE (or ECD) enter the community during community assembly, then a bias in "sampling" from the regional pool would exist. To incorporate this bias, we use the non-central hypergeometric distribution (McCullagh and Nelder 1989). This distribution incorporates additional parameters to estimate the bias in sampling from the different categories. Here, the sampling biases for ISE and ECD are represented as ω_I and ω_E, respectively. Thus, the probability of a particular number of species within a community whose character-state origin was by ISE, conditioned on the sampling biases, regional pool (D_I and D_E), and number of species within the community (n) is

$$P(x = d_I \mid \omega_I, \omega_E, n, D_I, D_E) = \omega_I^{d_I}\omega_E^{n-d_I}\frac{\binom{D_I}{d_I}\binom{D_E}{n - d_I}}{\binom{D_I + D_E}{n}}Q^{-1} \quad (2)$$

where Q is a normalization constant. Because ω_I and ω_E are interdependent (e.g., as one goes up the other must go down), we reparameterized the equation (following Munch and Conover 2003; see also McCullagh and Nelder 1989) to compare the bias parameters to each other, with the ratio $\psi = \omega_I / \omega_E$. Additionally, the terms that do not depend on d_I and d_E, can be taken out of the equation because those constant terms will also be in the normalization constant and thus will cancel out.

$$P(x = d_I \mid \psi, n, D_I, D_E) = \left(\frac{\psi^{d_I}}{d_I!(n-d_I)!(D_I-d_I)!(D_E-n+d_I)!} \right) Q^{-1} \tag{3}$$

where the normalization constant, Q, is equal to

$$Q = \sum_{i=0}^{n} \left(\frac{\psi^{i}}{i!(n-i)!(D_I-i)!(D_E-n+i)!} \right) \tag{4}$$

The standard (random assembly) and non-central hypergeometric models are compared via a likelihood ratio (LR) test, which can be used to compare nested models (Edwards 1972). Here, the random assembly model is a special case of (i.e., nested within) the biased assembly model when $\psi = 1$. The LR-test statistic is

$$LR = 2 \ln \frac{\lambda(\psi = \hat{\psi})}{\lambda(\psi = 1)} \tag{5}$$

where $\hat{\psi}$ = maximum likelihood estimate of the bias parameter. Given the random assembly model, this LR is expected to be asymptotically distributed as $\chi^2_{p,\alpha}$, where p = the number of free parameters differing between the two models and α = the desired level of statistical significance. In this case, $p = 1$ and we set $\alpha = 0.05$. We calculated the bias parameter estimate and likelihoods of the two models in MatLab (ver. 6.5, The MathWorks Inc., Natick, MA), and the code is available from the authors upon request.

We note here two important considerations. First, in theory, one could instead simply calculate the standard hypergeometric probability of the proportion of species in the community having their states for a character due to ISE (i.e., under the random assembly model only; equation (1) above) and compare this probability to a significance value, such as $\alpha = 0.05$. Under most circumstances, this should give very similar results to our approach. However, the advantage of our approach is that it is more general, allowing investigators to extend tests to more complicated questions. For example, the approach outlined above will be necessary if one wants to calculate whether two communities differ from each other (i.e., compare the likelihood of each community having its own unique bias parameter versus the likelihood that their bias parameters are the same). Second, the number of species within a community

(community size) is the effective sample size in these analyses, so this number will influence the power of statistical analyses. To quantitatively examine the influence of community size, we also conduct a simple simulation, varying the number of species in artificial communities and testing whether the ROTI was significantly different than the random expectation. To do this, we tested similar ROTI values (varied continuously from 0.0 to 1.0) for increasingly larger communities (varied from 2 to 30 species). For these analyses we used a regional pool of 180 species, 90 each with character-state origins due to ISE and ECD (D_I = 90, D_E = 90).

VARIATIONS ON THE MODEL

In theory, statistical significance of the ROTI may be influenced by the size or characterization of the regional species pool. Varying the regional pool, then, may reveal important drivers of significantly high or low ROTI values. For example, altering the probabilities of randomly sampling species from the regional pool in proportion to dispersal ability may reveal whether dispersal ability is more strongly correlated with one type of character-state origin (e.g. ECD) than another (ISE; see below). Alternatively, changing the geographic size of the regional pool may suggest at what scale dispersal limitation breaks down. For example, given a significantly high ROTI, we might suspect that localized ISE events and dispersal limitation lead to a predominance of ISE in a community (and thus a high ROTI). In this case, reducing the geographic extent of the regional pool should result in a ROTI going from significant to non-significant.

To address these situations, we examine two variations on the regional species pool. We first alter the regional pool by weighting species by a proxy for dispersal ability (see below for details). Second, we vary the geographic extent of the regional pool for communities in Costa Rica and Panama.

One way to alter the regional pool would be to weight species representation in the regional pool by overall abundance in the region, by the size of their geographic range within the region relative to the region's size as a whole, by known dispersal ability (which is unknown for many organisms), or by their frequency in the communities of the region. Herein we examine the latter weighting scheme [corresponding to the "occurrence distribution" of Connor and Simberloff (1978)]. In this analysis, our overall regional pool was limited to the species that occurred in the communities we considered, and each species occurred in the regional pool as many times as it occurred across our entire sample of communities (e.g., a species that occurred in five communities was listed five times in the regional pool, whereas a species that was only in one community was listed once, as before). The consequence of this characterization of the regional pool is to upweight the species that have dispersed widely throughout the region and downweight those with limited distributions. This might be more reasonable in cases where one type of trait origin (ISE or ECD) is found in widespread species, thus reducing the significance of seeing many communities with high amounts of that type of trait origin. For Middle American hylids, the original regional pool contains 73 species with character-state origins due to ISE of body size and 82 due to ECD for body size (i.e., a ratio of 73:82), and a ratio of 119:37 for larval habitat, whereas the ratios under the frequency-weighted regional pools were 146:110 and 151:105, respectively.

A second way to alter the regional pool is to change the geographic scale over which it occurs. Certainly, an optimal regional pool would be one within which all species can be expected to disperse freely (an assumption of many sampling models of community assembly, but see below for a discussion on this assumption in our model), but it can be quite difficult in practice to specify exactly such a pool (Connor and Simberloff 1978, Graves and Gotelli 1993). Thus, we examined the effect of progressively larger regional pools. For this analysis we examined the communities of Costa Rica and Panama, testing significance with the "regional pool" set at the scale of the individual countries, the two countries combined, and all of Middle America (cf. Swenson et al. 2006). The ratios of ISE to ECD in the two countries combined were 20:31 and 27:25 for body size and larval habitat, respectively. The ratios for Costa Rica only were 18:22 and 24:17, and those for Panama were 16:29 and 22:23 for body size and larval habitat, respectively.

RESULTS

The results for our null model analyses of each community's ROTI are presented in Tables S5–S6. In general, we found only communities with the most extreme deviations from the regional pool (i.e., very high or low ROTI) to be statistically significant. Though many communities were close to the null expectation of the regional pool (and thus would not expected to be significant), our data also illustrate the low statistical power experienced by analyses of small community size (e.g., community 1 vs. 2 for body size ROTI; Table S5).

Our simulation results of varied community size are presented in Fig. S4, showing the large increase in power with moving from communities of $n = 2$ (no ROTIs significant) to those of $n = 10$ (ROTI = 0.0–0.20 significantly low, 0.80–1.0 significantly high) to $n = 20$ (ROTI = 0.0–0.29, 0.71–1.0 significant). However, it should be noted that the primary aim of our empirical study of treefrogs is not to test for significant deviations from random expectations, but rather to test for correlates of ROTI among communities (e.g., with elevation).

Modification of the regional species pool strongly influenced the results. *P*-values for the ROTIs of both body size and larval habitat were often quite different when comparing the "standard" regional pool with the regional pool constructed by weighting species by their frequency across communities, though they were still correlated (Body size: $r_s = 0.624$, $P < 0.0001$; Larval habitat: $r_s = 0.619$, $P < 0.0001$). For body size, all ROTI values statistically significant under one regional pool were also significant under the other (Table S5). However, for larval habitat, statistical significance often changed based on the regional pool (Table S6), possibly reflecting the larger asymmetry in the ISE:ECD ratio in these two pools for larval habitat relative to the regional pools for body size.

When we varied the geographic scale of the regional pool for Panamanian communities, the general consequence of reducing the size of the regional pool was to make results more liberal for body size and more conservative for larval habitat. These results seem to be influenced largely by the relative shift in the symmetry of ISE to ECD events represented in the regional pool. Despite this tendency, communities with a significant larval habitat ROTI under the Middle American regional pool (i.e., the largest pool) were still statistically significant when the regional pool was reduced to Panama

alone (i.e., the smallest pool). Similar relationships extended to the analyses of Costa Rican communities. In both cases, it is clear from the results that the consequences of altering the regional pool will be highly data dependent, contingent on the ratio of ISE to ECD events in the regional pool. Thus, we suggest that future analyses under this framework similarly examine the influence of the regional pool and base conclusions under the most realistic regional pool if the results are not robust to the regional pool specification.

DISCUSSION OF MODEL ASSUMPTIONS

We note here two important model considerations. First, the idea of sampling from a regional pool to assemble communities is not realistic in many cases. In particular, here we are inferring the importance of evolution within a region (ISE) versus character-state origins from dispersal from outside the region (ECD). Clearly, then, the idea of a static regional pool from which species assemble into communities is not realistic. For ISE, character-states are presumably generated by in-situ evolution within certain types of communities (which are then represented by a sample of that type of community in our analyses, such as stream breeders in montane forests in hylids). In other words, at some level, the communities are helping to generate the regional pool, rather than strictly vice versa. Despite this discrepancy between the null model and our understanding of the evolution of a regional pool of species, we see our null models as useful because they form a method to point out whether a ROTI is significantly higher or lower under one type of random expectation. Violations of the null model form a basis for further investigation into the processes that create the patterns we are testing (instead of a basis for rejecting the methodology).

Second, many models of random community assembly from a regional pool assume no dispersal limitation among sites (i.e., all species within the regional pool could, in principle, be found in a given community; Vamosi et al. 2009). However, this is not an assumption of the ROTI. In fact, without dispersal limitation, we might not expect to see any significant deviations from a random draw from the species pool. For example, evolution within a small area within a region (ISE), coupled with dispersal limitation (e.g., at high elevations), would suggest that most species within communities from that area will have their character-state origins from ISE and thus would have a high ROTI.

It is important to distinguish here between our null model for the ROTI and the increasing use of very similar null models for detecting competition, environmental filtering, or other phenotype-specific processes in community assembly (e.g. Webb 2000; Kraft et al. 2007). In order to isolate the role of specific processes in community assembly (such as competition), one must assume dispersal equivalency in both the null and alternative models. However, the ROTI only relates to how many species within a community have a character state that originated within the region via ISE or ECD and makes no reference to the value of the character state itself (which *is* important in the former case of determining such processes as environmental filtering and competition). Thus, dispersal limitation is a perfectly valid alternative model to explain why a community has a high ROTI, as in the example given above.

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Table A3.1. Estimates of local species composition at 39 sites in Middle America based on data summarized by Duellman (2001). Locality numbers correspond to Table 3.2. References for body size and larval habitat data are found in Table A3.2.

Locality and elevation (country, state, specific location)	Species present	Body size	Larval habitat	Hylid clade	Subclade within Middle American clade
1) Mexico, Sonora, Alamos; 597 m	*Pachymedusa dacnicolor*	82.6	pond	Phyllomedusinae	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca fodiens	62.6	pond	Middle American	*Smilisca* clade
2) Mexico, Sinaloa, Mazatlan; 9 m	*Pachymedusa dacnicolor*	82.6	pond	Phyllomedusinae	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca fodiens	62.6	pond	Middle American	*Smilisca* clade
	Tlalocohyla smithii	26.0	pond	Middle American	*Tlalocohyla*
	Diaglena spatulata	85.9	pond	Middle American	*Smilisca* clade
3) Mexico, Durango, El Salto; 2603 m	*Hyla eximia*	35.0	pond	Middle American	*Hyla*
4) Mexico, Jalisco, Chamela; 11 m	*Dendropsophus sartori*	26.0	pond	*Dendropsophus*	
	Exerodonta smaragdina	26.0	stream	Middle American	*Plectrohyla* clade
	Pachymedusa dacnicolor	82.6	pond	Phyllomedusinae	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca fodiens	62.6	pond	Middle American	*Smilisca* clade
	Tlalocohyla smithii	26.0	pond	Middle American	*Tlalocohyla*
	Diaglena spatulata	85.9	pond	Middle American	*Smilisca* clade
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
5) Mexico, Michoacan, Nueva Italia (between Rio Marquez and Cuatro Caminos); 412 m	*Pachymedusa dacnicolor*	82.6	pond	Phyllomedusinae	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca fodiens	62.6	pond	Middle American	*Smilisca* clade
	Tlalocohyla smithii	26.0	pond	Middle American	*Tlalocohyla*

	Diaglena spatulata	85.9	pond	Middle American	*Smilisca* clade
6) Mexico, D.F., Xochimilco; 2240 m	*Hyla eximia*	35.0	pond	Middle American	*Hyla*
7) Mexico, Guerrero, Puerto del Gallo; 2078 m	*Charadrahyla trux*	81.0	stream	Middle American	*Charadrahyla* clade
	Exerodonta melanomma	29.9	stream	Middle American	*Plectrohyla* clade
	Exerodonta pinorum	34.5	stream	Middle American	*Plectrohyla* clade
	Plectrohyla hazelae	38.6	stream	Middle American	*Plectrohyla* clade
	Plectrohyla mykter	42.3	stream	Middle American	*Plectrohyla* clade
	Plectrohyla pentheter	52.1	stream	Middle American	*Plectrohyla* clade
	Plectrohyla thorectes	34.2	stream	Middle American	*Plectrohyla* clade
	Ptychohyla leonardschultzei	35.6	stream	Middle American	*Ptychohyla* clade
8) Mexico, Oaxaca, Puerto Escondido; 2 m	*Dendropsophus sartori*	26.0	pond	*Dendropsophus*	
	Pachymedusa dacnicolor	82.6	pond	Phyllomedusinae	
	Scinax staufferi	29.0	pond	*Scinax*	
	Tlalocohyla smithii	26.0	pond	Middle American	*Tlalocohyla*
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
	Diaglena spatulata	85.9	pond	Middle American	*Smilisca* clade
9) Mexico, Oaxaca, San Gabriel Mixtepec; 1768 m	*Charadrahyla altipotens*	75.0	stream	Middle American	*Charadrahyla* clade
	Exerodonta juanitae	35.8	stream	Middle American	*Plectrohyla* clade
	Exerodonta melanomma	29.9	stream	Middle American	*Plectrohyla* clade
	Exerodonta sumichrasti	27.7	stream	Middle American	*Plectrohyla* clade
	Megastomatohyla pellita	29.0	stream	Middle American	*Charadrahyla* clade
	Plectrohyla pentheter	52.1	stream	Middle American	*Plectrohyla* clade
	Plectrohyla thorectes	34.2	stream	Middle American	*Plectrohyla* clade
	Ptychohyla leonhardschultzii	35.6	stream	Middle American	*Ptychohyla* clade
10) Mexico, Oaxaca,	*Pachymedusa dacnicolor*	82.6	pond	Phyllomedusinae	

Tehauntepec; 53 m	*Scinax staufferi*	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Triprion petasatus	60.8	pond	Middle American	*Smilisca* clade
11) Mexico, Tamaulipas, Gomez Farias; 361 m	*Hyla eximia*	35.0	pond	Middle American	*Hyla*
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
12) Mexico, Hidalgo, El Chico; 2007 m	*Hyla eximia*	35.0	pond	Middle American	*Hyla*
	Hyla plicata	44.0	pond	Middle American	*Hyla*
	Plectrohyla robertsorum	47.9	pond	Middle American	*Plectrohyla* clade
13) Mexico, Puebla, ~14.4 km W of Huauchinango; 2253 m	*Ecnomiohyla miotympanum*	38.4	stream	Middle American	*Ptychohyla* clade
	Hyla euphorbiacea	29.6	pond	Middle American	*Hyla*
	Plectrohyla arborescandens	37.6	stream	Middle American	*Plectrohyla* clade
	Plectrohyla charadricola	44.4	stream	Middle American	*Plectrohyla* clade
14) Mexico, Veracruz, Mata de Oscura (5 km E); 767 m	*Scinax staufferi*	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla godmani	38.0	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
15) Mexico, Veracruz, Huatusco (3 km SW); 1369 m	*Bromeliohyla dendroscarta*	31.6	arboreal	Middle American	*Ptychohyla* clade
	Charadrahyla taeniopus	65.9	stream	Middle American	*Charadrahyla* clade
	Ecnomiohyla miotympanum	38.4	stream	Middle American	*Ptychohyla* clade
	Megastomatohyla mixomaculata	29.1	stream	Middle American	*Charadrahyla* clade
	Megastomatohyla nubicola	36.7	stream	Middle American	*Charadrahyla* clade

	Plectrohyla arborescandens	37.6	stream	Middle American	*Plectrohyla* clade
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
16) Mexico, Veracruz, Acultzingo; 2093 m	*Ecnomiohyla miotympanum*	38.4	stream	Middle American	*Ptychohyla* clade
	Hyla euphorbiacea	29.6	pond	Middle American	*Hyla*
	Plectrohyla arborescandens	37.6	stream	Middle American	*Plectrohyla* clade
	Plectrohyla bistincta	53.8	stream	Middle American	*Plectrohyla* clade
17) Mexico, Veracruz, Cuatlapan; 1041 m	*Agalychnis moreletii*	65.7	pond	Phyllomedusinae	
	Anotheca spinosa	68.5	arboreal	Middle American	*Smilisca* clade
	Bromeliohyla dendroscarta	31.6	arboreal	Middle American	*Ptychohyla* clade
	Ecnomiohyla miotympanum	38.4	stream	Middle American	*Ptychohyla* clade
	Hyla eximia	35.0	pond	Middle American	*Hyla*
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
18) Mexico, Veracruz, Los Tuxtlas; 1015 m	*Agalychnis moreletii*	65.7	pond	Phyllomedusinae	
	Anotheca spinosa	68.5	arboreal	Middle American	*Smilisca* clade
	Charadrahyla nephila	71.0	stream	Middle American	*Charadrahyla* clade
	Ecnomiohyla miotympanum	38.4	stream	Middle American	*Ptychohyla* clade
	Ecnomiohyla valancifer	77.7	?	Middle American	*Ptychohyla* clade
	Smilisca cyanosticta	56.0	pond	Middle American	*Smilisca* clade
19) Mexico, Veracruz, Estacion de Biologica Tropical, Los Tuxtlas; 350 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	

