

PHYLOGENETIC EVIDENCE FOR COMPETITIVELY DRIVEN DIVERGENCE: BODY-SIZE EVOLUTION IN CARIBBEAN TREEFROGS (HYLIDAE: *OSTEOPILUS*)

Daniel S. Moen^{1,2} and John J. Wiens^{1,3}

¹Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245

²E-mail: dmoen@life.bio.sunysb.edu

³E-mail: wiensj@life.bio.sunysb.edu

Received October 11, 2007

Accepted August 19, 2008

Understanding the role of competition in explaining phenotypic diversity is a challenging problem, given that the most divergent species may no longer compete today. However, convergent evolution of extreme body sizes across communities may offer evidence of past competition. For example, many treefrog assemblages around the world have convergently evolved species with very large and small body sizes. To better understand this global pattern, we studied body-size diversification within the small, endemic radiation of Caribbean treefrogs (*Osteopilus*). We introduce a suite of analyses designed to help reveal the signature of past competition. Diet analyses show that *Osteopilus* are generalist predators and that prey size is strongly associated with body size, suggesting that body-size divergence facilitates resource partitioning. Community assembly models indicate that treefrog body-size distributions in Jamaica and Hispaniola are consistent with expectations from competition. Phylogenetic analyses show that similar body-size extremes in Jamaica and Hispaniola have originated through parallel evolution on each island, and the rate of body-size evolution in *Osteopilus* is accelerated relative to mainland treefrogs. Together, these results suggest that competition may have driven the rapid diversification of body sizes in Caribbean treefrogs to the extremes seen in treefrog communities around the world.

KEY WORDS: Body size, Caribbean, community assembly, competition, diversification, phylogenetic analysis.

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 in-

dicates that competition was important in the past, nor does a lack of competition today prove that it was unimportant in the past. 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. Thus, explaining present-day patterns of phenotypic diversity in communities and clades also requires comparative approaches that address past diversification among species. 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 lacking 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 competitively 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, whereas 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 diversi-

fy 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 use 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 is 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 competitively 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 nonrandom 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. In this study, 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

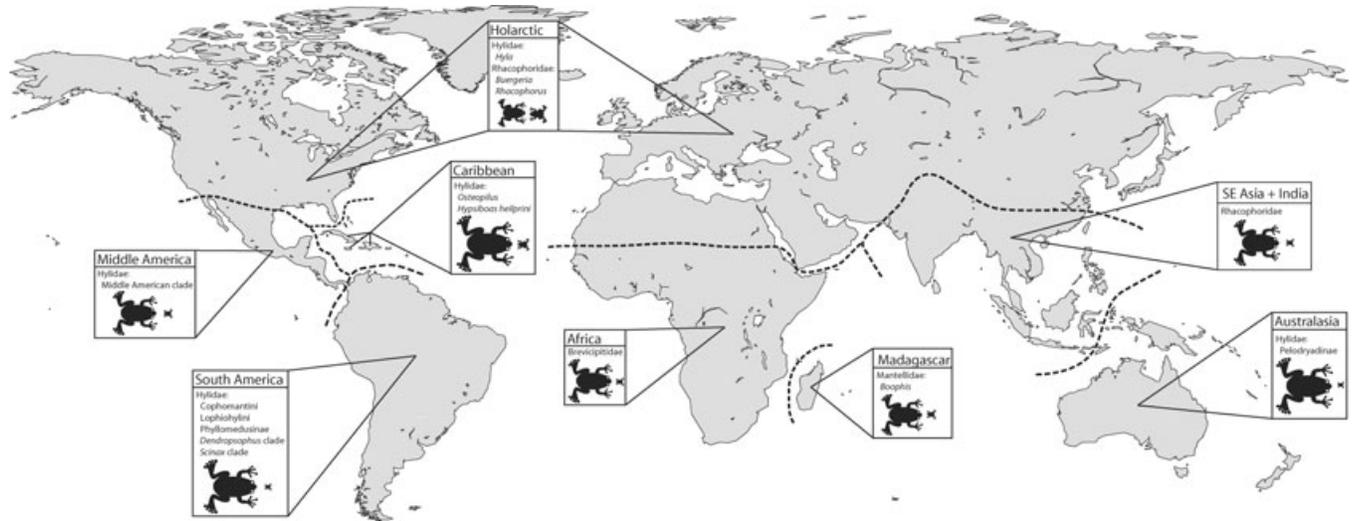


Figure 1. Body-size extremes of treefrog assemblages around the world. Dashed lines delineate approximate boundaries of regions of independent treefrog evolution (see Materials and Methods). Body sizes of cartoon frogs are directly proportional to the body size of the largest and smallest species within 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).

seen in other regions (Fig. 1, Table 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. Most importantly, 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 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; see 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*; nine species total) represent a relatively simple system in which to examine the evolution of body-size extremes. One species (*Osteopilus septentrionalis*) occurs in 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. pulchilineatus*; Hispaniola: *H. heilprini*, *O. dominicensis*, *O. pulchilineatus*, *O. vastus*). In Jamaica 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 1), and have similar body-size distributions (i.e., each island shows an approximately even number of

species across nonoverlapping 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. By 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 nonrandomness 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 in

Table 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 many of the local communities presented here. Clade ages are estimated crown-group ages of the predominant treefrog clades in each region (Caribbean: *Osteopilus* (Hylidae); South America: Hylidae; Middle America: Hylidae; Holarctic: (Hylidae); SE Asia and India: Rhacophoridae; Australasia: Pelodyadinae (Hylidae); 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 figure 3 of Bossuyt et al. (2006).

