

COMMUNITY ASSEMBLY THROUGH EVOLUTIONARY DIVERSIFICATION AND DISPERSAL IN MIDDLE AMERICAN TREEFROGS

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How are ecologically diverse organisms added to local assemblages to create the community structure we see today? In general, within a given region or community, a given trait (character state) may either evolve in situ or be added through dispersal after having evolved elsewhere. Here, we develop simple metrics to quantify the relative importance of these processes and then apply them to a case study in Middle American treefrogs. We examined two ecologically important characters (larval habitat and body size) among 39 communities, using phylogenetic and ecological information from 278 species both inside and outside the region. For each character, variation among communities reflects complex patterns of evolution and dispersal. Our results support several general hypotheses about community assembly, which may apply to many other systems: (1) elevation can play an important role in creating patterns of community structure within a region, (2) contrary to expectations, species can invade communities in which species with similar ecological traits are already present, (3) dispersal events tend to occur between areas with similar climatic regimes, and (4) the first lineage to invade a region diversifies the most ecologically, whereas later invasions show limited change.

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A major goal of evolutionary ecology is to understand the origins of ecological communities. Specifically, how does a set of species with a given set of ecological traits come to exist together in the same place? In recent years, there has been growing appreciation for the importance of using phylogenies to understand how communities have originated through evolutionary, ecological, and biogeographical processes (e.g., special issues of *Ecology* in 1996 and 2006 and reviews in Webb et al. 2002; Emerson and Gillespie 2008). Many recent studies have focused on the phylogenetic relatedness of co-occurring species and have used these patterns of relatedness to infer ecological processes (e.g., Webb

2000; Cavender-Bares et al. 2004; Horner-Devine and Bohannan 2006; Kembel and Hubbell 2006; Lovette and Hochachka 2006; Webb et al. 2006; Vamosi et al. 2009). In this article, we use a phylogenetic approach to infer the relative roles of trait evolution and biogeographic dispersal in creating patterns of community structure (defined here as the set of co-occurring species and their ecologically relevant character states).

Many different ecological and evolutionary processes may determine the structure of a community. However, in general, only two major processes seem likely to add a species with a given character state to a specific community. First, character states may

be added through in situ evolution within the community (in situ evolution or ISE hereafter). ISE may be determined by abiotic conditions and by interactions with co-occurring species (e.g., selection to exploit underutilized resources and reduce competition). Second, character states may be added through dispersal of lineages into the community that evolved these states elsewhere and retained them over time (ecologically conservative dispersal or ECD; Stephens and Wiens 2004). The ability of a species to invade and persist in a given community will be determined by the characteristics of the dispersing species and the abiotic and biotic conditions present there (Morin 1999).

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

What factors determine the extent to which communities are assembled through ISE versus ECD? We make four predictions that address such factors. (1) Systems (e.g., regions, communities) that are relatively closed to biogeographic dispersal are likely to be dominated by ISE, as species diversify to fill open niches (e.g., adaptive radiations on islands; Losos et al. 1998; Schluter 2000; Gillespie 2004; Harmon et al. 2008; Moen and Wiens 2009). Although often documented on islands, similar processes may be important in continental systems as well, given that biogeographic dispersal may be limited by climate as well as by physical separation (Janzen 1967; Wiens and Donoghue 2004; Lomolino et al. 2006). For example, mountain ranges may form islands of distinct climates within a region and may be important centers for ISE. Therefore, even in more open biogeographic systems, we might expect more ISE in montane regions relative to lowlands and on different isolated mountain ranges. (2) Given the potential constraints of climatic tolerances on biogeographic dispersal, we expect most ECD to occur between locations with similar climatic regimes. (3) Competition may also limit ECD, in that lineages from outside a region may be unable to invade communities in which the relevant niches are already “filled” (e.g., Morin 1999). Thus, ECD might only occur if lineages have character states dissimilar to those of species already present (although some theory predicts that ecological similarity might instead allow for long periods of co-occurrence; Leibold and McPeck 2006; Scheffer and van Nes 2006). (4) Competition may also prevent dispersing lineages from expanding into new niches (e.g., Schluter 2000), and so may determine whether invading lineages undergo ISE (but see Kozak et al. 2009). Thus, we may expect more ISE in the

first lineage to colonize a region and conservatism in lineages that arrived later. We test these four hypotheses for the first time here.