	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Ecnomiohyla valancifer	77.7	?	Middle American	*Ptychohyla* clade
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca cyanosticta	56.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
20) Mexico, Oaxaca, Vista Hermosa; 876 m	*Agalychnis moreletii*	65.7	pond	Phyllomedusinae	
	Anotheca spinosa	68.5	arboreal	Middle American	*Smilisca* clade
	Bromeliohyla dendroscarta	31.6	arboreal	Middle American	*Ptychohyla* clade
	Charadrahyla nephila	71.0	stream	Middle American	*Charadrahyla* clade
	Duellmanohyla ignicolor	30.9	stream	Middle American	*Ptychohyla* clade
	Ecnomiohyla echinata	57.0	?	Middle American	*Ptychohyla* clade
	Megastomatohyla mixe	30.8	stream	Middle American	*Charadrahyla* clade
	Plectrohyla arborescandens	37.6	stream	Middle American	*Plectrohyla* clade
	Ptychohyla acrochorda	36.3	?	Middle American	*Ptychohyla* clade
21) Mexico, Oaxaca, Tuxtepec; 30 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
22) Mexico, Chiapas, Rayon Mescalapan (6 km S); 1942 m	*Charadrahyla chaneque*	71.0	stream	Middle American	*Charadrahyla* clade
	Duellmanohyla chamulae	30.5	stream	Middle American	*Ptychohyla* clade

	Exerodonta bivocata	28.5	stream	Middle American	*Plectrohyla* clade
	Plectrohyla acanthodes	63.2	stream	Middle American	*Plectrohyla* clade
	Plectrohyla guatemalensis	76.1	stream	Middle American	*Plectrohyla* clade
	Plectrohyla ixil	41.6	stream	Middle American	*Plectrohyla* clade
23) Mexico, Yucatan, Piste; 30 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
	Triprion petasatus	60.8	pond	Middle American	*Smilisca* clade
24) Guatemala, El Peten, Tikal; 254 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
	Triprion petasatus	60.8	pond	Middle American	*Smilisca* clade
25) Honduras, Copan, Quebrada Grande; 1324 m	*Agalychnis moreletii*	65.7	pond	Phyllomedusinae	
	Bromeliohyla bromeliacia	29.5	arboreal	Middle American	*Ptychohyla* clade
	Duellmanohyla soralia	32.3	stream	Middle American	*Ptychohyla* clade
	Ecnomiohyla salvaje	86.0	arboreal	Middle American	*Ptychohyla* clade
	Plectrohyla guatemalensis	76.1	stream	Middle American	*Plectrohyla* clade
	Plectrohyla matudai	46.0	stream	Middle American	*Plectrohyla* clade
	Ptychohyla hypomykter	41.2	stream	Middle American	*Ptychohyla* clade

	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
26) Honduras, Copan, Laguna de Cerro; 1085 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Agalychnis moreletii	65.7	pond	Phyllomedusinae	
	Duellmanohyla soralia	32.3	stream	Middle American	*Ptychohyla* clade
	Plectrohyla matudai	46.0	stream	Middle American	*Plectrohyla* clade
	Ptychohyla hypomykter	41.2	stream	Middle American	*Ptychohyla* clade
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
27) Honduras, Gracias a Dios, Barra Patuka; 2 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
28) Honduras, Atlantida, Quebrada de Oro; 1132 m	*Duellmanohyla salvavida*	28.0	stream	Middle American	*Ptychohyla* clade
	Plectrohyla chrysopleura	65.6	stream	Middle American	*Plectrohyla* clade
	Ptycholyla spinipollex	41.2	stream	Middle American	*Ptychohyla* clade
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
29) Honduras, Atlantida, La Ceiba; 10 m	*Dendropsophus microcephalus*	25.0	pond	*Dendropsophus*	
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
	Tlalocohyla picta	21.4	pond	Middle American	*Tlalocohyla*
	Trachycephalus venulosus	101.0	pond	Lophiohylini	

30) Costa Rica, Heredia, Volcan Barba; 2802 m	*Isthmohyla angustilineata*	34.2	pond	Middle American	*Isthmohyla*
	Isthmohyla picadoi	32.8	arboreal	Middle American	*Isthmohyla*
	Isthmohyla pictipes	39.0	stream	Middle American	*Isthmohyla*
	Isthmohyla pseudopuma	41.4	pond	Middle American	*Isthmohyla*
	Isthmohyla rivularis	34.0	stream	Middle American	*Isthmohyla*
31) Costa Rica, Cartago, Moravia; 1172 m	*Agalychnis annae*	73.9	pond	Phyllomedusinae	
	Anotheca spinosa	68.5	arboreal	Middle American	*Smilisca* clade
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Duellmanohyla rufioculis	30.0	stream	Middle American	*Ptychohyla* clade
	Duellmanohyla uranochroa	36.8	stream	Middle American	*Ptychohyla* clade
	Hyloscirtus colymba	37.0	stream	Cophomantini	
	Isthmohyla lancasteri	33.6	stream	Middle American	*Isthmohyla*
	Isthmohyla pseudopuma	41.4	pond	Middle American	*Isthmohyla*
	Hylomantis lemur	40.8	pond	Phyllomedusinae	
	Smilisca phaeota	65.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*
32) Costa Rica, Heredia, La Selva; 54 m	*Cruziohyla calcarifer*	80.5	pond	Phyllomedusinae	
	Agalychnis callidryas	56.0	pond	Phyllomedusinae	
	Agalychnis saltator	46.7	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Dendropsophus phlebodes	23.6	pond	*Dendropsophus*	
	Hypsiboas rufitelus	49.2	pond	Cophomantini	
	Scinax boulengeri	48.7	pond	*Scinax*	
	Scinax elaeochrous	37.7	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca phaeota	65.0	pond	Middle American	*Smilisca* clade
	Smilisca puma	38.0	pond	Middle American	*Smilisca* clade
	Tlalocohyla loquax	44.7	pond	Middle American	*Tlalocohyla*

33) Costa Rica, Puntarenas, Rincon de Osa; 38 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Agalychnis spurrelli	75.6	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Hypsiboas rosenbergi	90.0	pond	Cophomantini	
	Hypsiboas rufitelus	49.2	pond	Cophomantini	
	Scinax boulengeri	48.7	pond	*Scinax*	
	Scinax elaeochrous	37.7	pond	*Scinax*	
	Smilisca phaeota	65.0	pond	Middle American	*Smilisca* clade
	Smilisca sila	45.0	stream	Middle American	*Smilisca* clade
	Smilisca sordida	45.0	stream	Middle American	*Smilisca* clade
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
34) Costa Rica, Las Canas, Finca Taboga; 13 m	*Dendropsophus microcephalus*	25.0	pond	*Dendropsophus*	
	Scinax boulengeri	48.7	pond	*Scinax*	
	Scinax staufferi	29.0	pond	*Scinax*	
	Smilisca baudinii	76.0	pond	Middle American	*Smilisca* clade
	Smilisca sordida	45.0	stream	Middle American	*Smilisca* clade
	Trachycephalus venulosus	101.0	pond	Lophiohylini	
35) Costa Rica, Puntarenas, Las Cruces; 1349 m	*Agalychnis annae*	73.9	pond	Phyllomedusinae	
	Anotheca spinosa	68.5	arboreal	Middle American	*Smilisca* clade
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Duellmanohyla rufioculis	30.0	stream	Middle American	*Ptychohyla* clade
	Ecnomiohyla miliaria	110.0	arboreal	Middle American	*Ptychohyla* clade
	Isthmohyla lancasteri	33.6	stream	Middle American	*Isthmohyla*
	Isthmohyla pseudopuma	41.4	pond	Middle American	*Isthmohyla*
	Ptychohyla legleri	36.7	stream	Middle American	*Ptychohyla* clade
	Smilisca sordida	45.0	stream	Middle American	*Smilisca* clade

36) Panama, Colon, Achiote; 27 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Dendropsophus phlebodes	23.6	pond	*Dendropsophus*	
	Hypsiboas rufitelus	49.2	pond	Cophomantini	
	Scinax boulengeri	48.7	pond	*Scinax*	
	Scinax ruber	41.0	pond	*Scinax*	
	Smilisca phaeota	65.0	pond	Middle American	*Smilisca* clade
37) Panama, Cocle, El Valle; 643 m	*Anotheca spinosa*	68.5	arboreal	Middle American	*Smilisca* clade
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Dendropsophus phlebodes	23.6	pond	*Dendropsophus*	
	Ecnomiohyla miliaria	110.0	arboreal	Middle American	*Ptychohyla* clade
	Hypsiboas crepitans	63.0	pond	Cophomantini	
	Hylomantis lemur	40.8	pond	Phyllomedusinae	
	Scinax altae	26.0	pond	*Scinax*	
	Smilisca sila	45.0	stream	Middle American	*Smilisca* clade
38) Panama, Darien, Rio Tuira at Rio Mono; 490 m	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	
	Agalychnis litodryas	70.2	pond	Phyllomedusinae	
	Dendropsophus ebraccatus	27.8	pond	*Dendropsophus*	
	Hypsiboas boans	132.0	pond	Cophomantini	
	Hypsiboas rosenbergi	90.0	pond	Cophomantini	
	Phyllomedusa venusta	86.3	pond	Phyllomedusinae	
	Smilisca phaeota	65.0	pond	Middle American	*Smilisca* clade
39) Panama, Barro Colorado	*Agalychnis callidryas*	56.0	pond	Phyllomedusinae	

Island; 31 m	*Agalychnis spurrelli*	75.6	pond	Phyllomedusinae	
	Cruziohyla calcarifer	80.5	pond	Phyllomedusinae	
	Dendropsophus microcephalus	25.0	pond	*Dendropsophus*	
	Dendropsophus phlebodes	23.6	pond	*Dendropsophus*	
	Hypsiboas rufitelus	49.2	pond	Cophomantini	
	Scinax boulengeri	48.7	pond	*Scinax*	
	Smilisca phaeota	65.0	pond	Middle American	*Smilisca* clade
	Smilisca sila	45.0	stream	Middle American	*Smilisca* clade
	Trachycephalus venulosus	101.0	pond	Lophiohylini	

Table A3.2. Data on body size (maximum male SVL) and larval habitat and original literature sources.

Species	SVL (mm)	Larval habitat	Source- male size (SVL)	Source - larval habitat
Acris crepitans	29	pond	Duellman 2001	Duellman 2001
Acris gryllus	29	pond	Lannoo 2005	IUCN et al. 2006
Agalychnis annae	73.9	pond	Duellman 2001	Duellman 2001
Agalychnis callidryas	56	pond	Duellman 2001	Duellman 2001
Agalychnis litodryas	70.2	pond	Duellman 2001	Duellman 2001
Agalychnis moreletii	65.7	pond	Duellman 2001	Duellman 2001
Agalychnis saltator	46.7	pond	Duellman 2001	Duellman 2001
Agalychnis spurrelli	75.6	pond	Duellman 2001	Duellman 2001
Anotheca spinosa	68.5	arboreal	Duellman 2001	Duellman 2001
Aparasphenodon brunoi	75	pond	Cochran 1955	IUCN et al. 2006
Aplastodiscus albofrenatus	40	stream	Lutz 1973	IUCN et al. 2006
Aplastodiscus albosignatus	42	direct	Heyer et al. 1990	IUCN et al. 2006
Aplastodiscus arildae	42	stream	Heyer et al. 1990	IUCN et al. 2006
Aplastodiscus callipygius	50.7	stream	Cruz and Peixoto 1984	IUCN et al. 2006
Aplastodiscus cavicola	38	stream	Duellman 2001	Duellman 2001
Aplastodiscus cochranae	46.5	pond	Garcia et al. 2001	IUCN et al. 2006
Aplastodiscus leucopygius	44	stream	Heyer et al. 1990	IUCN et al. 2006
Aplastodiscus perviridis	45	pond	Cei 1980	IUCN et al. 2006
Aplastodiscus weygoldti	?	stream		IUCN et al. 2006
Argenteohyla siemersi	70	pond	Cei 1980	IUCN et al. 2006
Bokermannohyla astartea	41.5	arboreal	Heyer et al. 1990	IUCN et al. 2006
Bokermannohyla circumdata	70	stream	Lutz 1973	IUCN et al. 2006
Bokermannohyla hylax	61.5	stream	Heyer et al. 1990	IUCN et al. 2006
Bokermannohyla martinsi	64	stream	Lutz 1973	IUCN et al. 2006
Bromeliohyla bromeliacia	29.5	arboreal	Duellman 2001	Duellman 2001
Bromeliohyla dendroscarta	31.6	arboreal	Duellman 2001	Duellman 2001
Charadrahyla altipotens	75	stream	Duellman 2001	Duellman 2001
Charadrahyla chaneque	71	stream	Duellman 2001	Duellman 2001
Charadrahyla nephila	71	stream	Duellman 2001	Duellman 2001

Charadrahyla taeniopus	65.9	stream	Duellman 2001	Duellman 2001
Charadrahyla trux	81	stream	Duellman 2001	Duellman 2001
Corythomantis greeningi	73	stream	Jared et al. 1999	IUCN et al. 2006
Cruziohyla calcarifer	80.5	pond	Duellman 2001	Duellman 2001
Cyclorana australis	100	pond	Cogger 1992	IUCN et al. 2006
Dendropsophus allenorum	21.4	pond	Duellman and Hoogmoed 1992	Duellman 2005
Dendropsophus anceps	40	pond	Lutz 1973	IUCN et al. 2006
Dendropsophus aperomeus	21.3	pond	Duellman 1982	Duellman 2001
Dendropsophus berthalutzae	21	stream	Lutz 1973	IUCN et al. 2006
Dendropsophus bifurcus	28	pond	Duellman 1978	Duellman 1978
Dendropsophus bipunctatus	25	pond	Lutz 1973	IUCN et al. 2006
Dendropsophus brevifrons	22	pond	Duellman 1978	Duellman 1978
Dendropsophus carnifex	27.7	pond	Duellman and Trueb 1983	IUCN et al. 2006
Dendropsophus ebraccatus	27.8	pond	Duellman 2001	Duellman 2001
Dendropsophus elegans	29.6	pond	Bastos and Haddad 1996	IUCN et al. 2006
Dendropsophus giesleri	25	pond	Weygoldt and Peixoto 1987	IUCN et al. 2006
Dendropsophus koechlini	24	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus labialis	43	pond	Amezquita 1999	IUCN et al. 2006
Dendropsophus leali	23	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus leucophyllatus	36	pond	Duellman 1978	Duellman 1978
Dendropsophus marmoratus	44	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus microcephalus	24.5	pond	Duellman 2001	Duellman 2001
Dendropsophus minusculus	20.6	pond	Duellman 1997	IUCN et al. 2006
Dendropsophus minutus	23	pond	Duellman 1997	IUCN et al. 2006
Dendropsophus miyatai	18.1	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus nanus	22	pond	Lutz 1973	IUCN et al. 2006
Dendropsophus parviceps	21.9	pond	Duellman 2005	IUCN et al. 2006
Dendropsophus pelidna	36.9	pond	Duellman and Hillis 1989	Duellman 2001
Dendropsophus phlebodes	23.6	pond	Duellman 2001	Duellman 2001
Dendropsophus rhodopeplus	24.2	pond	Duellman and Hoogmoed 1992	Duellman 2005
Dendropsophus riveroi	20	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus robertmertensi	26.4	pond	Duellman 2001	Duellman 2001
Dendropsophus rubicundulus	24	pond	Lutz 1973	IUCN et al. 2006

Dendropsophus sanborni	17	pond	Lutz 1973	IUCN et al. 2006
Dendropsophus sarayacuensis	29	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus sartori	26	pond	Duellman 2001	Duellman 2001
Dendropsophus schubarti	29.5	pond	Duellman 2005	IUCN et al. 2006
Dendropsophus seniculus	37.7	pond	Heyer et al. 1990	IUCN et al. 2006
Dendropsophus triangulum	28	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Dendropsophus walfordi	19.5	pond	Bokermann 1962	IUCN et al. 2006
Diaglena spatulata	85.9	pond	Duellman 2001	Duellman 2001
Duellmanohyla chamulae	30.5	stream	Duellman 2001	Duellman 2001
Duellmanohyla ignicolor	30.9	stream	Duellman 2001	Duellman 2001
Duellmanohyla rufioculis	30	stream	Duellman 2001	Duellman 2001
Duellmanohyla salvavida	28	stream	Duellman 2001	Duellman 2001
Duellmanohyla soralia	32.3	stream	Duellman 2001	Duellman 2001
Duellmanohyla uranochroa	36.8	stream	Duellman 2001	Duellman 2001
Ecnomiohyla echinata	57	?	Duellman 2001	Duellman 2001
Ecnomiohyla miliaria	110	arboreal	Duellman 2001	Duellman 2001
Ecnomiohyla minera	83.1	?	Duellman 2001	
Ecnomiohyla miotympanum	38.4	stream	Duellman 2001	Duellman 2001
Ecnomiohyla salvaje	86	arboreal	Duellman 2001	Duellman 2001
Ecnomiohyla valancifer	77.7	?	Duellman 2001	Duellman 2001
Exerodonta abdivita	27.5	?	Duellman 2001	
Exerodonta bivocata	28.5	stream	Duellman 2001	Duellman 2001
Exerodonta chimalapa	24.9	stream	Duellman 2001	Duellman 2001
Exerodonta juanitae	35.8	stream	Duellman 2001	Duellman 2001
Exerodonta melanomma	29.9	stream	Duellman 2001	Duellman 2001
Exerodonta perkinsi	?	stream		IUCN et al. 2006
Exerodonta pinorum	34.5	stream	Duellman 2001	Duellman 2001
Exerodonta smaragdina	26	stream	Duellman 2001	Duellman 2001
Exerodonta sumichrasti	27.7	stream	Duellman 2001	Duellman 2001
Exerodonta xera	27.9	stream	Duellman 2001	Duellman 2001
Hyla andersonii	51	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla annectans	35	pond	Fei et al. 1999	IUCN et al. 2006
Hyla arborea	50	pond	Arnold 2003	IUCN et al. 2006