| Region ¹ | Body size (mm) | | | Difference | Species richness ² | Age of predominant clade (mya) | Reference |
|--|----------------|---------|------------|------------|-------------------------------|--------------------------------|-------------------------------|
| | Smallest | Largest | Difference | | | | |
| Caribbean | 28.7 | 141.9 | 113.2 | 9 | 24.35 | 32.51 | Schwartz and Henderson (1991) |
| 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 | Heyer et al. (1990) |
| Boracéia, Brazil | 25 | 104 | 79 | 26 | | | Duellman (1978) |
| Santa Cecilia, Ecuador | 23 | 132 | 109 | 36 | | | Duellman (1978) |
| Middle America | 22.1 | 110.4 | 88.3 | 153 | 44.72 | 60.65 | Rand and Myers (1990) |
| Barro Colorado Island, Panamá | 27.8 | 113.7 | 85.9 | 10 | | | Duellman (2001) |
| Chamela, Jalisco, México | 28 | 113.7 | 85.7 | 8 | | | Duellman (2001) |
| Holarctic | 33 | 70 | 37 | 31 | 31.85 | 41.65 | Wright (2002) |
| Okfenokee Swamp, United States | 44 | 70 | 26 | 5 | | | Goris and Maeda (2004) |
| Ishigakijima and Iriomotejima, Japan | 37 | 67 | 30 | 4 | | | Tyler et al. (1983) |
| Australasia | 16 | 141 | 125 | 174 | 42.37 | 60.40 | Zweifel (1980) |
| Magela Creek system, Australia | 16 | 110 | 94 | 15 | | | Ziegler et al. (2006) |
| Huon Peninsula, Papua New Guinea | 40 | 141 | 101 | 12 | | | Lloyd et al. (1968) |
| Southeast Asia and India | 16 | 115 | 99 | 283 | 60.00 | 62.80 | Andreone (1994) |
| Phong Nha-Ke Bang National Park, Vietnam | 32 | 115 | 83 | 11 | | | Nussbaum et al. (1999) |
| Nanga Tekalit, Sarawak, Borneo | 35 | 90 | 55 | 10 | | | Drewes (2007) |
| Madagascar | 23 | 103 | 80 | 65 | 63.10 | 66.70 | Drewes and Vindum (1994) |
| Ranomafana National Park | 29 | 103 | 74 | 10 | | | |
| Andohahela National Park | 32 | 103 | 71 | 13 | | | |
| Africa | 20 | 110 | 90 | 242 | 91.00 | | |
| Arabuko-Sokoke Rain forest, Kenya | 21 | 90 | 69 | 12 | | | |
| Impenetrable Forest, Uganda | 21 | 62 | 41 | 15 | | | |

¹Extremes for entire regions include only species endemic to those regions, whereas extremes for local assemblages (indented) include all species.

²Includes only number of native treefrog species.

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 assemblages 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 Supporting Appendix S1.

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 Supporting Appendix S1.

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 “minimum 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 (Schlötter 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 S1 of Supporting Information), 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 Supporting Appendix S2 for specimen numbers). With one exception, between four and 10 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 SVL as a standard measure of body size throughout the article.

RESOURCE-USE DIVERGENCE

Within an island, different species of *Osteopilus* seem to use 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 $N = 4$ to $N = 34$, 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 that we examined contained prey).

For each specimen, we first measured its 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, although 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 ("sample size," i.e., as defined above rather than the total number of prey items in a species). 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

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

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 Futuyama 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 that 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 because 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, because 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 in Jamaica and Hispaniola are each structured nonrandomly, 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 assembly 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 potentially sampling from a postcompetition 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 Supporting Appendix S1). 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 S1 of Supporting Appendix S1. Hypergeometric probabilities of body-size distributions for Jamaica and Hispaniola were cal-

culated by hand. Specific details of the analysis, including the derivation of the probability models, can be found in Supporting Appendix S1.

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 noncentral hypergeometric distribution (McCullagh and Nelder 1989; see Supporting Appendix S1). 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 Supporting Appendix S1 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 (version 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 noncentral 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 competitively 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 in 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 in 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 10 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 Supporting Appendix S1, 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 dataset 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 datasets 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 nine 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 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. S1 and S2 in the Supporting information).

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 of the species (i.e., regardless of sex) as a standard index of body size. 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 Supporting Appendix S1.

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 South American and Caribbean hylids combined. 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 America, 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 in 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 (seven of eight) have a smallest species ≤ 30 mm and a largest species ≥ 100 mm, despite differing species numbers and ages (Table 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 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 the Caribbean, South America, Middle America, Southeast Asia and India, sub-Saharan Africa, Madagascar, and Australasia (Fig. 1).

MORPHOMETRIC ANALYSES

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

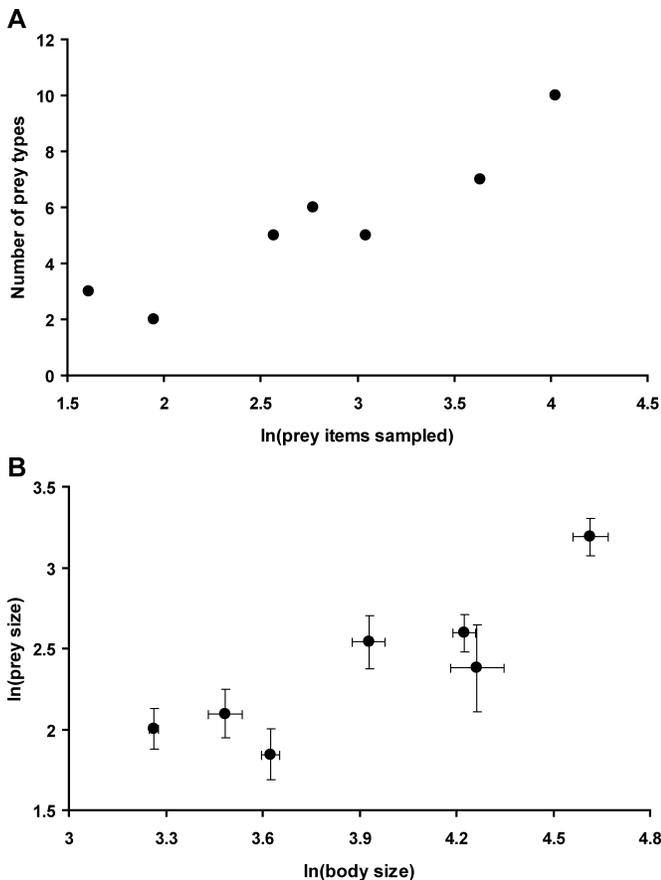


Figure 2. (A) Plot of total number of prey items sampled versus the number of different types of prey (identified to taxonomic order or class) found for each species. (B) Plot of body size versus mean prey size for resource-use analysis. Body size is represented as $\ln(\text{snout-to-vent length in mm})$, and prey size is additionally \ln -transformed. Bars represent one standard error of the mean for both body size and prey size.

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. 2A). Prey type overlap was generally quite high among species (Table S2 in the Supporting Information), with the exception of *O. pulchilineatus* (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). These observations support the idea that *Osteopilus* are dietary generalists that use 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* (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,

Table 2. Results of community assembly analyses: noncentral 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 that exclude 1.0 indicate statistical significance (i.e., when all ψ_i = 1.0, the noncentral model collapses to the standard 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 |
| Noncentral Hypergeometric | -4.83 | 3 | |

P = 0.10.

P < 0.0001; maximum prey size: r = 0.55, P < 0.0001; r_s = 0.61, P < 0.0001). This correlation was even stronger in interspecific correlation analyses of mean treefrog body size and mean prey size (Fig. 2B; 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 in Jamaica and Hispaniola with that of South American hyliids 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), 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). 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

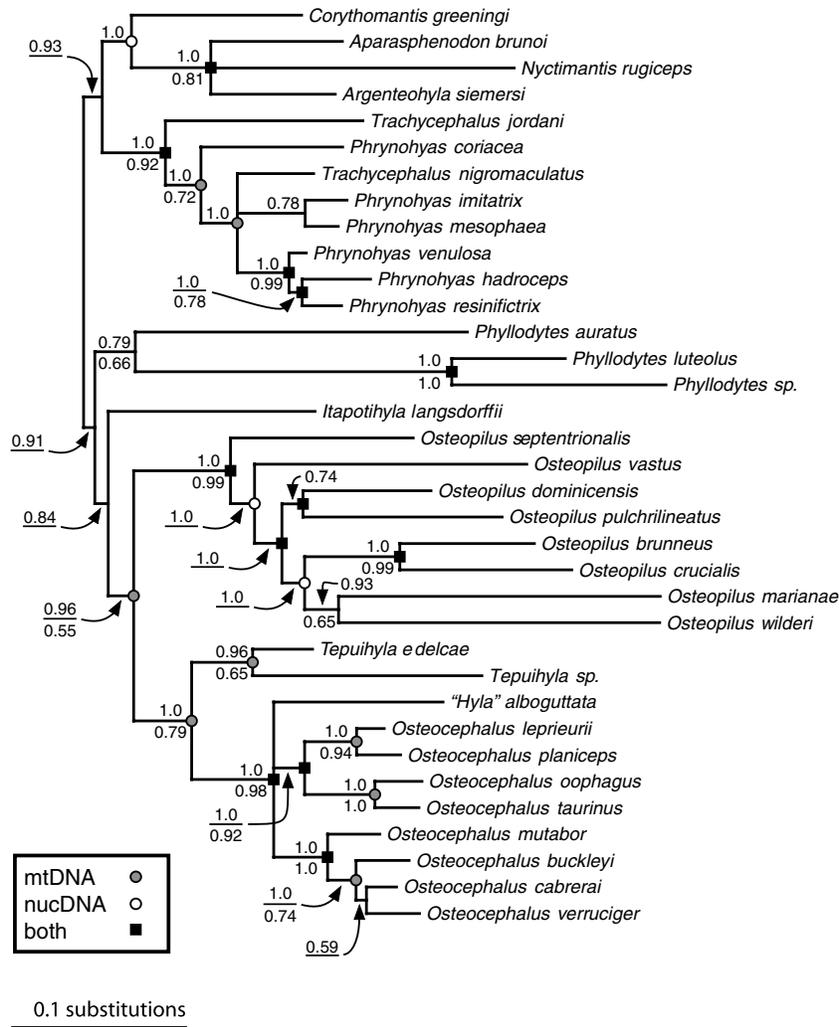


Figure 3. Phylogeny of Lophiohylii (Hylidae) based on combined Bayesian analysis of seven nuclear and six mitochondrial genes. Values above branches indicate the Bayesian Pp, and those below branches indicate parsimony bootstrap proportions for concordant clades. Nodes that were also recovered in separate Bayesian analyses of the mitochondrial and/or nuclear data are labeled with symbols. Unlabeled nodes were unique to the combined data analysis.

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 S1 and S2 of Supporting Appendix S1.