Hyla arenicolor	51.2	pond&stream	Duellman 2001	Duellman 2001
Hyla avivoca	39	pond	Lannoo 2005	IUCN et al. 2006
Hyla chinensis	32	pond	Fei et al. 1999	IUCN et al. 2006
Hyla chrysoscelis	60	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla cinerea	57	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla euphorbiacea	29.6	pond	Duellman 2001	Duellman 2001
Hyla eximia	35	pond	Duellman 2001	Duellman 2001
Hyla femoralis	44	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla gratiosa	70	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla japonica	39	pond	Goris and Maeda 2004	IUCN et al. 2006
Hyla meridionalis	65	pond	Arnold 2003	IUCN et al. 2006
Hyla plicata	44	pond	Duellman 2001	Duellman 2001
Hyla savignyi	40	pond	Tarkhnishvili and Gokhelashvili 1999	IUCN et al. 2006
Hyla squirella	41	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla versicolor	60	pond	Conant and Collins 1991	IUCN et al. 2006
Hyla walkeri	35.9	pond	Duellman 2001	Duellman 2001
Hyla wrightorum	44	pond	Degenhardt et al. 1996	Degenhardt et al. 1996
Hylomantis granulosa	37.4	stream	Cruz 1988	IUCN et al. 2006
Hylomantis lemur	40.8	pond	Duellman 2001	Duellman 2001
Hyloscirtus armatus	68.5	pond&stream	Duellman et al. 1997	IUCN et al. 2006
Hyloscirtus charazani	55	stream	Vellard 1970	IUCN et al. 2006
Hyloscirtus colymba	37	stream	Duellman 2001	Duellman 2001
Hyloscirtus lascinius	38	stream	Rivero 1969	IUCN et al. 2006
Hyloscirtus lindae	68.1	stream	Duellman and Altig 1978	IUCN et al. 2006
Hyloscirtus pacha	60.8	stream	Duellman and Hillis 1990	Duellman 2001
Hyloscirtus palmeri	45	stream	Duellman 2001	Duellman 2001
Hyloscirtus pantostictus	63	stream	Duellman and Berger 1982	IUCN et al. 2006
Hyloscirtus phyllognathus	34	stream	Duellman 1972	IUCN et al. 2006
Hyloscirtus simmonsi	37.8	stream	Duellman 1989	Duellman 2001
Hyloscirtus tapichalaca	63.8	stream	Kizirian et al. 2003	IUCN et al. 2006
Hypsiboas albomarginatus	55	pond	Lutz 1973	IUCN et al. 2006
Hypsiboas albopunctatus	75	pond	Cei 1980	IUCN et al. 2006

Hypsiboas andinus	60	pond	Cei 1980	IUCN et al. 2006
Hypsiboas balzani	50.4	stream	Duellman et al. 1997	IUCN et al. 2006
Hypsiboas benitezi	37	stream	Rivero 1961	IUCN et al. 2006
Hypsiboas bischoffi	46.1	pond	Heyer et al. 1990	IUCN et al. 2006
Hypsiboas boans	132	pond	Duellman 2001	Duellman 2001
Hypsiboas caingua	33.1	stream	Lavilla and Cei 2001	IUCN et al. 2006
Hypsiboas calcaratus	47.5	pond	Duellman and Hoogmoed 1992	IUCN et al. 2006
Hypsiboas cinerascens	44	pond	Rodríguez and Duellman 1994	Duellman 2005
Hypsiboas cordobae	50	pond	Lutz 1973	IUCN et al. 2006
Hypsiboas crepitans	63	pond	Lutz 1973	IUCN et al. 2006
Hypsiboas ericae	34	stream	Caramaschi and Cruz 2000	IUCN et al. 2006
Hypsiboas faber	104	pond	Heyer et al. 1990	IUCN et al. 2006
Hypsiboas fasciatus	40.3	pond	Duellman and Hoogmoed 1992	IUCN et al. 2006
Hypsiboas geographicus	62	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Hypsiboas guentheri	40	pond	Lutz 1973	IUCN et al. 2006
Hypsiboas heilprini	48	stream	Hedges 2006	IUCN et al. 2006
Hypsiboas joaquini	51.5	pond&stream	Lutz 1973	IUCN et al. 2006
Hypsiboas lanciformis	80	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Hypsiboas latistriatus	40.6	?	Caramaschi and Cruz 2004	
Hypsiboas lemai	30.4	stream	Duellman 1997	IUCN et al. 2006
Hypsiboas leptolineatus	31.6	pond	Cruz and Caramaschi 1998	IUCN et al. 2006
Hypsiboas lundii	76	stream	Bokermann and Sazima 1973	IUCN et al. 2006
Hypsiboas marginatus	51.1	stream	Caramaschi and Cruz 2000	IUCN et al. 2006
Hypsiboas marianitae	56.8	pond	Duellman et al. 1997	IUCN et al. 2006
Hypsiboas microderma	34	pond	Rodríguez and Duellman 1994	Rodríguez and Duellman 1994
Hypsiboas multifasciatus	57.3	pond	Duellman 1997	IUCN et al. 2006
Hypsiboas pardalis	69	pond	Lutz 1973	IUCN et al. 2006
Hypsiboas pellucens	61.6	pond	Cochran and Goin 1970	IUCN et al. 2006
Hypsiboas picturatus	?	stream		IUCN et al. 2006
Hypsiboas polytaenius	31.4	pond	Cruz and Caramaschi 1998	IUCN et al. 2006
Hypsiboas prasinus	55	pond&stream	Lutz 1973	IUCN et al. 2006
Hypsiboas pulchellus	50	pond	Cei 1980	IUCN et al. 2006
Hypsiboas punctatus	40	pond	Rodríguez and Duellman 1994	IUCN et al. 2006

Hypsiboas raniceps	71	pond	Caramaschi and Niemeyer 2003	IUCN et al. 2006
Hypsiboas riojanus	45	pond	Cei 1980	IUCN et al. 2006
Hypsiboas roraima	45.5	stream	Duellman and Hoogmoed 1992	IUCN et al. 2006
Hypsiboas rosenbergi	90	pond	Duellman 2001	Duellman 2001
Hypsiboas rufitelus	49.2	pond	Duellman 2001	Duellman 2001
Hypsiboas semiguttatus	42	stream	Lutz 1973	IUCN et al. 2006
Hypsiboas semilineatus	?	pond		IUCN et al. 2006
Hypsiboas sibleszi	34.9	pond	Duellman 1997	IUCN et al. 2006
Isthmohyla angustilineata	34.2	pond	Duellman 2001	Duellman 2001
Isthmohyla lancasteri	33.6	stream	Duellman 2001	Duellman 2001
Isthmohyla picadoi	32.8	arboreal	Duellman 2001	Duellman 2001
Isthmohyla pictipes	39	stream	Duellman 2001	Duellman 2001
Isthmohyla pseudopuma	41.4	pond	Duellman 2001	Duellman 2001
Isthmohyla rivularis	34	stream	Duellman 2001	Duellman 2001
Isthmohyla tica	34.1	stream	Duellman 2001	Duellman 2001
Isthmohyla zeteki	23.5	arboreal	Duellman 2001	Duellman 2001
Itapotihyla langsdorffii	77	pond	Lutz 1973	IUCN et al. 2006
Litoria aurea	85	pond	Cogger 1992	IUCN et al. 2006
Litoria caerulea	100	pond	Cogger 1992	IUCN et al. 2006
Litoria freycineti	45	pond	Cogger 1992	IUCN et al. 2006
Litoria infrafrenata	110	pond	Cogger 1992	IUCN et al. 2006
Litoria meiriana	20	pond	Cogger 1992	IUCN et al. 2006
Lysapsus laevis	22	pond	Parker 1935	IUCN et al. 2006
Lysapsus limellum	20	pond	Cei 1980	IUCN et al. 2006
Megastomatohyla mixe	30.8	stream	Duellman 2001	Duellman 2001
Megastomatohyla mixomaculata	29.1	stream	Duellman 2001	Duellman 2001
Megastomatohyla nubicola	36.7	stream	Duellman 2001	Duellman 2001
Megastomatohyla pellita	29	stream	Duellman 2001	Duellman 2001
Myersiohyla inparquesi	50.4	pond&stream	Ayarzagüena and Señaris 1993	IUCN et al. 2006
Myersiohyla kanaima	48	?	Goin and Woodley 1969	
Nyctimantis rugiceps	67.5	arboreal	Duellman and Trueb 1976	Duellman 1978
Nyctimystes foricula	40	pond&stream	Menzies 1977	IUCN et al. 2006
Osteocephalus alboguttatus	46	stream	Duellman 1978	IUCN et al. 2006

Osteocephalus buckleyi	48.1	stream	Rodríguez and Duellman 1994	IUCN et al. 2006
Osteocephalus cabrerai	?	stream		IUCN et al. 2006
Osteocephalus leprieurii	48	pond	Jungfer and Hödl 2002	IUCN et al. 2006
Osteocephalus mutabor	50.3	pond&stream	Jungfer and Hödl 2002	IUCN et al. 2006
Osteocephalus oophagus	47.2	arboreal	Jungfer and Schiesari 1995	IUCN et al. 2006
Osteocephalus planiceps	65.9	arboreal	Duellman and Mendelson 1995	IUCN et al. 2006
Osteocephalus taurinus	85	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Osteocephalus verruciger	54.3	pond	Trueb and Duellman 1971	IUCN et al. 2006
Osteopilus brunneus	52	arboreal	Hedges 2006	IUCN et al. 2006
Osteopilus crucialis	100	arboreal	Hedges 2006	IUCN et al. 2006
Osteopilus dominicensis	66	pond	Hedges 2006	IUCN et al. 2006
Osteopilus marianae	40	arboreal	Hedges 2006	IUCN et al. 2006
Osteopilus pulchrilineatus	32	pond	Hedges 2006	IUCN et al. 2006
Osteopilus septentrionalis	89	pond	Duellman 2001	Duellman 2001
Osteopilus vastus	109	stream	Hedges 2006	IUCN et al. 2006
Osteopilus wilderi	28	arboreal	Hedges 2006	IUCN et al. 2006
Pachymedusa dacnicolor	82.6	pond	Duellman 2001	Duellman 2001
Phasmahyla cochranae	33.9	stream	Heyer et al. 1990	IUCN et al. 2006
Phasmahyla guttata	35	stream	Cochran 1955	IUCN et al. 2006
Phrynomedusa marginata	31	stream	Izecksohn and Cruz 1976	IUCN et al. 2006
Phyllodytes auratus	29	arboreal	Murphy 1997	IUCN et al. 2006
Phyllodytes luteolus	23	arboreal	Bokermann 1966	IUCN et al. 2006
Phyllomedusa atelopoides	37.4	pond	Duellman and Hoogmoed 1992	IUCN et al. 2006
Phyllomedusa bicolor	115	pond	Duellman 1974	IUCN et al. 2006
Phyllomedusa duellmani	54.2	pond	Cannatella 1982	Cannatella 1982
Phyllomedusa hypochondrialis	40	pond	Cei 1980	IUCN et al. 2006
Phyllomedusa palliata	49.1	pond	Duellman 2005	IUCN et al. 2006
Phyllomedusa tarsius	97	pond	Duellman 1978	Duellman 1978
Phyllomedusa tetraploidea	69.4	pond	Pombal and Haddad 1992	IUCN et al. 2006
Phyllomedusa tomopterna	48	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Phyllomedusa vaillantii	59.9	pond&stream	Duellman and Mendelson 1995	Duellman 1978
Phyllomedusa venusta	86.3	pond	Duellman 2001	Duellman 2001
Plectrohyla acanthodes	63.2	stream	Duellman 2001	Duellman 2001

Plectrohyla ameibothalame	43.1	stream	Canseco-Márquez et al. 2002	Canseco-Márquez et al. 2002
Plectrohyla arborescandens	37.6	stream	Duellman 2001	Duellman 2001
Plectrohyla bistincta	53.8	stream	Duellman 2001	Duellman 2001
Plectrohyla calthula	56.1	stream	Duellman 2001	Duellman 2001
Plectrohyla charadricola	44.4	stream	Duellman 2001	Duellman 2001
Plectrohyla chrysopleura	65.6	stream	Duellman 2001	Duellman 2001
Plectrohyla cyclada	39.5	stream	Duellman 2001	Duellman 2001
Plectrohyla glandulosa	49.1	stream	Duellman 2001	Duellman 2001
Plectrohyla guatemalensis	76.1	stream	Duellman 2001	Duellman 2001
Plectrohyla hazelae	38.6	stream	Duellman 2001	Duellman 2001
Plectrohyla ixil	41.6	stream	Duellman 2001	Duellman 2001
Plectrohyla matudai	46	stream	Duellman 2001	Duellman 2001
Plectrohyla mykter	42.3	stream	Duellman 2001	Duellman 2001
Plectrohyla pentheter	52.1	stream	Duellman 2001	Duellman 2001
Plectrohyla robertsorum	47.9	pond	Duellman 2001	Duellman 2001
Plectrohyla siopela	46.2	stream	Duellman 2001	Duellman 2001
Plectrohyla thorectes	34.2	stream	Duellman 2001	Duellman 2001
Pseudacris brachyphona	38	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudacris brimleyi	32	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudacris cadaverina	36	stream	Duellman 2001	IUCN et al. 2006
Pseudacris clarkii	29	pond	Duellman 2001	Duellman 2001
Pseudacris crucifer	37	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudacris feriarum	40	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudacris illinoensis	48	pond	Conant and Collins 1991 (as *P. streckeri*)	IUCN et al. 2006
Pseudacris kalmi	40	pond	Conant and Collins 1991 (as *P. triseriata*)	IUCN et al. 2006
Pseudacris maculata	37	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudacris nigrita	32	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudacris ocularis	15.5	pond	Lannoo 2005	IUCN et al. 2006
Pseudacris ornata	39	pond	Lannoo 2005	IUCN et al. 2006
Pseudacris regilla	37.8	pond	Duellman 2001	Duellman 2001
Pseudacris streckeri	39	pond	Lannoo 2005	IUCN et al. 2006

Pseudacris triseriata	40	pond	Conant and Collins 1991	IUCN et al. 2006
Pseudis minuta	40	pond	Cei 1980	IUCN et al. 2006
Pseudis paradoxa	57	pond	Duellman and Hoogmoed 1992	Duellman 2005
Ptychohyla acrochorda	36.3	?	Duellman 2001	Duellman 2001
Ptychohyla dendrophasma	84.1	unknown	Duellman 2001	IUCN et al. 2006
Ptychohyla euthysanota	38.1	stream	Duellman 2001	Duellman 2001
Ptychohyla hypomykter	41.2	stream	Duellman 2001 (as *P. spinipollex*)	Duellman 2001
Ptychohyla legleri	36.7	stream	Duellman 2001	Duellman 2001
Ptychohyla leonhardschultzei	35.6	stream	Duellman 2001	Duellman 2001
Ptychohyla salvodorensis	34.2	stream	Duellman 2001	Duellman 2001
Ptychohyla spinipollex	41.2	stream	Duellman 2001	Duellman 2001
Ptychohyla zophodes	37.4	stream	Duellman 2001	Duellman 2001
Scarthyla goinorum	21	stream	Rodríguez and Duellman 1994	IUCN et al. 2006
Scinax acuminatus	45	pond	Lutz 1973	IUCN et al. 2006
Scinax altae	26	pond	Duellman 2001	Duellman 2001
Scinax berthae	22.2	pond	Faivovich 2005	IUCN et al. 2006
Scinax boulengeri	48.7	pond	Duellman 2001	Duellman 2001
Scinax catharinae	35.1	pond	Faivovich 2005	IUCN et al. 2006
Scinax crospedospilus	33.3	pond	Heyer et al. 1990	IUCN et al. 2006
Scinax elaeochrous	37.7	pond	Duellman 2001	Duellman 2001
Scinax fuscovarius	47.1	pond	de la Riva 1993	IUCN et al. 2006
Scinax garbei	42.2	pond	Duellman and Wiens 1993	IUCN et al. 2006
Scinax nasicus	37	pond	Lutz 1973	IUCN et al. 2006
Scinax ruber	41.2	pond	Duellman and Wiens 1993	IUCN et al. 2006
Scinax squalirostris	29	pond	Lutz 1973	IUCN et al. 2006
Scinax staufferi	29	pond	Duellman 2001	Duellman 2001
Scinax sugillatus	42	pond	Duellman 1973	IUCN et al. 2006
Scinax uruguayus	25.8	pond	Langone 1990	IUCN et al. 2006
Smilisca baudinii	76	pond	Duellman 2001	Duellman 2001
Smilisca cyanosticta	56	pond	Duellman 2001	Duellman 2001
Smilisca fodiens	62.6	pond	Duellman 2001	Duellman 2001
Smilisca phaeota	65	pond	Duellman 2001	Duellman 2001
Smilisca puma	38	pond	Duellman 2001	Duellman 2001

Smilisca sila	45	stream	Duellman 2001	Duellman 2001
Smilisca sordida	45	stream	Duellman 2001	Duellman 2001
Sphaenorhynchus dorisae	29	pond	Rodríguez and Duellman 1994	IUCN et al. 2006
Sphaenorhynchus lacteus	41.5	pond	Duellman and Hoogmoed 1992	Duellman 2005
Sphaenorhynchus orophilus	32	pond	Heyer et al. 1990	IUCN et al. 2006
Tepuihyla edelcae	40.2	pond	Mijares-Urrutia et al. 1999	IUCN et al. 2006
Tlalocohyla godmani	38	pond	Duellman 2001	Duellman 2001
Tlalocohyla loquax	44.7	pond	Duellman 2001	Duellman 2001
Tlalocohyla picta	21.4	pond	Duellman 2001	Duellman 2001
Tlalocohyla smithii	26	pond	Duellman 2001	Duellman 2001
Trachycephalus coriaceus	63	arboreal	Rodríguez and Duellman 1994	IUCN et al. 2006
Trachycephalus hadroceps	53.9	arboreal	Duellman and Hoogmoed 1992	Duellman 2001
Trachycephalus imitatrix	57.1	pond	Lutz 1973	IUCN et al. 2006
Trachycephalus jordani	75.9	stream	Dan Moen, unpublished	IUCN et al. 2006
Trachycephalus mesophaeus	85	pond	Lutz 1973	IUCN et al. 2006
Trachycephalus nigromaculatus	86	pond	Cochran 1955	IUCN et al. 2006
Trachycephalus resinifrictix	76	arboreal	Rodríguez and Duellman 1994	IUCN et al. 2006
Trachycephalus venulosus	101	pond	Duellman 2001	Duellman 2001
Triprion petasatus	60.8	pond	Duellman 2001	Duellman 2001
Xenohyla truncata	?	pond		IUCN et al. 2006

Table A3.3. Morphometric data for hylid frogs. All measurements are in millimeters and were conducted on males. Variables are described in the text and labeled here as follows: (1) snout-to-vent length (SVL); (2) tibia length (TIBL); (3) foot length (FOOT); (4) head length (HLEN); (5) head width (HWID); (6) interorbital distance (IOD); (7) internarial distance (IND); (8) eye-to-nostril distance (ENOS); (9) eye diameter (EYE); (10) hand length (HNDL); (11) thumb length (THBL); (12) radioulnar length (RDL); (13) maximum width of terminal digit of finger 3 (DIG3); and (14) tympanum width (TYMP).

Species	Museum number	SVL	TIBL	FOOT	HLEN	HWID	IOD	IND	ENOS	EYE	HNDL	THBL	RDL	DIG3	TYMP
Acris crepitans	USNM 514868	22.24	12.2	11.49	6.87	8.35	1.68	1.9	1.9	2.49	5.64	1.85	4.52	0.6	1.19
Acris crepitans	USNM 514841	21.18	11.5	11.92	6.51	7.63	1.55	2.2	2.02	2.29	6.04	1.73	4.74	0.46	1.16
Agalychnis callidryas	USNM 563405	44.63	23.3	14.94	13.78	14.77	5.25	3.4	4.49	5.09	10.2	4.13	12.3	2.03	2.96
Agalychnis callidryas	USNM 563406	51.2	26.7	16.84	15.21	16.88	6.05	4	5.29	5.08	13.18	5.44	13.4	2.87	2.89
Anotheca spinosa	USNM 219621	67.05	36.1	28.87	23.2	26.28	9.25	5.5	6.65	6.19	22.56	8.05	18.6	4.41	6.08
Anotheca spinosa	USNM 219622	66.84	33.6	30.92	20.66	23.52	8.65	4.9	6.25	6.36	24.07	6.43	18.9	3.81	5.37
Aparasphenodon brunoi	USNM 164158	44.38	17.2	13.42	15.2	11.76	5.78	2.7	6.94	4.06	10.51	4.1	8.89	1.38	2.23
Aparasphenodon brunoi	USNM 164160	39.58	16.2	11.68	15.17	12.04	5.95	2.1	6.47	4.04	10.6	3.96	9.07	1.29	2.28
Aplastodiscus leucopygius	USNM 208406	42.93	21.5	18.04	14.27	14.83	6.18	3	5.7	3.39	11.89	4.56	10.4	2.28	3.4
Aplastodiscus perviridis	USNM 303652	36.06	17.7	18.33	11.09	12.61	3.71	3.3	2.99	3.52	12.18	4.25	10.1	1.34	1.89
Argenteohyla siemersi	USNM 200048	43.32	19.3	16.89	13.45	13.89	5.55	3.3	4.32	3.6	11.46	3.88	10.1	1.39	2.69
Bokermannohyla hylax	USNM 247811	55.74	29.3	23.88	18.93	20.22	7.2	4.1	6.1	5.51	16.34	6.72	14.8	3.03	3.67
Bromeliohyla bromeliacia	USNM 523171	28.36	14	10.37	9.75	9.58	3.47	2.3	3.1	3.25	6.57	3.17	6.53	1.36	1.49
Bromeliohyla bromeliacia	USNM 523172	29.52	15.1	11.65	9.92	10.09	4.01	2.6	3.18	3.03	6.64	3.42	7.67	1.26	1.61
Corythomantis greeningi	USNM 565106	66.01	27.7	22.89	20.45	19.2	8.99	4.6	6.82	5.32	16.78	5.01	14.9	2.48	3.32
Cruziohyla calcarifer	USNM 559748	68.48	35.1	24.63	23.1	24.21	7.54	5.8	7.16	4.96	19.52	7.62	18.7	4.81	4.95

Cruziohyla calcarifer	USNM 563933	69.81	39.6	26	21.71	24.65	8.93	6.3	7.03	4.61	20.07	9.32	19.2	4.26	4.65
Cyclorana australis	USNM 128236	56.73	27	21.88	23.03	24.53	5.1	4.7	6.1	5.55	13.31	6.74	15.2	0.8	4.38
Cyclorana australis	USNM 203883	58.17	24.6	22.77	22.6	25.57	5.29	4.5	5.34	5.88	14.04	6.09	15.7	0.44	3.44
Dendropsophus leucophyllatus	USNM 288971	27.75	14.6	12.78	7.67	9.97	3.8	2.9	2.75	2.93	8.23	3.04	6.72	1.33	1.54
Dendropsophus leucophyllatus	USNM 288974	28.88	14.2	11.44	9.22	10.17	3.45	1.8	2.55	3.04	7.34	2.95	6.74	1.36	1.52
Dendropsophus marmoratus	USNM 560322	36.01	18.3	15.61	10	11.98	3.7	3.1	3.49	3.63	10.99	3.91	8.34	1.74	2.25
Dendropsophus marmoratus	USNM 560331	34.48	17.3	15.45	9.82	11.67	3.44	2.7	3.51	3.98	10.94	3.78	8.55	1.98	2.05
Dendropsophus microcephalus	USNM 242778	21.25	11.6	9.22	6.3	6.57	2.73	1.7	1.8	2.12	5.36	2.13	5.59	0.87	1.06
Dendropsophus microcephalus	USNM 242784	19.98	10	7.5	5.43	6.07	2.09	1.8	1.72	2.29	4.93	1.65	4.79	0.84	1.11
Dendropsophus parviceps	USNM 345223	19.01	10.3	7.91	5.75	7.1	2.78	1.7	1.93	2.48	5.39	1.58	5.35	1.01	1.11
Dendropsophus parviceps	USNM 345224	19.18	10.4	7.9	6.49	6.52	2.21	1.7	1.86	2.59	5.22	1.42	5.17	0.98	1.24
Dendropsophus parviceps	USNM 345229	20.22	10.6	8.19	5.76	6.98	2.6	1.7	1.98	2.6	5.77	1.78	5.22	0.96	1.06
Dendropsophus parviceps	USNM 345231	20.31	10.3	8.4	5.93	7.07	2.92	1.8	1.93	2.67	5.95	1.86	5.32	1.05	1.16
Dendropsophus parviceps	USNM 345233	19.77	10.3	8.02	5.64	7.12	2.67	1.5	1.91	2.61	5.58	1.54	5.07	1.01	1.1
Duellmanohyla soralia	USNM 514515	29.3	14.5	10.57	9.67	9.24	3.69	2.2	3.06	2.94	8.07	3.09	7.94	1.3	1.58
Duellmanohyla soralia	USNM 514520	28.6	14.6	11.57	9.48	9.79	3.61	2.8	2.79	2.66	8.51	2.9	7.89	1.29	1.39
Ecnomiohyla miliaria	USNM 563949	97.39	46.7	47.2	31.85	37.66	11.2	7.3	9.47	8.41	32.14	10.9	23.7	6.45	6.02
Ecnomiohyla miliaria	USNM 563950	94.71	48.8	45.37	31.33	37.23	10.9	7.1	10.63	7.55	33.78	12.5	24.1	6.51	6.06
Ecnomiohyla miotympanum	USNM 304929	29.62	16	12.72	9.46	9.95	3.04	2.3	2.87	2.89	8.34	2.31	7.83	1.78	1.6

Ecnomiohyla miotympanum	USNM 304929	27.58	14.4	11.22	8.45	9.83	2.86	2.3	2.59	2.72	7.47	2.3	7.21	1.21	1.34
Exerodonta sumichrasti	USNM 114190	21.08	11.2	8.44	7.08	7	3.26	1.9	2.46	2.04	5.63	1.84	4.8	0.86	1.05
Hyla cinerea	USNM 530227	37.62	17.7	14.38	10.21	11.21	3.79	2.7	3.08	3.11	8.86	2.47	8.7	1.47	2.08
Hyla cinerea	USNM 530233	38.38	17.9	15.95	10.28	11.75	3.69	2.7	3.2	3.29	9.86	3.25	8.43	1.55	2.48
Hylomantis lemur	USNM 286444	42.89	20.3	14.57	13.04	13.54	4.75	3.5	4.29	4.66	9.39	4.26	12.1	1.95	1.51
Hylomantis lemur	USNM 286449	41.15	20.4	14.43	13.42	12.89	4.93	3.4	4.05	4.56	10.95	4.43	11.5	2.19	1.98
Hyloscirtus phyllognathus	USNM 298222	34.46	17.3	13.73	9.56	11.48	3.78	2.6	2.58	3.19	9.71	4.09	8.82	1.69	1.4
Hyloscirtus phyllognathus	USNM 298226	34.86	16.7	13.92	10.86	11.19	4.51	2.9	3.04	3.09	10.31	3.54	9.03	2	1.8
Hypsiboas boans	USNM 298726	91.71	50.5	39.04	32.15	34.94	12.3	5.9	12.26	7.6	27.18	12.4	20.8	5.07	4.68
Hypsiboas boans	USNM 298727	93.77	50.4	41.64	29.6	32.63	10.7	5.9	11.66	7.6	27.85	11.8	24.2	4.87	4.85
Hypsiboas geographicus	USNM 298853	50.74	26.9	19.25	17.72	19.09	6.71	3.6	5.97	5.68	14.09	6.01	12.5	2.66	4.31
Hypsiboas geographicus	USNM 298855	43.82	22.4	16.38	13.99	15.02	4.58	3	4.94	4.53	12.02	4.11	9.99	2.29	2.69
Hypsiboas geographicus	USNM 298858	49.31	25.1	17.36	15.97	17.45	5.18	3.1	5.4	4.74	13.57	4.49	11.2	2.62	3.03
Hypsiboas geographicus	USNM 298859	45.62	23	17.07	15.29	15.81	5.1	3.2	5.1	4.8	12.29	4.33	11	2.25	2.78
Hypsiboas geographicus	USNM 342938	46.67	22.9	16.8	15.82	17.16	5.12	3.2	5.07	4.85	12.47	5.26	10.9	2.22	3.3
Hypsiboas lanciformis	USNM 317318	66.67	47.2	32.47	23.74	19.99	6.78	5.6	8.46	6.24	20.42	9.82	17	2.75	4.31
Hypsiboas lanciformis	USNM 317320	71.28	47.8	35.14	26.14	21.94	8.29	6	8.04	7.44	21.72	9.59	17.5	3.06	4.5
Isthmohyla pseudopuma	USNM 219895	39.13	20.4	18.7	12.66	11.8	4.49	2.5	3.33	4.17	10.45	4.26	10.4	2.07	2.68
Isthmohyla pseudopuma	USNM 219896	36.81	20.5	17.03	11.22	11.38	4.13	2.6	3.28	3.6	10.05	3.09	10.3	1.87	2.06
Itapotihyla langsdorffii	USNM 121337	82.86	44.5	32.8	25.73	26.22	10.8	6	8.51	7.6	25.88	8.96	19.1	4.78	4.84
Litoria aurea	USNM 149672	73.48	35.9	33.3	23.63	24.17	5.49	4.2	6.04	6.09	20.08	7.57	18	2.21	4.82
Litoria aurea	USNM 149674	72.89	35.5	33.34	23.45	24.2	5.76	4.2	5.34	6.6	19.92	7.09	17.4	2.04	5.1
Litoria bicolor	USNM 195493	19.41	9.88	7.33	5.24	5.89	2.33	1.8	2.1	2.23	4.16	1.53	4.22	0.68	1.13

Litoria caerulea	USNM 195501	78.65	30.1	28.77	20.82	25.65	7.47	6.1	6.55	5.76	20.25	7.08	16.4	4.65	3.87
Litoria caerulea	USNM 212762	75.75	30.5	27.67	21.53	26.13	6.84	5.9	6.45	6.06	18.91	5.81	22.1	4.47	4.39
Litoria eucnemis	USNM 166199	36.57	23.7	14.6	11.47	12.84	4.03	3.5	4.29	3.85	10.98	3.98	9.98	1.91	2.43
Litoria eucnemis	USNM 166200	44.4	25	18.31	15.68	16	4.83	3.6	4.8	5.02	11.46	3.84	11	2.18	3.23
Litoria ewingii	USNM 63177	33.02	16.7	14.46	9.76	11.05	3.58	2.7	3.19	3.83	8.37	3.25	9.88	1.45	2.38
Litoria gracilenta	USNM 203913	33.37	17	13.24	9.3	11.85	4.71	3	2.76	3.29	7.89	2.24	8.18	1.6	2.43
Litoria lesueurii	USNM 203916	54.74	35.1	27.03	17.64	18.92	5.78	4.6	5.99	5.41	15.54	7.11	14.6	1.89	3.77
Litoria nannotis	USNM 269406	43.7	24.9	18.47	13.67	15.96	4.52	4.1	4.06	4.11	12.2	5.04	12.5	2.19	0
Litoria nasuta	USNM 212347	42.22	29.3	24.13	15.11	12.56	3.48	3.9	4.23	3.66	10.7	5.47	10.1	0.83	3.16
Litoria peronii	USNM 203920	51.24	27.7	24.86	14.22	16.2	4.65	3.9	4.54	4.69	16.56	6.42	12.9	3.09	3.38
Litoria peronii	USNM 203921	50.22	28.9	23.89	16.12	17.43	6.37	3.5	4.62	4.63	18.18	6.59	12.9	3.03	3.94
Litoria rubella	USNM 199224	32.45	12.1	11.21	6.98	9.93	3.24	2.3	3.25	2.78	7.87	2.56	6.96	1.39	2.17
Litoria rubella	USNM 199225	32.34	12.7	11.09	8.23	9.6	3.44	2.4	2.94	2.9	7.88	3.28	7.36	1.4	2.1
Litoria thesaurensis	USNM 340152	50.05	27.3	22.16	15.13	15.51	6.53	3.6	5.55	4.17	14.15	5.35	12.3	2.68	2.58
Litoria thesaurensis	USNM 340155	50.15	27.6	20.99	16.03	15.85	5.34	3.6	4.76	4.59	14.09	5.76	12.6	2.62	2.82
Myersiohyla kanaima	USNM 561828	46.7	23.9	17.21	17.01	16.05	4.59	3.5	6.09	5.49	12.62	5.89	12.8	2.5	2.67
Myersiohyla kanaima	USNM 561829	44.1	23.1	15.98	16.9	16.09	3.65	3.1	5	5.01	12.45	5.81	11.9	2.2	2.43
Nyctimantis rugiceps	USNM 198707	63.59	32.3	25.9	22.23	22.64	7.6	5.6	8.11	6.5	19.21	6.92	15.8	3.91	4.12
Nyctimantis rugiceps	USNM 198708	59.95	32.2	24.15	20.99	22.3	8.14	5.6	7.13	5.5	17.17	6.49	15.8	2.22	4.02
Nyctimystes cheesmani	USNM 269473	34.66	19.3	13.99	11.52	12.26	3.45	3.3	3.32	3.99	9.92	3.8	9.12	1.26	1.56
Nyctimystes cheesmani	USNM 269475	33.36	18.8	14.2	11.73	11.85	3.55	3.2	3.3	3.5	10.4	3.42	9.16	1.44	1.74
Osteocephalus leprieurii	USNM 342602	50.91	30	22.44	16.63	16.62	5.88	3.6	5.66	5.1	15.87	6.05	13.6	2.87	4.02
Osteocephalus leprieurii	USNM 343216	44.6	25.8	19.65	14.79	15.07	5.51	3.2	4.59	4.05	12.73	4.72	12.2	2.32	3.35
Osteocephalus taurinus	USNM 222205	74.33	38.1	30.18	21.81	24	8.38	5	8.06	6.23	24.23	7.88	18.9	4.73	6.09