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 (Fig. 3), with no strongly supported incongruence. Separate parsimony analyses of the two datasets 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. 3). Parsimony bootstrap proportions generally were low for deep nodes, but most previously recognized subclades (Faivovich et al. 2005) were strongly supported (Fig. 3).

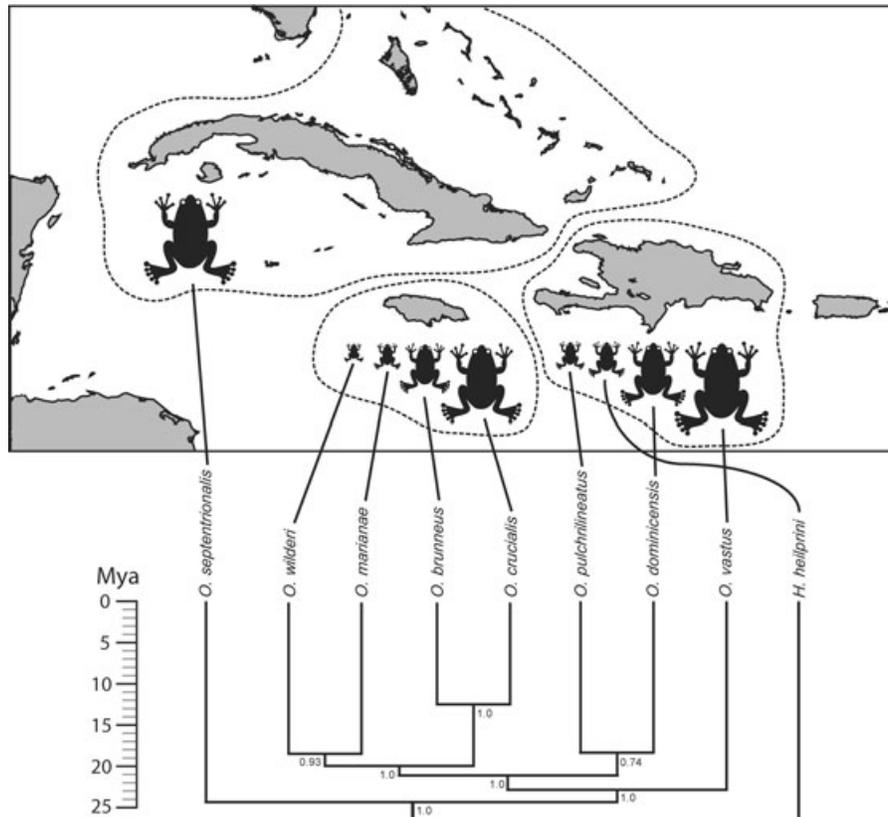


Figure 4. Body-size evolution and biogeography of Greater Antillean treefrogs (*Osteopilus* and *Hypsiboas heilprini*). The phylogeny is from the Bayesian analysis of the combined data (Fig. 3), with branch lengths proportional to time (as determined using penalized-likelihood analysis). The scale bar indicates branch lengths resulting from the younger calibration point in dating analyses, in millions of years ago (mya). Note that the branch leading to *H. heilprini* stems from the South American clade Cophomantini and is not drawn proportional to time, 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.

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*. The Cuban species *O. septentrionalis* is sister to the Jamaica–Hispaniola clade. These results suggest that body-size diversification in Jamaica and

Hispaniola occurred in replicate on each island, as predicted under the model of competitively driven divergence (Fig. 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 $[\ln \text{ mm}]^2$ per million years; see Table 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

Table 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).

| Group | SVL ¹ | Ages ² | | Rates | |
|---|------------------|-------------------|-----------------|--------------|------------|
| | | Younger root | Older root | Younger root | Older root |
| Cophomantini | 53.3 ± 17.4 | 51.67 | 73.55 | 0.00330 | 0.00227 |
| <i>Dendropsophus</i> | 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 |
| <i>Scinax</i> clade | 33.9 ± 8.5 | 53.77 | 75.95 | 0.00237 | 0.00169 |
| Lophiohylini (without <i>Osteopilus</i>) | 57.1 ± 24.5 | 35.90 | 48.59 | 0.00720 | 0.00522 |
| <i>Osteopilus</i> | 86.3 ± 46.1 | 24.35 | 32.51 | 0.01500 | 0.01128 |
| South American hylids ³ | 45.3 ± 20.6 | 64.97 | 92.90 | 0.00404 | 0.00284 |
| | | | LR ⁴ | 9.79 | 10.62 |
| | | | P = | 0.0016 | 0.0008 |

¹Reported as mean (± one standard deviation) SVL of entire clade, calculated as the average of the maximum reported SVL of each species within each clade.

²Ages of the most recent common ancestor of all the species sampled within this study, in millions of years ago. Root categories refer to the two sets of root dates used to calibrate the chronograms for clades (see text for details).

³Includes the Cophomantini, *Dendropsophus*, Phyllomedusinae, *Scinax* clade, and Lophiohylini (without *Osteopilus*)

⁴Likelihood-ratio tests (LR, as defined in Supporting Appendix S1) 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)

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; Ta-

per 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 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. 1; Table 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 use 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). 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 in 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. 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 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, because 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 would be valuable. 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 that occurs both allopatrically and sympatrically with other species of *Osteopilus* (e.g., *O. 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 *O. 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 although 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 *O. 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, in 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 the 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. For example, 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 S6 in the Supporting Information). 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, unpubl. data), 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 assumed 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

Although 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 (Table S6), 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 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 3 have at least 55 species). Our results add to the increasing number of studies that have found a pattern of species diversification with limited phenotypic diversification after an initial diversification of morphotypes, including studies of *Anolis* 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 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 in 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 in both Jamaica and Hispaniola, why are there no native treefrogs in Puerto Rico and only one in 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, *O. 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 article, 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).

ACKNOWLEDGMENTS

We thank S. B. Hedges for his generosity in sharing *Osteopilus* tissues, without which this project would not have been possible. We are grateful to the many other individuals and institutions who provided tissue samples that were used in the phylogenetic analyses, including K. de Queiroz (U.S. National Museum); W. E. Duellman and J. Simmons (University of Kansas); and B. P. Noonan. Morphometric work at the U.S. National Museum was facilitated by K. de Queiroz, W. R. Heyer, R. W. McDiarmid, and K. Tighe. We thank R. M. Brown (University of Kansas), K. de Queiroz (U. S. National Museum), and S. P. Rogers (Carnegie Museum) for specimen loans and permission to examine *Osteopilus* gut contents. DNA sequencing was performed in the Stony Brook MEAD laboratory, which is funded through a National Science Foundation (NSF) instrumentation grant and Stony Brook University. We thank S. B. Munch for help with the community analyses, S. A. Smith for advice in acquiring the molecular data, and W. E. Aguirre, P. Espinosa, D. J. Futuyma, K. H. Kozak, S. Munch, D. K. Padilla, D. W. Pfennig, C. Ulloa, and two anonymous reviewers for useful comments on the manuscript. This work was supported by National Science Foundation (NSF) grant EF-0334923 to JJW and an NSF Graduate Research Fellowship to DSM.

LITERATURE CITED

- Andreone, F. 1994. The amphibians of Ranomafana rain forest, Madagascar: preliminary community analysis and conservation considerations. *Oryx* 28:207–214.
- Arnold, E. N. 2003. A field guide to the reptiles and amphibians of Europe. Princeton Univ. Press, Princeton, NJ.
- Arthur, W. 1987. The niche in competition and evolution. Wiley, New York, NY.
- Barker, J., G. C. Grigg, and M. J. Tyler. 1995. A field guide to Australian frogs. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Berry, P. Y. 1975. Amphibian fauna of peninsular Malaysia. Tropical Press, Kuala Lumpur, Malaysia.
- Bolnick, D. I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* 58:608–618.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulseley, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161:1–28.
- Borror, D. J., and R. E. White. 1970. A field guide to the insects. Houghton-Mifflin, New York, NY.
- Bossuyt, F., R. M. Brown, D. M. Hillis, D. C. Cannatella, and M. C. Milinkovitch. 2006. Phylogeny and biogeography of a cosmopolitan frog radiation: late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. *Syst. Biol.* 55:579–594.
- Brandl, R., A. Kristín, and B. Leisler. 1994. Dietary niche breadth in a local community of passerine birds, an analysis using phylogenetic contrasts. *Oecologia* 98:109–116.
- Burton, T. M. 1976. An analysis of feeding ecology of the salamanders (Amphibia: Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. *J. Herpetol.* 10:187–204.
- Channing, A. 2001. Amphibians of central and southern Africa. Comstock Publishing Associates, Cornell Univ. Press, Ithaca, NY.
- Churchfield, S., V. A. Nesterenko, and E. A. Shvarts. 1999. Food niche overlap and ecological separation amongst six species of coexisting forest shrews (Insectivora: Soricidae) in the Russian Far East. *J. Zool.* 248:349–359.
- Collar, D. C., T. J. Near, and P. C. Wainwright. 2005. Comparative analysis of morphological diversity: does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution* 59:1783–1794.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567–576.
- Colwell, R. K., and D. W. Winkler. 1984. A null model for null models in biogeography. Pp. 344–359 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. 1984. Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton, NJ.
- Conant, R., and J. T. Collins. 1998. A field guide to reptiles and amphibians of eastern and central North America. 3rd ed. Houghton-Mifflin, New York, NY.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.
- . 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661–696.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.* 61:1–12.
- Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, MA.
- Daniel, J. C. 2002. The book of Indian reptiles and amphibians. Bombay Natural History Society and Oxford Univ. Press, Mumbai, India.
- Dayan, T. and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. *Ecol. Lett.* 8:875–894.
- Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–357.
- Doebeli, M. 1996. An explicit genetic model for ecological character displacement. *Ecology* 77:510–520.
- Drewes, R. C. 2007. Frogs of the Arabuko-Sokoke Forest, Kenya. <http://www.calacademy.org/research/herpetology/frogs/kfrogs.html>. Accessed on 25 June 2007.
- Drewes, R. C., and J. V. Vindum. 1994. Amphibians of the Impenetrable Forest, Uganda. *J. Afr. Zool.* 108:55–70.
- Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 65:1–352.
- . 2001. The hylid frogs of Middle America. 2nd ed. Society for the Study of Amphibians and Reptiles, Lawrence, KS.