Osteocephalus taurinus	USNM 222210	78.77	39.6	32.74	24.05	24.47	9.21	5.1	8.24	6.97	25.12	8.84	18.3	4.6	5.8
Osteocephalus taurinus	USNM 247614	78.34	41.2	32.67	22.58	24.41	9.22	4.9	7.82	6.35	22.9	7.66	19.3	4.38	5.31
Osteopilus vastus	KU 264729	105	56.3	46.54	32.03	36.18	11.6	9	8.68	8.72	34.54	14.6	27.6	6.59	4.99
Osteopilus vastus	KU 264734	108.1	58.1	46.62	32.18	35.4	13.4	9.3	9.2	9.25	30.83	11.9	27.5	6.59	4.92
Osteopilus wilderi	KU 287833	24.75	13.7	9.51	8.02	8.82	3.55	2	2.47	2.16	6.52	2.35	6.24	1.02	1.15
Osteopilus wilderi	KU 287849	25.85	14	9.44	8.17	9.1	3.42	1.8	2.51	2.35	6.76	1.9	6.18	1.11	1.35
Pachymedusa dacnicolor	USNM 238118	63.95	25.3	22.99	18.52	19.71	6.24	5.3	5.11	6.2	16.49	6.37	17.7	2.36	3.87
Pachymedusa dacnicolor	USNM 238125	65.89	25.4	21.66	19.39	20.59	7.12	5.3	6.32	6.04	17.76	6.94	16.6	1.88	3.99
Phyllodytes auratus	USNM 244419	31.43	14.6	11.38	10.13	10.56	3.85	1.9	3.29	2.81	8	2.85	7.03	1.49	0
Phyllomedusa atelopoides	USNM 342650	35.8	14.4	11.44	12.44	14.04	5.56	3.4	3.42	4.24	8.9	3.36	13.2	0.88	3.11
Phyllomedusa tarsius	USNM 560397	81.95	38.3	27.39	23.91	25.85	7.94	6.5	7.2	7.88	23.14	8.67	24.1	3.44	3.59
Phyllomedusa tarsius	USNM 560398	80.92	37.9	26.95	23.34	26.17	9.68	6.3	6.97	7.66	21.97	9.37	24.7	3.07	3.63
Phyllomedusa tomopterna	USNM 343278	45.19	21.8	15.3	14.04	15.1	5.16	3.8	4.08	4.69	12.06	4.38	14	1.82	2.73
Phyllomedusa tomopterna	USNM 343279	41.91	20.1	14.51	12.64	13.76	4.97	3.4	3.92	4.72	10.78	4.27	13.5	1.87	2.47
Phyllomedusa tomopterna	USNM 537736	43.3	20.5	14.82	14.28	14.35	5.18	3.2	4.03	4.83	10.6	4.17	13.2	1.58	2.78
Phyllomedusa tomopterna	USNM 537737	40.63	22.4	15.64	13.08	13.64	5	3.5	4.09	4.32	11.25	5.09	13.8	2.09	2.73
Plectrohyla guatemalensis	USNM 523195	52.22	26.7	24.18	14.89	16.73	5.05	4.4	3.66	4.83	16	6.07	14.3	2.29	2.47
Plectrohyla guatemalensis	USNM 523200	51.7	26	23.18	13.5	17.23	5.21	4.5	3.33	4.48	16.11	5.42	14.4	2.55	?
Pseudacris crucifer	USNM 534798	29.14	14.6	12.22	8.67	9.8	2.89	2.3	2.66	2.8	6.1	2.31	7.67	1	1.42
Pseudacris crucifer	USNM 534820	29.44	13.5	12.13	8.72	10.32	3.22	2.4	2.84	3.02	7.83	2.32	7.03	1.09	1.81
Pseudis limellum	USNM 341861	17.33	10.6	8.82	5.8	6.53	1.66	0.9	1.65	1.9	5.02	2.3	4.26	0.3	1.74
Pseudis limellum	USNM 341875	19.11	12	10.01	6.23	7.06	1.92	1.1	1.72	1.69	6.08	2.66	4.76	0.36	1.57

Pseudis paradoxus	USNM341880	49.97	24	22.16	15.17	17.34	3.31	3.3	3.11	4.5	11.92	6.11	13.2	0.49	4.23
Pseudis paradoxus	USNM341885	48.72	26	25.54	14.63	17.59	3.22	3.1	3.21	4.34	10.5	6.3	12.7	0.4	3.72
Ptychohyla spinipollex	USNM 514366	37.02	18.8	15.11	10.77	11.38	3.9	3.2	2.82	3.77	10.09	3.62	8.93	1.6	1.77
Ptychohyla spinipollex	USNM 514381	40.29	19.2	15.76	11.47	12.07	3.89	3.6	3.08	3.89	10.59	4.1	9.59	1.71	1.9
Scarthyla goinorum	USNM 342385	16.74	10	7.78	5.53	5.01	2.23	1.8	1.88	1.93	4.76	1.68	4.36	0.65	1.12
Scinax acuminatus	USNM 303691	42.42	21.2	16.23	14.38	15.37	4.06	3	5.17	3.69	11.25	4.38	9.49	1.97	2.71
Scinax catharinae	USNM 217742	28.83	15.9	12.37	9.95	9.22	2.8	2.2	3.52	3.15	8.81	3.23	7.35	1.54	1.61
Scinax catharinae	USNM 217742	30.55	17.2	12.55	9.73	9.63	2.91	2.3	3.72	3.44	8.73	3.8	7.13	1.51	1.98
Scinax garbei	USNM 537707	38.38	20.5	16.3	13.8	11.25	3.83	3.2	5.4	3.49	11.64	4.54	9	2.42	2.23
Scinax garbei	USNM 537708	38.7	21.8	16.53	12.79	12.73	3.99	3.3	5.29	3.33	11.57	4.93	9.46	2.03	2.07
Scinax ruber	USNM 346097	33.43	15.4	13.12	10.7	10.4	3.87	2.6	3.73	3.56	8.67	3.09	7.86	1.63	1.96
Scinax ruber	USNM 346100	34.71	16.9	13.95	11	10.44	3.79	2.6	4.07	3.01	9.24	3.82	7.65	1.81	2.03
Scinax staufferi	USNM 514439	26.16	11.6	8.95	7.15	8.51	2.57	1.9	2.89	2.31	5.69	2	5.64	1.04	1.39
Scinax staufferi	USNM 514440	26.9	11.5	9.06	7.73	9.11	3.49	2.1	3.04	2.37	6.78	2.29	5.68	1.11	1.61
Smilisca baudinii	USNM 559240	56.63	27.7	23.48	17.1	19.67	6.5	4.1	4.56	5.81	14.75	4.99	13.8	2.5	4.23
Smilisca baudinii	USNM 559253	57.15	27.8	23.9	18.36	20.14	6.01	4.1	4.59	5.55	15.91	5.14	13.4	2.68	3.63
Sphaenorhynchus lacteus	USNM 281733	30.42	15	14.68	7.21	9.52	4.62	2.3	3.1	2.66	9.75	3.03	7.85	1.29	1.13
Sphaenorhynchus lacteus	USNM 281746	37.25	18.1	15.78	8.47	10.75	4.68	2.6	3.32	3.15	10.38	3.81	8.3	1.5	1.27
Tlalocohyla godmani	USNM 514229	40.57	20.6	17.56	11.23	13.62	4.92	3.5	3.19	3.63	12.05	4.04	10	1.36	2.17
Tlalocohyla godmani	USNM 514229	41.17	20.3	16.67	11.25	13.65	5.46	3.5	3.59	3.68	11.95	4.21	9.72	1.94	2.31
Tlalocohyla picta	USNM 333083	17.53	9.3	7.18	5.4	5.73	3	1.6	1.84	2	4.33	1.49	4.24	0.68	0.94
Trachycephalus jordani	USNM 285292	70.22	34.6	29.75	20.85	22.19	10.1	4.5	7.89	5.47	19.8	7.73	17	3.74	4.22
Trachycephalus jordani	USNM 285294	70.45	33.4	28.07	22.17	22.51	10.9	4.1	7.81	5.11	22	7.53	16.6	3.62	4.09
Trachycephalus	USNM 247254	72.68	33.3	29.08	20.97	22.24	6.27	5	5.66	5.92	22.16	8.34	16.8	3.39	4.55

venulosus															
Trachycephalus venulosus	USNM 247255	65.84	31.1	26.62	19.38	21.62	6.29	5	5.85	4.83	20.28	7.47	16.3	3.24	3.65
Trachycephalus venulosus	USNM 247616	62.88	30.4	26.14	18.64	20.33	5.71	4.8	5.55	5.22	18.93	7.56	15.7	3.44	3.5
Trachycephalus venulosus	USNM 342966	64.79	30.3	24.68	18.63	19.3	6.38	4.6	5.33	6.06	19.45	6.05	15.2	3.41	4.07
Trachycephalus venulosus	USNM 343219	68.97	32.9	27.7	19.76	22.52	6.61	4.8	5.98	5.73	20.79	7.03	17	3.93	3.9
Triprion petasatus	USNM 118660	51.95	21.4	16.86	17.68	14.63	11.5	1.7	7.49	4.41	11.92	3.82	10.8	2.23	3.1
Triprion petasatus	USNM 118661	50.61	21.2	17.34	17.92	14.69	11.3	1.8	8.2	3.25	13.31	4.52	10.2	2.2	2.69
Xenohyla truncata	USNM 565111	34.73	14.9	13.33	8.44	11.87	5.47	2.1	3.78	2.58	9.02	3.35	7.88	1.72	1.64

Table A3.4. Results of principal components analysis (PCA) on the hylid morphometric data (Table A3.3), showing the loadings of each original variable on PC1 (left) and the proportion of the total variation represented by each PC axis (right). Variable acronyms are as above in Table A3.3. We only present the principal components loadings for the first PC axis due to the low amount of variation represented by all other axes. "All hylids" represents a PCA conducted on the data from a sample of all hylid species (i.e., regardless of region), while "MA hylids" represents the same analysis conducted on a subset of the data that includes only Middle American species.

	PC1 loadings			*% Variation*	
Variable	All hylids	MA hylids	PC Axis	All hylids	MA hylids
SVL	0.27724	0.27534	1	91.227	92.870
TIBL	0.27323	0.27393	2	2.481	3.481
FOOT	0.27095	0.27203	3	1.730	1.114
HLEN	0.27504	0.27527	4	1.268	0.888
HWID	0.27456	0.27572	5	0.995	0.598
IOD	0.25232	0.24225	6	0.599	0.273
IND	0.26377	0.25789	7	0.437	0.217
ENOS	0.25873	0.25502	8	0.400	0.172
EYE	0.26756	0.26353	9	0.277	0.145
HNDL	0.27547	0.27386	10	0.184	0.087
THBL	0.27144	0.27101	11	0.171	0.067
RDL	0.27189	0.27254	12	0.087	0.046
DG3	0.25380	0.26753	13	0.084	0.026
TYMP	0.25371	0.26339	14	0.061	0.018

Table A3.5. Results of ROTI null model analyses for body size, showing ROTI value for each community and its associated *P*-value under different regional pools. Community numbers refer to communities as listed in Table S1. Communities with significant P-values are boldfaced.

Community	Number of species	Body Size ROTI	Whole region	Freq. weighted	Costa Rica + Panama	Costa Rica	Panama
1	**3**	**1.00**	**0.033**	0.065			
2	**5**	**1.00**	**0.006**	**0.017**			
3	1	0.00	0.259	0.194			
4	8	0.75	0.100	0.279			
5	**5**	**1.00**	**0.006**	**0.017**			
6	1	0.00	0.259	0.194			
7	8	0.50	0.866	0.685			
8	6	0.67	0.326	0.622			
9	8	0.75	0.100	0.279			
10	**4**	**1.00**	**0.013**	**0.033**			
11	3	0.67	0.492	0.730			
12	**3**	**0.00**	**0.050**	**0.024**			
13	4	0.25	0.359	0.190			
14	4	0.75	0.251	0.449			
15	7	0.43	0.818	0.445			
16	4	0.50	0.907	0.777			
17	9	0.56	0.602	0.930			
18	6	0.83	0.061	0.162			
19	8	0.63	0.371	0.746			
20	9	0.44	0.870	0.440			
21	8	0.50	0.866	0.685			
22	6	0.67	0.326	0.622			
23	7	0.57	0.587	0.993			
24	8	0.63	0.371	0.746			
25	8	0.75	0.100	0.279			
26	8	0.63	0.371	0.746			
27	7	0.57	0.587	0.993			
28	4	0.75	0.251	0.449			
29	6	0.50	0.885	0.727			
30	**5**	**0.00**	**0.011**	**0.003**	**0.022**	**0.011**	
31	11	0.36	0.457	0.157	0.828	0.502	
32	12	0.58	0.418	0.922	0.128	0.274	
33	11	0.55	0.609	0.867	0.249	0.461	
34	6	0.50	0.885	0.727	0.573	0.792	
35	10	0.40	0.642	0.268	0.955	0.716	
36	7	0.43	0.818	0.445	0.834		0.667
37	9	0.56	0.602	0.930	0.279		0.174
38	7	0.43	0.818	0.445	0.834		0.667
39	10	0.60	0.399	0.842	0.142		0.076

Table A3.6. Results of ROTI null model analyses for larval habitat, showing ROTI value for each community and its associated *P*-value under different regional pools. Community numbers refer to communities as listed in Table S1. Communities with significant P-values are boldfaced.

Community	Number of species	Larval Habitat ROTI	Whole region	Freq. weighted	Costa Rica + Panama	Costa Rica	Panama
1	3	0.67	0.705	0.779			
2	5	0.80	0.840	0.308			
3	1	0.00	0.090	0.183			
4	8	0.63	0.372	0.828			
5	5	0.80	0.840	0.308			
6	1	0.00	0.090	0.183			
7	**8**	**1.00**	**0.035**	**0.003**			
8	6	0.33	0.023	0.201			
9	**8**	**1.00**	**0.035**	**0.003**			
10	4	0.50	0.250	0.720			
11	3	0.33	0.113	0.371			
12	3	0.33	0.113	0.371			
13	4	0.75	0.952	0.494			
14	4	0.75	0.952	0.494			
15	**7**	**1.00**	**0.049**	**0.006**			
16	4	0.75	0.952	0.494			
17	9	0.56	0.160	0.839			
18	6	0.83	0.668	0.190			
19	8	0.63	0.372	0.828			
20	**9**	**0.89**	0.324	**0.042**			
21	**8**	**0.38**	**0.016**	0.215			
22	**6**	**1.00**	0.069	**0.011**			
23	7	0.57	0.255	0.927			
24	8	0.50	0.098	0.607			
25	8	0.88	0.414	0.070			
26	8	0.75	0.931	0.328			
27	7	0.43	0.053	0.387			
28	**4**	**1.00**	0.139	**0.038**			
29	6	0.50	0.156	0.658			
30	**5**	**1.00**	0.097	**0.020**	**0.008**	**0.017**	
31	11	0.64	0.330	0.736	0.383	0.690	
32	**12**	**0.33**	**0.001**	0.066	0.143	**0.038**	
33	**11**	**0.27**	**0.000**	**0.029**	0.065	**0.015**	
34	**6**	**0.33**	**0.023**	0.201	0.334	0.183	
35	10	0.70	0.639	0.453	0.201	0.397	
36	**7**	**0.14**	**0.000**	**0.013**	**0.027**		**0.039**
37	**9**	**0.33**	**0.005**	0.114	0.221		0.298
38	**7**	**0.14**	**0.000**	**0.013**	**0.027**		**0.039**
39	**10**	**0.20**	**0.000**	**0.010**	**0.022**		**0.035**

Figures A3.1–A3.3. Phylogeny of Hylidae that was used for all analyses, estimated by (1) separate Bayesian analyses of each major South American clade (from Moen and Wiens 2009) and the Middle American Clade (Smith et al. 2007), (2) converting branch lengths into units of time using the program r8s, and (3) connecting these clades together by placing on an ultrametric phylogeny (with branch lengths in units of time) of the Hylidae, as estimated by Wiens et al. (2006b). See Methods for further details. Branch lengths are in units of time, with the scale bar reflecting divergence times estimated using the younger set of calibration dates. Branch colors reflect biogeographic designations (for species at tips) and ancestral-state estimates (for internal nodes), estimated under the DEC model of Ree and Smith (2008). This model distinguishes between range evolution along branches with changes that occur at cladogenesis events; thus, we show changes as occurring mid-branch (for changes along branches) or as vertical branches differing from their common ancestor (for changes at cladogenesis). Note that the position of changes along branches could not be inferred, so our mid-branch designation for changes is arbitrary and was chosen for visual clarity. Branch colors reflect states with the highest likelihood, and dashed branches represent cases where alternative reconstructions fell within two ln-likelihood units (Ree and Smith 2008). In most of these latter cases the displayed resolution still had a much higher likelihood than all other possible resolutions, with the exception of the nodes in the vicinity of the Middle American *Hyla* in Fig. A3.3. Because of the extreme amount of ambiguity in this case (no potential resolution had a normalized likelihood higher than 0.44 and 3–5 alternative resolutions were possible), we considered it most likely that *Hyla* recolonized Middle America only once. However, considering this clade as representing multiple colonization events did not influence our results (not shown).

Figure A3.1

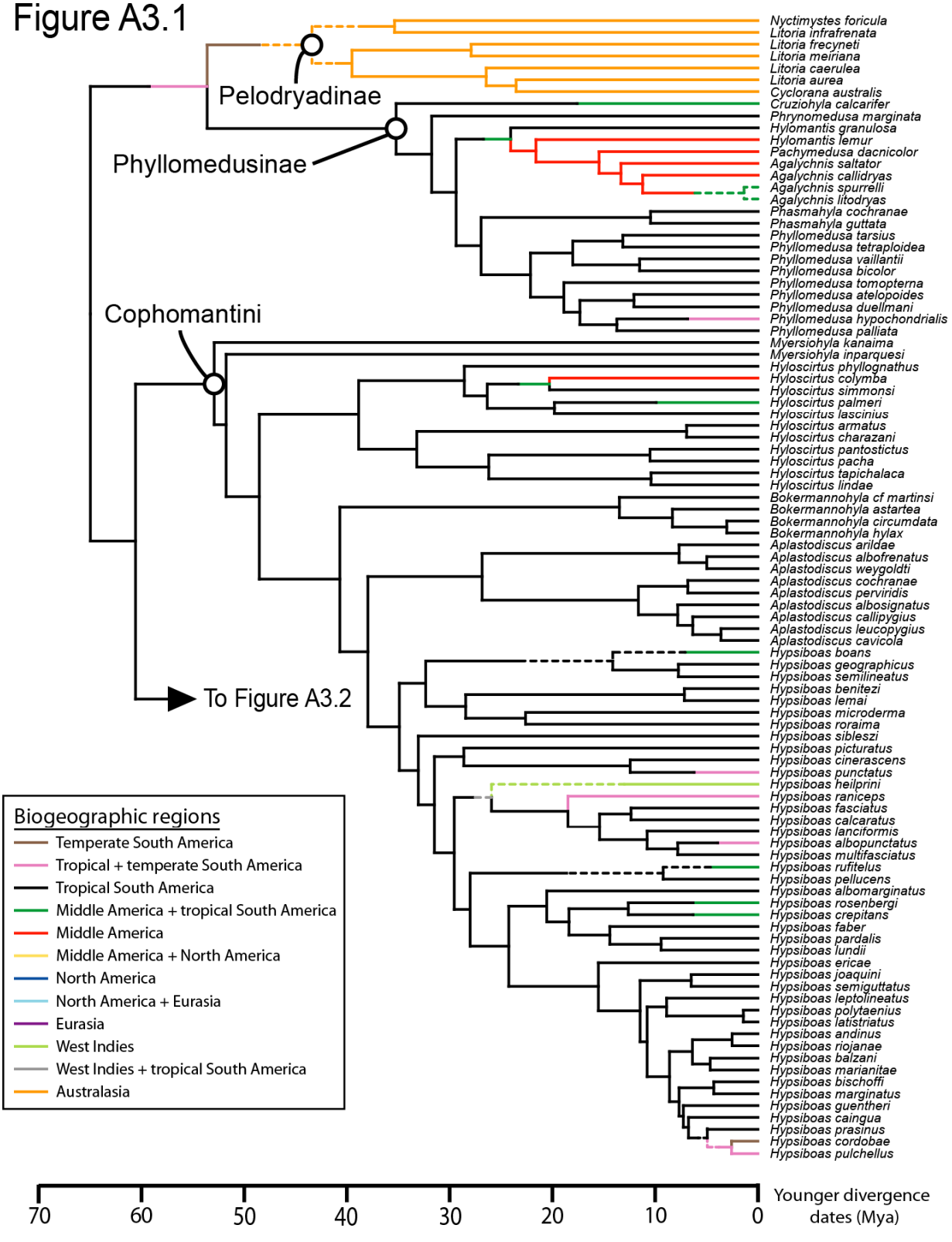

Pelodryadinae
Phyllomedusinae
Cophomantini
To Figure A3.2
Nyctimystes foricula
Litoria infrafrenata
Litoria frecyneti
Litoria meiriana
Litoria caerulea
Litoria aurea
Cyclorana australis
Cruziohyla calcarifer
Phrynomedusa marginata
Hylomantis granulosa
Hylomantis lemur
Pachymedusa dacnicolor
Agalychnis saltator
Agalychnis callidryas
Agalychnis spurrelli
Agalychnis litodryas
Phasmahyla cochranae
Phasmahyla guttata
Phyllomedusa tarsius
Phyllomedusa tetraploidea
Phyllomedusa vaillantii
Phyllomedusa bicolor
Phyllomedusa tomopterna
Phyllomedusa atelopoides
Phyllomedusa duellmani
Phyllomedusa hypochondrialis
Phyllomedusa palliata
Myersiohyla kanaima
Myersiohyla inparquesi
Hyloscirtus phyllognathus
Hyloscirtus colymba
Hyloscirtus simmonsi
Hyloscirtus palmeri
Hyloscirtus lascinius
Hyloscirtus armatus
Hyloscirtus charazani
Hyloscirtus pantostictus
Hyloscirtus pacha
Hyloscirtus tapichalaca
Hyloscirtus lindae
Bokermannohyla cf martinsi
Bokermannohyla astartea
Bokermannohyla circumdata
Bokermannohyla hylax
Aplastodiscus arildae
Aplastodiscus albofrenatus
Aplastodiscus weygoldti
Aplastodiscus cochranae
Aplastodiscus perviridis
Aplastodiscus albosignatus
Aplastodiscus callipygius
Aplastodiscus leucopygius
Aplastodiscus cavicola
Hypsiboas boans
Hypsiboas geographicus
Hypsiboas semilineatus
Hypsiboas benitezi
Hypsiboas lemai
Hypsiboas microderma
Hypsiboas roraima
Hypsiboas sibleszi
Hypsiboas picturatus
Hypsiboas cinerascens
Hypsiboas punctatus
Hypsiboas heilprini
Hypsiboas raniceps
Hypsiboas fasciatus
Hypsiboas calcaratus
Hypsiboas lanciformis
Hypsiboas albopunctatus
Hypsiboas multifasciatus
Hypsiboas rufitelus
Hypsiboas pellucens
Hypsiboas albomarginatus
Hypsiboas rosenbergi
Hypsiboas crepitans
Hypsiboas faber
Hypsiboas pardalis
Hypsiboas lundii
Hypsiboas ericae
Hypsiboas joaquini
Hypsiboas semiguttatus
Hypsiboas leptolineatus
Hypsiboas polytaenius
Hypsiboas latistriatus
Hypsiboas andinus
Hypsiboas riojanae
Hypsiboas balzani
Hypsiboas marianitae
Hypsiboas bischoffi
Hypsiboas marginatus
Hypsiboas guentheri
Hypsiboas caingua
Hypsiboas prasinus
Hypsiboas cordobae
Hypsiboas pulchellus
Biogeographic regions
Temperate South America
Tropical + temperate South America
Tropical South America
Middle America + tropical South America
Middle America
Middle America + North America
North America
North America + Eurasia
Eurasia
West Indies
West Indies + tropical South America
Australasia
70
60
50
40
30
20
10
0
Younger divergence dates (Mya)

Figure A3.2

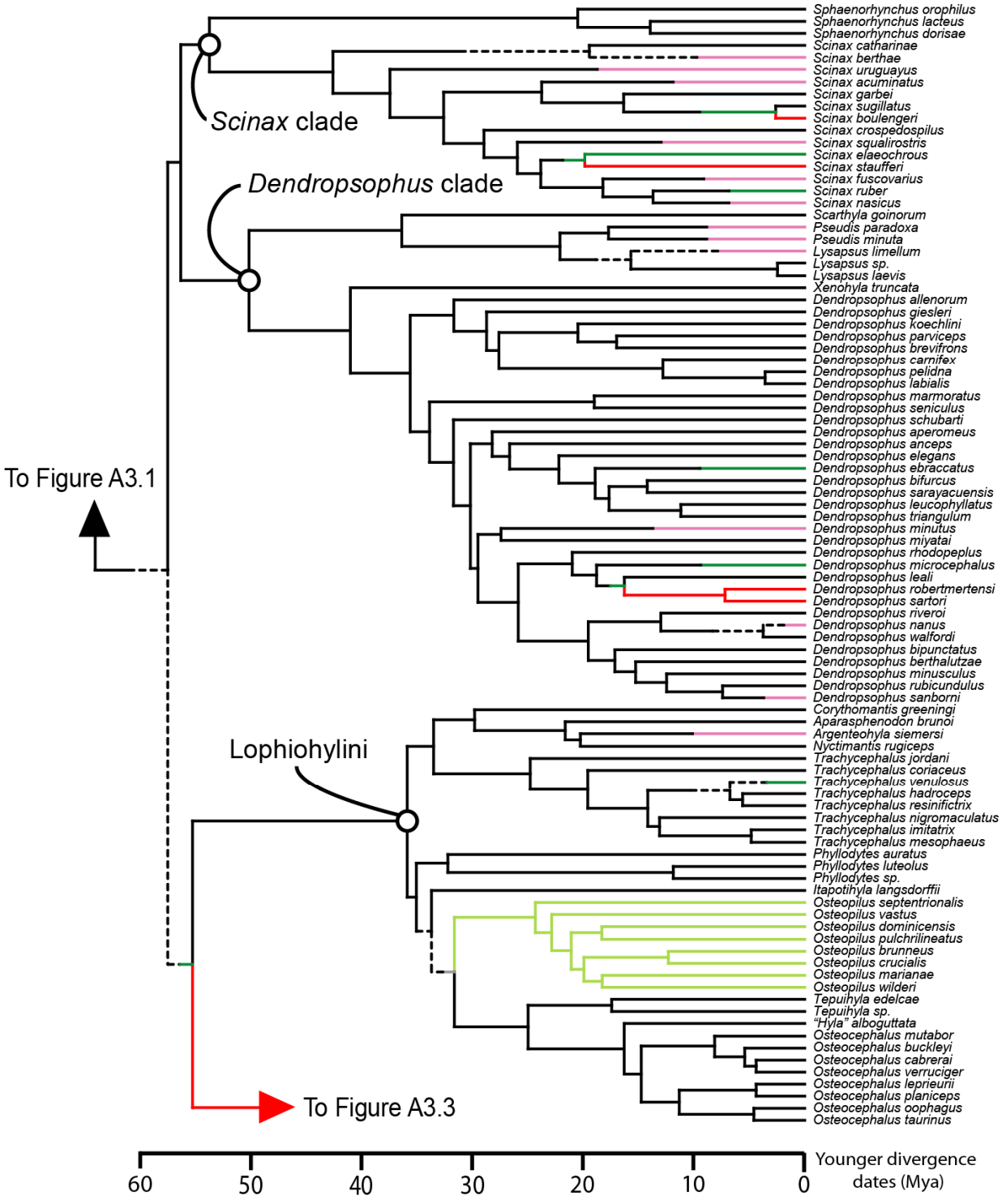
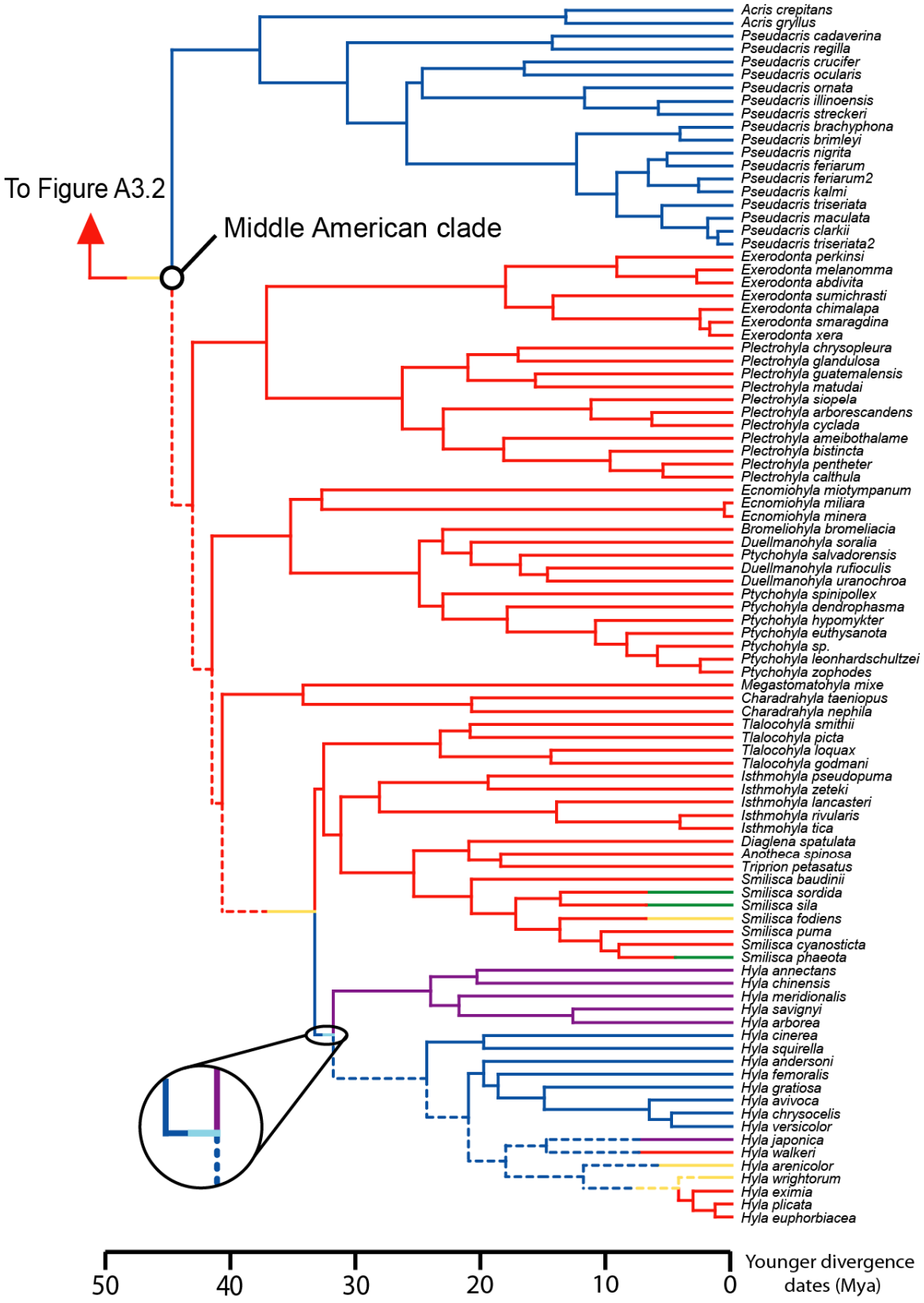

Sphaenorhynchus orophilus
Sphaenorhynchus lacteus
Sphaenorhynchus dorisae
Scinax catharinae
Scinax berthae
Scinax uruguayus
Scinax acuminatus
Scinax garbei
Scinax sugillatus
Scinax boulengeri
Scinax crospedospilus
Scinax squalirostris
Scinax elaeochrous
Scinax staufferi
Scinax fuscovarius
Scinax ruber
Scinax nasicus
Scarthyla goinorum
Pseudis paradoxa
Pseudis minuta
Lysapsus limellum
Lysapsus sp.
Lysapsus laevis
Xenohyla truncata
Dendropsophus allenorum
Dendropsophus giesleri
Dendropsophus koechlini
Dendropsophus parviceps
Dendropsophus brevifrons
Dendropsophus carnifex
Dendropsophus pelidna
Dendropsophus labialis
Dendropsophus marmoratus
Dendropsophus seniculus
Dendropsophus schubarti
Dendropsophus aperomeus
Dendropsophus anceps
Dendropsophus elegans
Dendropsophus ebraccatus
Dendropsophus bifurcus
Dendropsophus sarayacuensis
Dendropsophus leucophyllatus
Dendropsophus triangulum
Dendropsophus minutus
Dendropsophus miyatai
Dendropsophus rhodopeplus
Dendropsophus microcephalus
Dendropsophus leali
Dendropsophus robertmertensi
Dendropsophus sartori
Dendropsophus riveroi
Dendropsophus nanus
Dendropsophus walfordi
Dendropsophus bipunctatus
Dendropsophus berthalutzae
Dendropsophus minusculus
Dendropsophus rubicundulus
Dendropsophus sanborni
Corythomantis greeningi
Aparasphenodon brunoi
Argenteohyla siemersi
Nyctimantis rugiceps
Trachycephalus jordani
Trachycephalus coriaceus
Trachycephalus venulosus
Trachycephalus hadroceps
Trachycephalus resinifictrix
Trachycephalus nigromaculatus
Trachycephalus imitatrix
Trachycephalus mesophaeus
Phyllodytes auratus
Phyllodytes luteolus
Phyllodytes sp.
Itapotihyla langsdorffii
Osteopilus septentrionalis
Osteopilus vastus
Osteopilus dominicensis
Osteopilus pulchrilineatus
Osteopilus brunneus
Osteopilus crucialis
Osteopilus marianae
Osteopilus wilderi
Tepuihyla edelcae
Tepuihyla sp.
"Hyla" alboguttata
Osteocephalus mutabor
Osteocephalus buckleyi
Osteocephalus cabrerai
Osteocephalus verruciger
Osteocephalus leprieurii
Osteocephalus planiceps
Osteocephalus oophagus
Osteocephalus taurinus
Scinax clade
Dendropsophus clade
Lophiohylini
To Figure A3.1
To Figure A3.3
60
50
40
30
20
10
0
Younger divergence dates (Mya)

Figure A3.3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Middle American clade
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Acris gryllus
Pseudacris cadaverina
Pseudacris regilla
Pseudacris crucifer
Pseudacris ocularis
Pseudacris ornata
Pseudacris illinoensis
Pseudacris streckeri
Pseudacris brachyphona
Pseudacris brimleyi
Pseudacris nigrita
Pseudacris feriarum
Pseudacris feriarum2
Pseudacris kalmi
Pseudacris triseriata
Pseudacris maculata
Pseudacris clarkii
Pseudacris triseriata2
Exerodonta perkinsi
Exerodonta melanomma
Exerodonta abdivita
Exerodonta sumichrasti
Exerodonta chimalapa
Exerodonta smaragdina
Exerodonta xera
Plectrohyla chrysopleura
Plectrohyla glandulosa
Plectrohyla guatemalensis
Plectrohyla matudai
Plectrohyla siopela
Plectrohyla arborescandens
Plectrohyla cyclada
Plectrohyla ameibothalame
Plectrohyla bistincta
Plectrohyla pentheter
Plectrohyla calthula
Ecnomiohyla miotympanum
Ecnomiohyla miliara
Ecnomiohyla minera
Bromeliohyla bromeliacia
Duellmanohyla soralia
Ptychohyla salvadorensis
Duellmanohyla rufioculis
Duellmanohyla uranochroa
Ptychohyla spinipollex
Ptychohyla dendrophasma
Ptychohyla hypomykter
Ptychohyla euthysanota
Ptychohyla sp.
Ptychohyla leonhardschultzei
Ptychohyla zophodes
Megastomatohyla mixe
Charadrahyla taeniopus
Charadrahyla nephila
Tlalocohyla smithii
Tlalocohyla picta
Tlalocohyla loquax
Tlalocohyla godmani
Isthmohyla pseudopuma
Isthmohyla zeteki
Isthmohyla lancasteri
Isthmohyla rivularis
Isthmohyla tica
Diaglena spatulata
Anotheca spinosa
Triprion petasatus
Smilisca baudinii
Smilisca sordida
Smilisca sila
Smilisca fodiens
Smilisca puma
Smilisca cyanosticta
Smilisca phaeota
Hyla annectans
Hyla chinensis
Hyla meridionalis
Hyla savignyi
Hyla arborea
Hyla cinerea
Hyla squirella
Hyla andersoni
Hyla femoralis
Hyla gratiosa
Hyla avivoca
Hyla chrysocelis
Hyla versicolor
Hyla japonica
Hyla walkeri
Hyla arenicolor
Hyla wrightorum
Hyla eximia
Hyla plicata
Hyla euphorbiacea
50
40
30
20
10
0
Younger divergence dates (Mya)

Figure A3.4. Effect of community size on the power of ROTI null model analyses. The vertical axis is represented as 1 – *P*, or one minus the *P*-value from the likelihood ratio test (i.e., values ≥ 0.95 favor rejecting the null model). Thus, these are analogous to power curves, but are different in that power curves instead compare the proportion of overlap of an alternative distribution with that of a null distribution. Note that we varied the ROTI continuously from 0.0 to 1.0 to aid visual demonstration of the change in power, but this also means that many of these ROTIs correspond to fractions of ISE events per community (especially in smaller communities), so it should be understood that many of the values along these curves are only of theoretical interest.