- . 2005. Cusco Amazónico. Comstock Publishing Associates, Cornell Univ. Press, Ithaca, NY.
- Duellman, W. E., and J. R. Mendelson III. 1995. Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. *Sci. Bull. Nat. His. Mus. Univ. Kansas* 55:329–376.
- Duellman, W. E., and L. Trueb. 1986. *Biology of amphibians*. McGraw-Hill, New York, NY.
- Faivovich, J., C. F. B. Haddad, P. C. A. Garcia, D. R. Frost, J. A. Campbell, and W. C. Wheeler. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bull. Am. Mus. Nat. Hist.* 294:1–240.
- Fei, L., C. Y. Ye, Y. A. Huang, and M. Y. Liu. 1999. *Atlas of amphibians of China*. Henan Science and Technical Press, Zhengzhou, China.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Fisher, D. O., and C. R. Dickman. 1993. Body size-prey size relationships in insectivorous marsupials: tests of three hypotheses. *Ecology* 74:1871–1883.
- Frost, D. R. 2007. *Amphibian Species of the World: an online reference*. Version 5.0 (1 February 2007). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, NY.
- Gerhardt, H. C., and F. Huber. 2002. *Acoustic communication in insects and anurans*. Univ. of Chicago Press, Chicago, IL.
- Gillespie, R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303:356–359.
- Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* 67:540–554.
- Glaw, F. and M. Vences. 1994. *A fieldguide to the amphibians and reptiles of Madagascar*. Moos Druck, Leverkusen, and FARBO, Köln, Germany.
- Glor, R. E., J. J. Kolbe, R. Powell, A. Larson, and J. B. Losos. 2003. Phylogenetic analysis of ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). *Evolution* 57:2383–2397.
- Glor, R. E., M. E. Gifford, A. Larson, J. B. Losos, L. Rodríguez-Schettino, A. R. Chamizo-Lara, and T. R. Jackman. 2004. Partial island submergence and speciation in an adaptive radiation: a multilocus analysis of the Cuban green anoles. *Proc. R. Soc. Lond. B* 271:2257–2265.
- Goris, R. C., and N. Maeda. 2004. *Guide to the amphibians and reptiles of Japan*. Krieger Publishing Company, Malabar, FL.
- Gray, S. M., and B. W. Robinson. 2002. Experimental evidence that competition between stickleback species favours adaptive character divergence. *Ecol. Lett.* 5:264–272.
- Griffiths, D. 1980. Foraging costs and relative prey size. *Am. Nat.* 116:743–752.
- Grimaldi, D., and M. S. Engel. 2005. *Evolution of the insects*. Cambridge Univ. Press, New York, NY.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *Am. Nat.* 140:539–572.
- Hass, C. A. 1991. Evolution and biogeography of West Indian *Sphaerodactylus* (Sauria: Gekkonidae): a molecular approach. *J. Zool.* 225:525–561.
- Hedges, S. B. 1989. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. Pp. 305–370 in C. A. Woods, ed. *Biogeography of the West Indies*. Sandhill Crane Press, Gainesville, FL.
- Heinicke, M. P., W. E. Duellman, and S. B. Hedges. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proc. Natl. Acad. Sci. USA* 104:10092–10097.
- Hendry, A. P., M. L. Kelly, M. T. Kinnison, and D. N. Reznick. 2006. Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of wild guppies. *J. Evol. Biol.* 19:741–754.
- Heyer, W. R., A. S. Rand, C. A. G. Cruz, O. L. Peixoto, and C. E. Nelson. 1990. Frogs of Boracéia. *Arquivos de Zoologia Sao Paulo* 31:231–410.
- Hill, J. L., P. J. Curran, and G. M. Foody. 1994. The effect of sampling on the species-area curve. *Global Ecol. Biogeogr. L.* 4:97–106.
- Hoskin, C. J., M. Higgie, K. R. McDonald, and C. Moritz. 2005. Reinforcement drives rapid allopatric speciation. *Nature* 437:1353–1356.
- Inger, R. F., and B. Greenburg. 1966. Ecological and competitive relations among three species of frogs (Genus *Rana*). *Ecology* 47:746–759.
- IUCN, Conservation International, and NatureServe. 2006. *Global Amphibian Assessment*. Available at <http://www.globalamphibians.org>. Accessed June 30, 2007.
- Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). *Evolution* 59:2000–2016.
- Krzysik, A. J. 1979. Resource allocation, coexistence, and the niche structure of a streambank salamander community. *Ecol. Monogr.* 49:173–194.
- Langerhans, R. B., M. E. Gifford, and E. O. Joseph. 2007. Ecological speciation in *Gambusia* fishes. *Evolution* 61:2056–2074.
- Lannoo, M., ed. 2005. *Amphibian declines*. Univ. of California Press, Berkeley, CA.
- Lim, B. K., and M. D. Engstrom. 2005. Mammals of Iwokrama forest. *Proc. Acad. Natl. Sci. Phila.* 154:71–108.
- Lima, A. P., and W. E. Magnusson. 1998. Partitioning seasonal time: interactions among size, foraging activity and diet in leaf-litter frogs. *Oecologia* 116:259–266.
- Lima, A. P., and G. Moreira. 1993. Effects of prey size and foraging mode on the ontogenetic change in feeding niche of *Colostethus stepheni* (Anura: Dendrobatidae). *Oecologia* 95:93–102.
- Lloyd, M., R. F. Inger, and F. W. King. 1968. On the diversity of reptile and amphibian species in a Bornean rain forest. *Am. Nat.* 102:497–515.
- Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. *Am. Nat.* 125:310–316.
- Losos, J. B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution* 44:558–569.
- . 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annu. Rev. Ecol. Syst.* 25:467–493.
- . 1996. Phylogenetic perspectives on community ecology. *Ecology* 77:1344–1354.
- . 2004. Adaptation and speciation in Greater Antillean anoles. Pp. 335–343 in U. Dieckmann, M. Doebeli, J. A. J. Metz, and D. Tautz, eds. *Adaptive speciation*. Cambridge Univ. Press, Cambridge, United Kingdom.
- Losos, J. B., and D. Schluter. 2000. Analysis of an evolutionary species-area relationship. *Nature* 408:847–850.
- Losos, J. B., R. E. Glor, J. J. Kolbe, and K. Nicholson. 2006. Adaptation, speciation, and convergence: a hierarchical analysis of adaptive radiation in Caribbean *Anolis* lizards. *Ann. Mo. Bot. Gard.* 93:24–33.
- Lyman, R. L., and K. M. Ames. 2007. On the use of species-area curves to detect the effects of sample size. *J. Archaeol. Sci.* 34:1985–1990.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101:377–385.
- Manly, B. F. J. 1994. *Multivariate statistical methods: a primer*. 2nd ed. Chapman and Hall, New York, NY.
- Manthey, U., and W. Grossman. 1997. *Amphibien und Reptilien Südostasiens*. Natur und Tier, Münster, Germany.
- Martins, E. P. 1994. Estimating the rate of phenotypic evolution from comparative data. *Am. Nat.* 144:193–209.
- . 2004. COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data. Distributed by the author