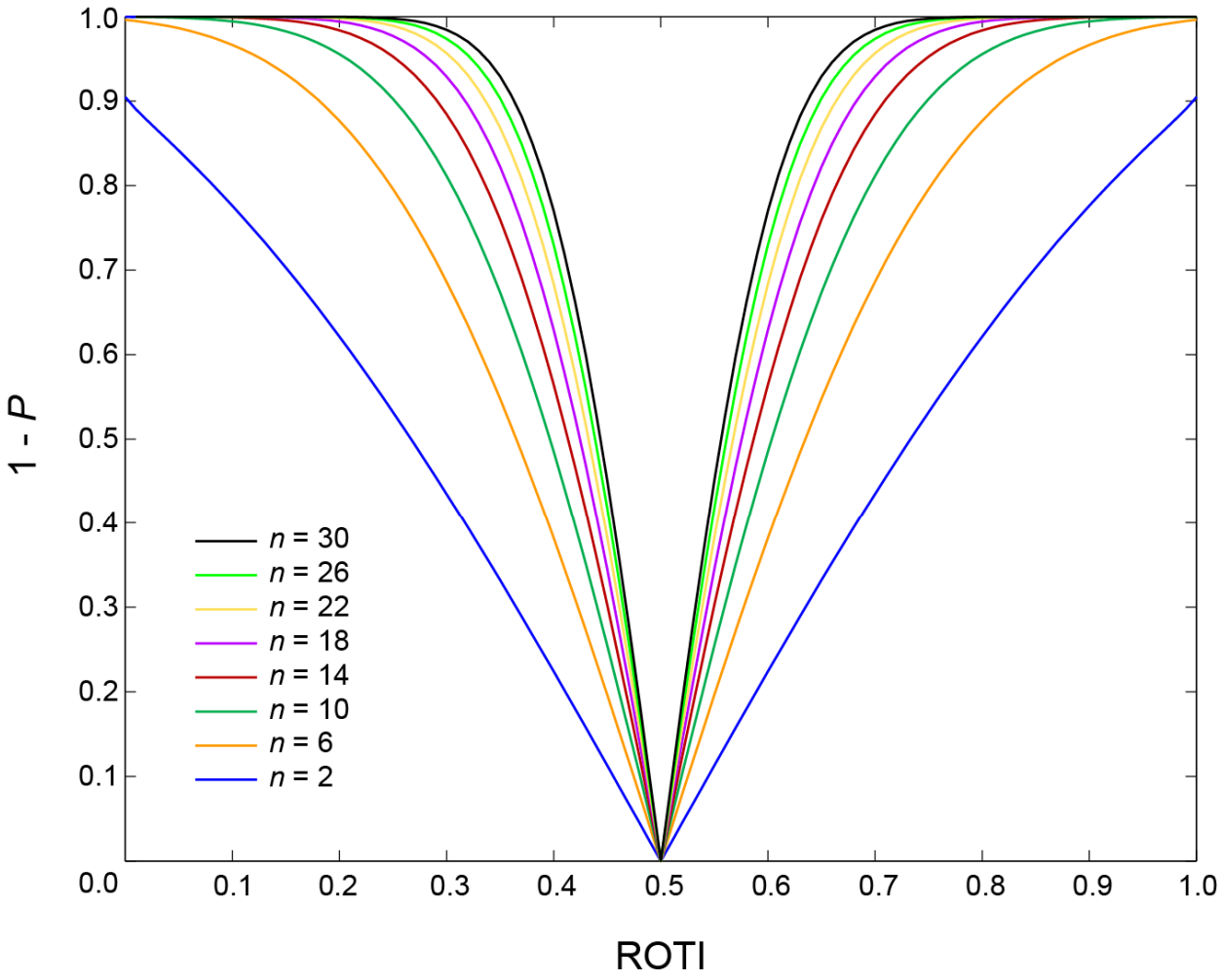
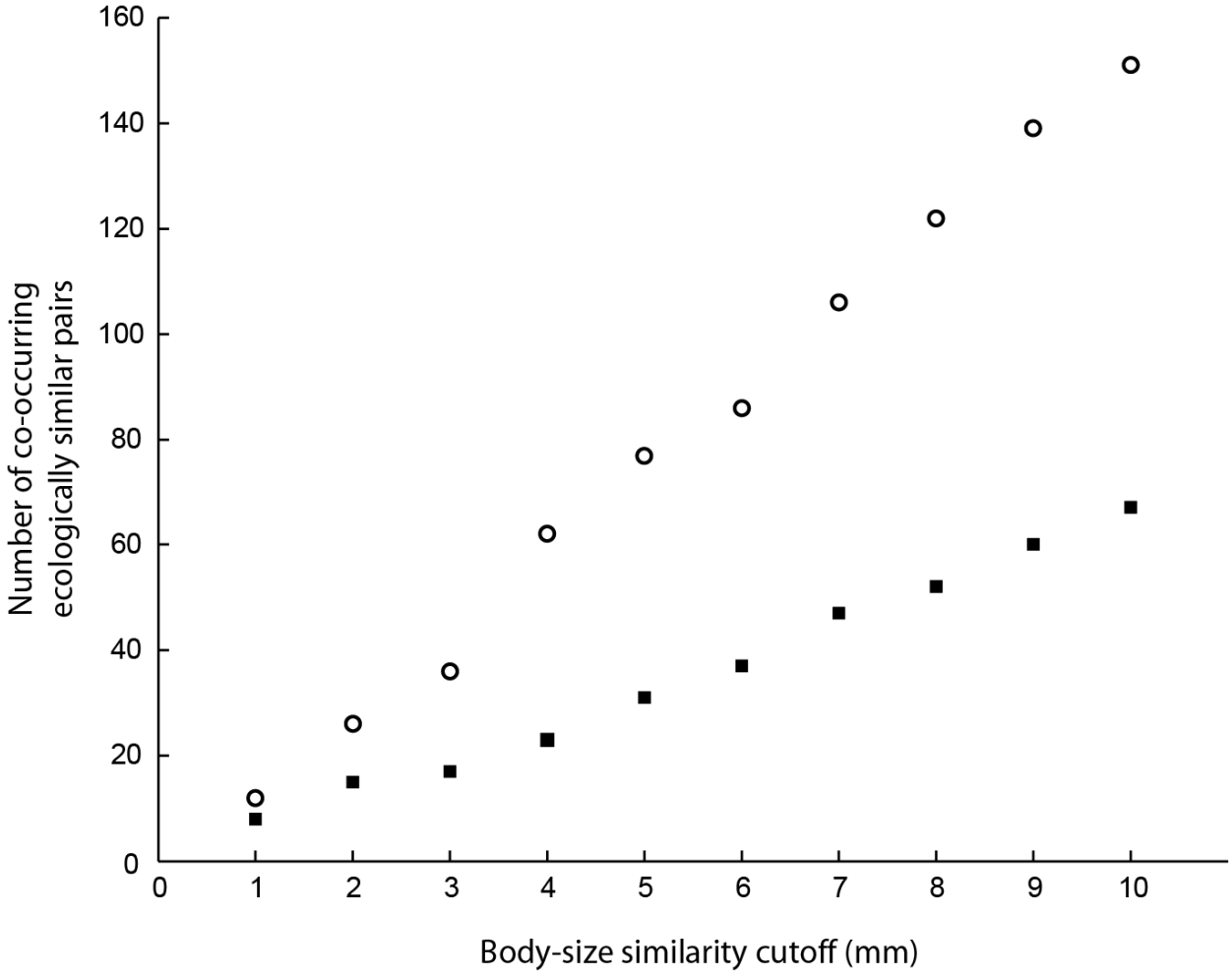


Figure A3.5. Results of varying the body-size cutoff for our ecological similarity analyses. Even under very stringent similarity criteria (e.g. same larval habitat and body sizes within 1 or 2 mm), we see many instances of similar species co-occurring (open circles), with many of those co-occurrences a consequence of independent colonizations of Middle America (opaque squares).



Appendix 4: Species means for performance and morphology from Chapter 4.

Table A4.1. Performance data (species mean ± 1 standard error).

Location	Species	Jumping performance				
		N	Peak velocity (m/s)	Peak acceleration (m/s^2)	Peak power (W/kg)	Angle (º)
Fogg Dam, NT, Australia						
	Limnodynastes convexiusculus	5	2.11±0.08	60.82±4.20	78.56±5.82	37.00±2.20
	Litoria australis	6	2.66±0.09	50.19±2.10	99.04±7.70	40.21±6.86
	Litoria bicolor	7	2.61±0.09	96.36±5.17	181.63±19.20	35.78±3.97
	Litoria caerulea	6	2.55±0.11	39.42±3.48	71.97±9.03	45.12±3.61
	Litoria dahlii	8	2.61±0.07	62.53±3.69	112.63±10.45	41.23±4.99
	Litoria inermis	1	2.74	85.36	163.83	38.87
	Litoria longipes	6	2.07±0.09	57.06±4.62	79.12±8.11	33.51±3.49
	Litoria nasuta	7	3.87±0.12	137.91±7.01	367.81±39.84	47.38±2.45
	Litoria pallida	2	3.58±0.57	120.08±23.37	295.17±101.44	44.42±3.21
	Litoria rothii	6	3.36±0.11	90.20±6.41	213.83±15.90	48.48±6.14
	Litoria rubella	6	2.13±0.05	69.83±3.22	101.00±7.20	39.95±4.76
	Litoria tornieri	8	3.14±0.07	123.03±5.14	255.55±14.51	43.15±2.57
	Platyplectrum ornatum	6	2.12±0.09	81.52±6.02	111.89±13.34	47.87±4.81
	Uperloia lithomoda	3	1.21±0.06	50.03±1.76	32.98±3.12	35.91±3.26
Baoshan, Yunnan, China						
	Amolops tuberodepressus	5	2.32±0.15	55.48±6.05	79.14±2.74	26.64±5.48
	Babina pleuraden	6	2.65±0.05	76.46±3.80	120.35±6.74	42.39±2.45
	Calluella yunnanensis	1	1.98	71.17	89.95	35.03
	Chiromantis doriae	5	2.14±0.07	67.80±6.29	94.97±10.83	29.21±4.57
	Duttaphrynus melanostictus	3	1.10±0.20	20.69±6.45	15.63±5.85	32.21±3.34
	Hyla annectans	5	1.81±0.06	47.03±3.73	57.80±8.82	32.78±2.24

Microhyla ornata	5	2.51±0.19	108.23±2.21	175.95±15.69	47.28±3.21
Nanorana yunnanensis	1	2.68	57.07	98.28	32.93
Odorrana grahami	6	3.37±0.12	73.68±2.09	148.16±7.15	31.10±2.07
Rhacophorus dugritei	5	1.73±0.03	35.59±2.38	41.92±2.37	21.52±1.57
Rhacophorus rhodopus	6	2.02±0.13	43.02±2.86	64.68±6.98	38.28±4.62
Leticia, Amazonas, Colombia					
Adenomera hylaedactyla	5	2.10±0.09	90.08±3.82	121.35±4.86	39.52±7.33
Allobates femoralis	1	2.26	114.54	168.16	37.86
Ameerega trivittata	2	2.12±0.29	59.60±16.86	86.30±28.71	38.38±1.32
Chiasmocleis bassleri	5	1.97±0.04	80.78±3.95	108.62±5.79	35.80±2.89
Dendropsophus rhodopeplus	1	2.54	98.05	169.77	33.10
Dendropsophus sarayacuensis	7	2.96±0.14	124.14±8.85	251.90±30.72	44.29±1.74
Dendropsophus triangulum	7	2.63±0.09	101.10±3.15	178.95±10.20	33.26±3.66
Hamptophryne boliviana	3	1.95±0.07	82.51±7.28	102.35±13.35	42.13±8.32
Hypsiboas hobbsi	7	2.43±0.07	60.76±3.90	104.37±8.26	34.59±2.93
Hypsiboas lanciformis	8	3.35±0.09	64.57±3.89	148.58±7.93	37.11±3.12
Hypsiboas punctatus	7	2.30±0.08	54.85±5.68	79.23±10.87	30.27±1.41
Leptodactylus leptodactyloides	7	2.38±0.10	91.12±10.41	142.45±21.31	37.91±3.24
Leptodactylus rhodomystax	8	2.49±0.05	56.16±2.83	91.26±4.89	34.95±2.72
Oreobates quixensis	4	2.72±0.09	78.83±6.02	137.43±11.83	34.95±1.73
Osteocephalus planiceps	6	3.61±0.10	84.23±9.27	219.74±23.00	33.62±3.20
Rhinella margaritifera	7	1.72±0.06	35.18±1.98	38.04±2.36	38.95±2.39
Rhinella proboscidea	2	1.34±0.10	28.06±1.06	23.61±2.20	37.59±13.94
Scinax ruber	6	2.72±0.09	92.82±3.09	169.74±6.20	30.64±1.91
Sphaenorhynchus lacteus	1	2.47	61.04	107.58	28.46

Location	Species	Swimming performance				Cling performance	
		N	Peak velocity (m/s)	Peak acceleration (m/s^2)	Peak power (W/kg)	*N*	Maximum angle (º)
Fogg Dam, NT, Australia							
	Limnodynastes convexiusculus	5	0.82±0.04	23.71±3.28	12.88±1.79	5	84.2±9.66
	Litoria australis	6	1.12±0.07	25.19±2.00	18.74±2.24	6	59.0±2.86
	Litoria bicolor	7	1.29±0.03	42.46±4.22	37.29±4.05	7	180.0±0.00
	Litoria caerulea	6	0.97±0.06	19.66±1.96	12.61±1.71	6	146.3±8.47
	Litoria dahlii	8	1.73±0.10	44.97±4.21	52.71±7.70	8	65.4±3.71
	Litoria inermis	1	1.20	53.80	39.32	1	127.0
	Litoria longipes	6	0.75±0.06	18.43±3.20	9.59±2.30	6	79.3±8.64
	Litoria nasuta	7	1.78±0.07	45.99±3.75	55.86±5.60	7	125.1±3.49
	Litoria pallida	2	1.50±0.21	48.89±13.18	48.65±18.19	2	110.0±32.00
	Litoria rothii	6	1.36±0.09	32.46±4.56	31.13±5.96	6	166.3±4.58
	Litoria rubella	6	0.91±0.03	29.02±1.79	17.82±1.52	6	179.8±0.17
	Litoria tornieri	8	1.70±0.07	51.01±5.23	55.41±6.95	8	160.9±7.32
	Platyplectrum ornatum	6	0.92±0.04	29.06±5.06	16.75±3.57	6	101.5±11.80
	Uperloia lithomoda	3	0.34±0.00	13.20±2.55	3.12±0.70	3	167.7±7.22
Baoshan, Yunnan, China							
	Amolops tuberodepressus	4	1.49±0.10	36.37±6.44	36.20±7.75	5	117.0±4.74
	Babina pleuraden	6	1.39±0.11	39.22±5.41	36.86±7.74	6	78.5±6.60
	Calluella yunnanensis	1	0.71	29.00	12.37	1	82.0
	Chiromantis doriae	5	1.03±0.05	35.07±4.32	25.32±3.64	5	180.0±0.00
	Duttaphrynus melanostictus	5	0.44±0.06	7.85±2.09	2.16±0.66	5	36.6±3.33
	Hyla annectans	5	0.71±0.05	17.64±1.26	8.68±0.99	5	151.8±4.78
	Microhyla ornata	5	1.11±0.05	42.91±8.10	32.29±9.46	5	159.0±12.60
	Nanorana yunnanensis	3	1.34±0.35	35.22±5.88	32.32±14.84	3	63.7±13.25

Odorrana grahami	6	2.05±0.10	42.63±4.59	56.89±6.43	6	68.3±2.56
Rhacophorus dugritei	5	0.77±0.12	20.13±3.52	12.12±4.40	5	156.2±6.55
Rhacophorus rhodopus	6	0.88±0.05	21.36±1.41	12.82±1.34	6	175.8±3.60
Leticia, Amazonas, Colombia						
Adenomera hylaedactyla	5	0.84±0.08	22.85±2.63	14.20±4.16	5	144.0±7.06
Allobates femoralis	1	0.91	22.74	12.31	1	172.0
Ameerega trivittata	2	1.02±0.16	21.26±3.39	15.24±3.70	2	83.0±1.00
Chiasmocleis bassleri	5	0.70±0.04	26.78±5.28	12.22±3.09	5	180.0±0.00
Dendropsophus rhodopeplus	1	1.22	41.73	28.32	1	180.0
Dendropsophus sarayacuensis	7	1.25±0.05	39.32±2.39	33.12±3.06	7	180.0±0.00
Dendropsophus triangulum	7	1.12±0.05	25.92±2.65	18.76±1.99	7	180.0±0.00
Hamptophryne boliviana	4	0.82±0.09	23.23±3.20	12.48±2.38	4	170.8±9.25
Hypsiboas hobbsi	7	1.64±0.11	36.31±3.58	43.33±6.89	7	176.6±2.57
Hypsiboas lanciformis	8	1.48±0.11	28.05±3.75	29.77±6.48	8	125.4±2.74
Hypsiboas punctatus	7	1.12±0.05	25.99±2.53	19.80±2.70	7	180.0±0.00
Leptodactylus leptodactyloides	7	1.25±0.09	36.07±4.38	30.40±5.43	7	102.4±10.01
Leptodactylus rhodomystax	8	1.39±0.04	28.18±1.60	25.58±2.08	8	48.5±2.23
Oreobates quixensis	4	1.17±0.09	38.47±8.87	31.96±6.07	4	76.5±9.91
Osteocephalus planiceps	6	1.59±0.15	28.69±3.63	32.59±7.01	6	131.3±2.92
Rhinella margaritifera	7	0.53±0.03	8.44±1.21	3.11±0.60	7	59.6±3.52
Rhinella proboscidea	2	0.46±0.11	9.12±1.76	2.84±1.13	2	87.0±22.00
Scinax ruber	6	1.12±0.09	30.66±3.96	23.47±5.15	6	169.8±6.46
Sphaenorhynchus lacteus	1	1.20	29.62	24.73	1	138.0

Table A4.2. Morphological data (species mean ± 1 standard error). First 10 variables (from SUL to hand) are in mm. Relative leg mass is a proportion. Metatarsal tubercle, foot webbing, toe tip, and finger tip are in mm^2. See main text for variable descriptions.

Location	Species	*N*	SUL	Femur	Tibiofibula	Metatarsal	Foot
Fogg Dam, NT, Australia							
	Limnodynastes convexiusculus	5	44.01±2.07	18.99±0.73	18.38±0.88	10.00±0.46	19.96±0.65
	Litoria australis	6	68.46±1.58	34.38±0.69	32.41±0.70	16.28±0.50	28.24±0.76
	Litoria bicolor	7	25.74±0.66	12.13±0.37	12.68±0.41	6.54±0.23	9.39±0.23
	Litoria caerulea	6	73.44±1.60	32.57±0.39	31.16±0.21	17.28±0.44	28.42±0.43
	Litoria dahlii	8	53.97±1.61	26.87±0.96	26.58±1.00	13.20±0.55	26.19±1.02
	Litoria inermis	1	33.03	16.66	17.98	8.94	15.64
	Litoria longipes	6	41.67±1.40	18.29±0.62	16.45±0.54	8.72±0.36	16.99±0.66
	Litoria nasuta	7	37.55±0.58	20.82±0.34	24.33±0.58	11.56±0.28	21.32±0.52
	Litoria pallida	2	35.36±0.90	18.19±0.92	20.88±0.88	9.57±0.82	16.85±0.64
	Litoria rothii	6	45.19±0.70	23.30±0.48	23.94±0.31	11.81±0.21	19.12±0.51
	Litoria rubella	6	30.44±0.36	12.48±0.07	11.84±0.07	6.38±0.13	10.82±0.17
	Litoria tornieri	8	30.74±0.26	16.83±0.18	18.49±0.23	8.48±0.14	15.77±0.14
	Platyplectrum ornatum	6	30.89±1.59	15.30±0.97	14.22±0.73	5.84±0.45	14.85±0.85
	Uperloia lithomoda	1	23.88±0.23	8.92±0.16	7.81±0.11	4.72±0.21	8.74±0.23
Baoshan, Yunnan, China							
	Amolops tuberodepressus	5	49.95±3.84	27.87±1.59	29.14±1.44	13.92±0.76	26.62±1.92
	Babina pleuraden	6	45.22±1.54	21.86±0.42	21.82±0.43	10.87±0.20	24.42±0.51
	Calluella yunnanensis	1	33.19	16.19	16.02	7.52	17.67
	Chiromantis doriae	5	26.49±0.77	12.14±0.48	12.66±0.48	7.37±0.39	11.54±0.54
	Duttaphrynus melanostictus	5	81.16±13.47	32.69±4.50	30.75±4.69	18.70±2.80	31.28±5.10
	Hyla annectans	5	30.20±1.01	14.53±0.47	14.60±0.47	7.95±0.22	13.74±0.53
	Microhyla ornata	5	23.62±0.41	10.65±0.21	12.05±0.34	5.60±0.33	12.42±0.38
	Nanorana yunnanensis	3	73.53±12.05	38.89±5.02	37.29±5.44	20.18±3.17	35.21±4.72
	Odorrana grahami	6	64.57±1.08	37.94±1.21	39.76±0.70	18.74±0.44	37.43±0.71

	Rhacophorus dugritei	5	39.67±1.39	18.25±0.43	16.47±0.30	8.60±0.28	17.71±0.38
	Rhacophorus rhodopus	6	35.20±0.30	16.95±0.24	16.48±0.11	8.06±0.26	15.02±0.25
Leticia, Amazonas, Colombia							
	Adenomera hylaedactyla	5	24.48±0.66	10.41±0.46	11.70±0.30	6.67±0.35	13.18±0.54
	Allobates femoralis	1	26.96	10.96	12.66	6.20	11.82
	Ameerega trivittata	2	38.97±2.90	17.83±1.61	20.25±0.89	10.76±0.55	18.21±1.18
	Chiasmocleis bassleri	5	20.43±1.72	8.83±0.75	9.52±0.55	5.64±0.49	8.79±0.41
	Dendropsophus rhodopeplus	1	21.82	10.76	11.94	6.61	9.03
	Dendropsophus sarayacuensis	7	25.83±0.47	13.04±0.31	14.17±0.39	8.10±0.17	11.63±0.28
	Dendropsophus triangulum	7	22.77±0.57	11.27±0.21	11.99±0.38	6.68±0.17	10.17±0.36
	Hamptophryne boliviana	4	22.25±0.78	10.21±0.56	10.51±0.38	6.26±0.28	11.52±0.41
	Hypsiboas hobbsi	7	40.56±0.70	20.50±0.21	21.27±0.33	11.98±0.28	15.60±0.33
	Hypsiboas lanciformis	8	66.09±0.80	35.77±0.83	39.50±0.93	22.70±0.51	29.35±0.72
	Hypsiboas punctatus	7	35.03±0.66	17.75±0.49	17.56±0.24	10.09±0.09	14.56±0.29
	Leptodactylus leptodactyloides	7	32.73±1.26	15.03±0.78	16.03±0.97	8.38±0.45	18.19±0.81
	Leptodactylus rhodomystax	8	75.24±3.00	35.35±1.25	36.39±1.38	17.52±0.56	37.53±1.32
	Oreobates quixensis	4	39.31±3.92	20.15±2.02	21.21±1.99	10.18±1.02	20.11±1.83
	Osteocephalus planiceps	6	68.11±4.79	35.00±2.49	38.45±2.68	18.05±1.41	28.19±2.16
	Rhinella margaritifera	7	51.96±0.56	23.48±0.37	22.94±0.40	12.22±0.15	18.69±0.15
	Rhinella proboscidea	2	41.06±9.58	18.50±4.92	17.62±4.50	9.38±2.51	14.80±3.69
	Scinax ruber	6	30.79±0.60	13.74±0.27	15.04±0.32	8.64±0.27	12.70±0.24
	Sphaenorhynchus lacteus	3	38.86	19.20	19.02	9.49	16.46

Location	Species	*N*	Head Length	Head Width	Humerus	Radioulna	Hand
Fogg Dam, NT, Australia							
	Limnodynastes convexiusculus	5	15.26±0.43	16.51±0.55	7.76±0.30	8.69±0.33	10.16±0.30
	Litoria australis	6	26.61±0.49	30.48±0.52	11.88±0.29	14.64±0.37	16.96±0.49
	Litoria bicolor	7	7.72±0.23	7.20±0.21	4.30±0.17	3.63±0.18	6.18±0.19
	Litoria caerulea	6	20.76±0.59	25.22±0.83	13.17±0.17	13.34±0.45	21.12±0.41

Litoria dahlii	8	16.69±0.46	16.94±0.42	9.14±0.25	9.88±0.41	13.40±0.46
Litoria inermis	1	11.48	11.41	5.41	6.35	8.27
Litoria longipes	6	14.06±0.39	16.92±0.32	6.30±0.24	9.80±0.42	10.00±0.42
Litoria nasuta	7	13.57±0.20	12.14±0.17	6.86±0.21	7.60±0.21	9.68±0.27
Litoria pallida	2	12.28±0.31	11.67±0.44	7.00±0.05	7.41±0.29	9.41±0.68
Litoria rothii	6	13.72±0.30	14.44±0.22	8.74±0.47	8.21±0.17	12.24±0.47
Litoria rubella	6	7.21±0.16	8.14±0.10	5.14±0.27	4.87±0.12	7.13±0.05
Litoria tornieri	8	10.98±0.14	10.73±0.09	5.69±0.11	6.42±0.17	7.84±0.11
Platyplectrum ornatum	6	9.46±0.43	12.23±0.60	6.30±0.55	6.71±0.59	7.64±0.54
Uperloia lithomoda	1	5.86±0.11	7.63±0.15	4.53±0.06	4.85±0.19	5.70±0.10
Baoshan, Yunnan, China						
Amolops tuberodepressus	5	13.77±0.80	15.51±0.88	10.13±0.60	10.71±0.57	16.62±1.12
Babina pleuraden	6	14.57±0.70	15.40±0.57	6.85±0.24	7.62±0.21	11.09±0.22
Calluella yunnanensis	1	7.43	10.59	5.87	6.54	11.02
Chiromantis doriae	5	7.39±0.29	7.93±0.37	4.88±0.49	5.00±0.20	7.50±0.45
Duttaphrynus melanostictus	5	21.67±2.94	29.30±4.99	13.63±1.83	18.97±2.82	19.49±2.90
Hyla annectans	5	8.47±0.08	9.81±0.37	5.83±0.20	6.35±0.38	9.59±0.37
Microhyla ornata	5	6.11±0.25	7.64±0.20	4.13±0.13	4.22±0.21	6.49±0.72
Nanorana yunnanensis	3	23.15±3.57	29.05±4.74	11.79±1.43	13.42±1.82	19.51±2.83
Odorrana grahami	6	20.03±0.88	22.05±0.54	13.80±0.55	14.87±0.31	19.37±0.27
Rhacophorus dugritei	5	12.03±0.52	14.74±0.34	6.89±0.28	8.87±0.35	12.53±0.34
Rhacophorus rhodopus	6	10.02±0.19	12.16±0.19	6.79±0.23	6.80±0.24	10.26±0.31
Leticia, Amazonas, Colombia						
Adenomera hylaedactyla	5	7.78±0.32	8.49±0.22	5.20±0.26	4.54±0.10	5.73±0.19
Allobates femoralis	1	8.78	8.66	6.16	6.20	6.82
Ameerega trivittata	2	10.53±0.53	10.90±0.62	10.16±0.55	9.86±0.16	11.02±0.63
Chiasmocleis bassleri	5	4.45±0.31	5.52±0.30	3.98±0.47	3.79±0.46	4.00±0.42
Dendropsophus rhodopeplus	1	6.37	7.25	5.13	4.01	5.56
Dendropsophus sarayacuensis	7	7.04±0.14	9.01±0.11	5.30±0.16	5.11±0.07	7.38±0.20
Dendropsophus triangulum	7	6.65±0.14	7.82±0.23	4.38±0.13	5.14±0.18	6.86±0.22

	Hamptophryne boliviana	4	5.80±0.15	7.42±0.17	4.46±0.28	4.13±0.26	6.30±0.33
	Hypsiboas hobbsi	7	11.62±0.15	14.15±0.15	8.01±0.28	8.26±0.25	12.02±0.13
	Hypsiboas lanciformis	8	21.85±0.29	20.24±0.26	12.16±0.35	12.31±0.22	19.04±0.37
	Hypsiboas punctatus	7	10.14±0.25	12.21±0.22	7.38±0.21	6.92±0.18	10.43±0.11
	Leptodactylus leptodactyloides	7	10.11±0.39	11.46±0.48	7.24±0.26	6.19±0.25	8.78±0.43
	Leptodactylus rhodomystax	8	25.55±1.13	29.99±1.43	16.64±0.81	17.68±0.75	18.60±0.62
	Oreobates quixensis	4	13.24±1.59	16.07±1.74	9.29±0.89	9.49±0.86	11.04±1.10
	Osteocephalus planiceps	6	21.07±1.64	21.53±1.50	12.26±0.87	14.44±1.10	20.33±1.78
	Rhinella margaritifera	7	15.36±0.24	18.36±0.26	11.10±0.41	14.09±0.14	13.58±0.22
	Rhinella proboscidea	2	12.34±2.41	14.39±2.85	9.64±1.14	11.11±2.44	10.65±2.09
	Scinax ruber	6	9.50±0.24	10.01±0.22	5.47±0.20	5.69±0.19	7.77±0.15
	Sphaenorhynchus lacteus	3	7.93	11.64	7.76	7.33	11.04

Location	Species	*N*	Relative leg mass	Metatarsal tubercle	Foot webbing	Toe tip	Finger tip
Fogg Dam, NT, Australia							
	Limnodynastes convexiusculus	5	0.065±0.004	2.51±0.46	0.85±0.19	3.24±0.18	2.28±0.06
	Litoria australis	6	0.073±0.002	6.81±0.38	22.14±3.18	8.64±0.64	6.01±0.56
	Litoria bicolor	7	0.063±0.003	0.31±0.03	6.70±0.38	3.36±0.21	3.02±0.18
	Litoria caerulea	6	0.043±0.002	4.80±0.39	64.73±3.90	49.21±4.39	52.93±4.58
	Litoria dahlii	8	0.080±0.004	2.57±0.23	130.96±11.46	6.26±0.57	3.53±0.15
	Litoria inermis	1	0.083	0.99	14.16	1.76	0.83
	Litoria longipes	6	0.043±0.003	2.37±0.12	4.16±0.54	3.71±0.32	3.26±0.21
	Litoria nasuta	7	0.108±0.004	1.36±0.18	24.88±1.74	4.67±0.34	3.09±0.22
	Litoria pallida	2	0.103±0.006	1.14±0.32	22.55±2.07	2.67±0.14	2.27±0.62
	Litoria rothii	6	0.068±0.002	1.35±0.08	52.45±7.98	14.05±0.74	14.65±1.06
	Litoria rubella	6	0.057±0.003	0.55±0.05	4.81±0.30	4.63±0.28	4.72±0.12
	Litoria tornieri	8	0.091±0.003	0.98±0.10	10.93±0.90	2.12±0.15	1.67±0.17
	Platyplectrum ornatum	6	0.070±0.002	2.18±0.42	8.89±1.95	2.66±0.60	1.93±0.14
	Uperloia lithomoda	1	0.044±0.002	2.08±0.04	0.79±0.09	0.86±0.10	0.52±0.04

Baoshan, Yunnan, China						
Amolops tuberodepressus	5	0.087±0.006	2.78±0.39	72.75±9.70	17.18±2.79	18.02±1.47
Babina pleuraden	6	0.086±0.003	2.01±0.21	16.29±2.07	4.27±0.53	2.59±0.34
Calluella yunnanensis	1	0.063	3.54	22.29	2.11	1.86
Chiromantis doriae	5	0.051±0.009	0.31±0.08	1.61±0.25	3.54±0.54	4.25±0.72
Duttaphrynus melanostictus	5	0.046±0.002	10.29±3.24	24.91±6.21	12.43±4.19	13.01±4.27
Hyla annectans	5	0.025±0.004	0.75±0.02	5.53±0.73	4.05±0.42	4.40±0.39
Microhyla ornata	5	0.070±0.005	0.58±0.03	0.77±0.16	1.64±0.25	1.45±0.12
Nanorana yunnanensis	3	0.082±0.009	8.17±1.07	157.84±49.99	12.63±3.99	9.78±1.67
Odorrana grahami	6	0.104±0.003	4.18±0.52	198.20±14.48	15.82±0.58	9.92±0.50
Rhacophorus dugritei	5	0.039±0.004	1.64±0.12	9.64±1.86	10.14±1.67	12.39±0.88
Rhacophorus rhodopus	6	0.029±0.003	0.98±0.07	24.02±2.26	7.80±0.48	9.95±0.84
Leticia, Amazonas, Colombia						
Adenomera hylaedactyla	5	0.079±0.004	0.48±0.05	0.15±0.04	1.61±0.15	0.84±0.13
Allobates femoralis	1	0.075	0.76	0.66	3.89	2.15
Ameerega trivittata	2	0.076±0.004	1.63±0.15	0.37±0.03	5.81±0.14	4.35±0.34
Chiasmocleis bassleri	5	0.064±0.006	0.22±0.08	0.09±0.02	1.71±0.25	0.53±0.15
Dendropsophus rhodopeplus	1	0.063	0.31	8.54	2.96	3.66
Dendropsophus sarayacuensis	7	0.062±0.001	0.56±0.08	12.39±0.61	5.23±0.52	4.88±0.32
Dendropsophus triangulum	7	0.052±0.002	0.42±0.06	11.38±0.84	4.69±0.54	4.16±0.26
Hamptophryne boliviana	4	0.078±0.002	0.67±0.13	0.33±0.04	2.19±0.12	1.36±0.09
Hypsiboas hobbsi	7	0.175±0.114	1.94±0.09	36.29±2.12	11.17±0.48	10.77±0.56
Hypsiboas lanciformis	8	0.087±0.001	2.59±0.15	85.36±3.09	24.10±0.50	23.30±0.56
Hypsiboas punctatus	7	0.047±0.002	0.90±0.09	11.15±0.77	8.56±0.55	8.81±0.34
Leptodactylus leptodactyloides	7	0.090±0.004	1.12±0.07	1.03±0.20	2.55±0.38	1.78±0.30
Leptodactylus rhodomystax	8	0.078±0.005	6.23±0.56	3.85±0.97	14.16±1.82	11.43±1.58
Oreobates quixensis	4	0.082±0.005	1.84±0.44	0.21±0.08	2.63±0.57	2.15±0.37
Osteocephalus planiceps	6	0.090±0.004	4.34±0.67	81.77±13.76	33.08±5.80	37.80±6.44
Rhinella margaritifera	7	0.051±0.002	3.40±0.32	11.41±1.20	6.03±0.58	4.95±0.43

Rhinella proboscidea	2	0.045±0.005	1.93±0.46	8.01±4.50	5.44±1.83	3.84±2.12
Scinax ruber	6	0.055±0.002	0.55±0.05	12.79±1.48	6.87±0.40	6.72±0.36
Sphaenorhynchus lacteus	3	0.062	1.38	36.19	14.55	12.82