- at <http://compare.bio.indiana.edu/>. Department of Biology, Indiana University, Bloomington, IN.
- Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* 149:646–667.
- May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proc. Natl. Acad. Sci. USA* 69:1109–1113.
- McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. 2nd ed. Chapman and Hall/CRC, New York, NY.
- Melville, J. 2002. Competition and character displacement in two species of scincid lizards. *Ecol. Lett.* 5:386–393.
- Menzies, J. I. 2006. The frogs of New Guinea and the Solomon Islands. Pensoft, Sofia, Bulgaria.
- Meshaka, W. E., Jr. 2001. The Cuban treefrog in Florida: life history of a successful colonizing species. Univ. Press of Florida, Gainesville, FL.
- Nosil, P., and B. J. Crespi. 2006. Experimental evidence that predation promotes divergence in adaptive radiation. *Proc. Natl. Acad. Sci. USA* 103:9090–9095.
- Nussbaum, R. A., C. J. Raxworthy, A. P. Raselimanana, and J.-B. Ramanamanjato. 1999. Amphibians and reptiles of the Reserve Naturelle Integrale d'Andohahela, Madagascar. *Fieldiana Zool.* 94:155–174.
- O'Meara, B. C., C. Ané, M. J. Sanderson, and P. C. Wainwright. 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution* 60:922–933.
- Pfennig, K. S., and D. W. Pfennig. 2005. Character displacement as the “best of a bad situation”: fitness trade-offs resulting from selection to minimize resource and mate competition. *Evolution* 59:2200–2208.
- Pfennig, D. W., A. M. Rice, and R. A. Martin. 2007. Field and experimental evidence for competition's role in phenotypic divergence. *Evolution* 61:257–271.
- Pough, F. H., C. M. Janis, and J. B. Heiser. 2002. Chapter 11: Salamanders, anurans and caecilians. Pp. 221–269 in *Vertebrate life*, 6th edn. Prentice-Hall, Upper Saddle River, NJ.
- Radtkey, R. R., S. M. Fallon, and T. J. Case. 1997. Character displacement in some *Cnemidophorus* lizards revisited: a phylogenetic analysis. *Proc. Natl. Acad. Sci. USA* 94:9740–9745.
- Rand, A. S., and C. W. Myers. 1990. The herpetofauna of Barro Colorado Island, Panama: an ecological survey. Pp. 386–409 in A. H. Gentry, ed. *Four neotropical rainforests*. Yale Univ. Press, New Haven, CT.
- Ridgely, R. S., D. Agro, and L. Joseph. 2005. Birds of Iwokrama forest. *Proc. Acad. Natl. Sci. Phila.* 154:109–121.
- Rodrigues, M., L. A. Carrara, L. P. Farla, and H. P. Gomes. 2005. The birds of Parque Nacional da Serra do Cipó: the Rio Cipó valley, Minas Gerais, Brasil. *Rev. Bras. Zool.* 22:326–338.
- Roelants, K., D. J. Gower, M. Wilkinson, S. P. Loader, S. D. Biju, K. Guillaume, and F. Bossuyt. 2007. Patterns of diversification in the history of modern amphibians. *Proc. Natl. Acad. Sci. USA* 104:887–892.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37:317–350.
- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univ. Press, New York, NY.
- Roughgarden, J. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. *Am. Nat.* 108:429–442.
- Ryan, M. J. 1988. Constraints and patterns in the evolution of anuran communication. Pp 637–677 in B. Fritzsch, M. Ryan, W. Wilczynski, T. Hetherington, and W. Walkowiak, eds. *The evolution of the amphibian auditory system*. Wiley, New York, NY.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Mol. Biol. Evol.* 19:101–109.
- . 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* 19:301–302.
- Schötz, A. 1999. Treefrogs of Africa. Edition Chimaira, Frankfurt am Main, Germany.
- Schluter, D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. *Am. Nat.* 131:799–824.
- . 1990. Species-for-species matching. *Am. Nat.* 136:560–568.
- . 1996. Ecological causes of adaptive radiation. *Am. Nat.* 148:S40–S64.
- . 2000a. Ecological character displacement in adaptive radiation. *Am. Nat.* 156:S4–S16.
- . 2000b. *The ecology of adaptive radiation*. Oxford Univ. Press, New York, NY.
- Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size of the lizard *Anolis conspersus*. *Science* 155:474–478.
- . 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- . 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- . 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- . 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240–285.
- Schoener, T. W., and G. C. Gorman. 1968. Some niche differences in three Lesser-Antillean lizards of the genus *Anolis*. *Ecology* 49:819–830.
- Schwartz, A., and R. W. Henderson. 1991. *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*. Univ. of Florida Press, Gainesville, FL.
- Shoemaker, V. H. 1992. Exchange of water, ions, and respiratory gases in terrestrial amphibians. Pp. 81–124 in M. E. Feder and W. W. Burggren, eds. *Environmental physiology of the amphibians*. Univ. of Chicago Press, Chicago, IL.
- Simpson, G. G. 1953. *The major features of evolution*. Columbia Univ. Press, New York, NY.
- Slatkin, M. 1980. Ecological character displacement. *Ecology* 61:163–177.
- Smith, S. A., P. R. Stephens, and J. J. Wiens. 2005. Replicate patterns of species richness, historical biogeography, and phylogeny in Holarctic treefrogs. *Evolution* 59:2433–2450.
- Smith, S. A., A. Nieto Montes de Oca, T. W. Reeder, and J. J. Wiens. 2007. A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: why so few species in lowland tropical rainforests? *Evolution* 61:1188–1207.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. 3rd edn. W. H. Freeman, New York.
- Sondaar, P. Y. 1977. Insularity and its effect on mammal evolution. Pp. 671–707 in M. K. Hecht, P. C. Goody, and B. M. Hecht, eds. *Major patterns of vertebrate evolution*. Plenum, New York, NY.
- Stebbins, R. C. 2003. *A field guide to western reptiles and amphibians*. 3rd edn. Houghton-Mifflin, New York, NY.
- Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.* 161:112–128.
- Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. 1984. *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, Princeton, NJ.
- Taper, M. L., and T. J. Case. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66:355–371.
- . 1992. Coevolution among competitors. Pp 63–111 in D. Futuyma and J. Antonovics, eds. *Oxford surveys in evolutionary biology*. Volume 8. Oxford Univ. Press, Oxford, UK.

- Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* 45:131–141.
- . 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *J. Herpetol.* 15:139–144.
- . 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- Trueb, L., and M. J. Tyler. 1974. Systematics and evolution of the Greater Antillean hylid frogs. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* 24:1–60.
- Tyler, M. J., G. A. Cook, and M. Davies. 1983. Reproductive biology of the frogs of the Magela Creek system, Northern Territory. *Rec. S. Aust. Mus.* 18:415–440.
- Vernes, K., S. Green, A. Howes, and L. Dunn. 2006. Species richness and habitat associations of non-flying mammals in Gibraltar Range National Park. *P. Linn. Soc. N. S. W.* 127:93–105.
- Vitt, L. J., S. S. Sartorius, T. C. S. Avila-Pires, M. C. Espósito, and D. B. Miles. 2000. Niche segregation among sympatric Amazonian teiid lizards. *Oecologia* 122:410–420.
- Vitt, L. J., S. S. Sartorius, T. C. S. Avila-Pires, P. A. Zani, and M. C. Espósito. 2005. Small in a big world: ecology of leaf-litter geckos in New World tropical forests. *Herpetol. Monogr.* 19:137–152.
- Wassersug, R. J., H. Yang, J. J. Sepkoski, and D. M. Raup. 1979. The evolution of body size on islands: a computer simulation. *Am. Nat.* 114:287–295.
- Wiens, J. J. 2007. Global patterns of species richness and diversification in amphibians. *Am. Nat.* 170:S86–S106.
- Wiens, J. J., J. W. Fetzner, C. L. Parkinson, and T. W. Reeder. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. *Syst. Biol.* 54:778–807.
- Wiens, J. J., M. C. Brandley, and T. W. Reeder. 2006a. Why does a trait evolve multiple times within a clade? Repeated evolution of snake-like body form in squamate reptiles. *Evolution* 60:123–141.
- Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006b. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *Am. Nat.* 168:579–596.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. *Lizard ecology: studies of a model organism*. Harvard Univ. Press, Cambridge, MA.
- Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* 71:1063–1074.
- Wright, A. H. 2002. *Life-histories of the frogs of the Okefinokee Swamp, Georgia*. Comstock Publishing Associates, Cornell Univ. Press, Ithaca, NY.
- Ziegler, T., A. Ohler, N. T. Vu, K. Q. Le, X. T. Nguyen, H. T. Dinh, and N. T. Bui. 2006. Review of the amphibian and reptile diversity of Phong Nha–Ke Bang National Park and adjacent areas, central Truong Son, Vietnam. Pp. 247–262 in M. Vences, J. Köhler, T. Ziegler, W. Böhm, eds. *Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica*. Societas Europaea Herpetologica, Bonn, Germany.
- Zweifel, R. G. 1980. Results of the Archbold expeditions. No. 103. Frogs and lizards from the Huon Peninsula, Papua New Guinea. *B. Am. Mus. Nat. Hist.* 165:387–434.

Associate Editor: D. Pfennig

Supporting Information

The following supporting information is available for this article:

Figures S1 and S2. 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).

Table S1. Maximum snout-to-vent length (SVL) data used to determine SVL ranges of treefrog assemblages and the species pool of the community analyses. SVL_{max} in millimeters (mm).

Table S2. Proportion of diet overlap, as assessed by Schoener's (1970) index of proportional overlap (see Methods).

Table S3. Setup of community assembly analyses.

Table S4. Genbank accession numbers for DNA sequences analyzed in the analysis of Lophiohylini.

Table S5. Primers used to amplify and sequence DNA sequence data.

Table S6. Ratios of body sizes of Jamaican and Hispaniolan treefrogs.

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

(This link will take you to the article abstract).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting informations supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.