In this article, we combine ecological, phylogenetic, and distributional data to quantify the relative importance of regional dispersal and ISE in 39 hylid frog communities in Middle America (Mexico to Panama), and to address the hypotheses described above. Middle American hylids offer an attractive study system because an extensive monograph (Duellman 2001) describes the morphology, geographic distribution, and natural history of each species. Furthermore, new phylogenies (Faivovich et al. 2005; Smith et al. 2005; Wiens et al. 2005, 2006b; Smith et al. 2007) provide a framework for analyzing patterns of biogeography and character evolution. Hylids are a monophyletic group (Faivovich et al. 2005; Wiens et al. 2005) and a distinctive ecological guild; they are the dominant group of arboreal frogs in Middle America and the only arboreal frogs there that use aquatic habitats for breeding (excepting the more geographically restricted centrolenids and hemiphraetids; Duellman 2001; Savage 2002).

To illustrate our approach, we focus on two ecologically important characters, adult body size and larval habitat. In general, hylids are dietary generalists (on arthropods), in which prey size is strongly associated with body size (e.g., Meshaka 2001; Duellman 2005; Moen and Wiens 2009). Thus, body size seems to determine whether different species consume the same prey items. Furthermore, body size appears to be the main axis of morphological diversification in hylid frogs (see Results). In Middle American hylids (Duellman 2001), larvae may be deposited in standing water (“ponds” hereafter), streams, or in arboreal sites (e.g., bromeliads, treeholes), depending upon the species. Larval habitat determines whether larvae of different species may potentially co-exist and compete, and seems to be strongly associated with microhabitat preferences of adults (Zimmerman and Bierregaard 1986; Donnelly and Guyer 1994; Duellman 2001; Ernst and Rödel 2008), at least during the breeding season (i.e., pond-breeding hylids are usually found on vegetation in or near ponds, whereas stream-breeding hylids are found on vegetation near streams; Duellman 2001).

In this study, we develop simple indices to quantify the relative importance of ISE and ECD at the regional and local scales. To examine the origins of character states (traits) at the regional scale, we map character evolution and biogeographic shifts onto phylogenies. If an ecological character changed after dispersal into the region, then we consider this a character-state origin through ISE. If a lineage dispersed into the region with a character state that evolved before the dispersal event, we consider this dispersal event a case of ECD. Using these criteria, we quantify for each character the number of trait origins in the region through ISE and ECD. We also trace the origin of character states in 39 local communities to ISE or ECD at the regional scale, assigning the character state of each species in each community to ISE or

ECD within Middle America. We then quantify the proportion of species having their character states through ISE or ECD and test whether the proportion of ISE in each community is related to the elevation of that community (with the expectation that higher elevation communities will be isolated by their climate and therefore dominated by ISE). We also examine how widespread each trait origin has become among communities, and whether some communities are characterized by unusually widespread or locally restricted character-state origins (e.g., are some geographically isolated communities dominated by local ISE?). Finally, we also address (1) the rate of ISE in each lineage relative to its timing of colonization of Middle America, (2) whether ECD occurs from areas of similar or dissimilar climatic regimes outside the region, and (3) whether invading lineages are able to colonize communities in which ecologically similar species are already present.

Materials and Methods

LOCAL COMMUNITY STRUCTURE AND CHARACTER DATA

We considered 39 local-scale hylid communities, most of which were described by Duellman (2001). We define a community as the assemblage of species within a single locality. The exact spatial limits of these sites have not been strictly defined, but each consists of a single collecting locality within an area of no more than a few square kilometers. Each consists of a single general habitat type (e.g., cloud forest) but encompasses multiple microhabitats within that habitat (e.g., forest, stream edge). For many lowland communities, community composition is relatively homogeneous across localities (Duellman 2001; Table S1), so that the exact area should have little impact. For highland communities, species composition may change dramatically among localities over a smaller spatial scale, but this is related to differences in habitat types (e.g., cloud forest vs. pine forest vs. montane rainforest), whereas we focus on localities encompassing a single habitat type. Overall, these sites have been visited repeatedly by herpetologists over several decades, and some sites have been the subject of long-term studies. Thus, we are confident that the hylid fauna at each site has been adequately documented.

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

signed species to character states for these communities based on Duellman's (2001) overall characterizations for these species. Species composition of communities and character states of these species are given in Table S1.

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

Because communities in close geographical proximity may be similar in species composition (and therefore nonindependent in our correlation analyses), we tested for spatial autocorrelation among communities. We expect communities separated by very long distances to be relatively independent, so we only conducted analyses within Mexico (with 23 of 39 communities), and within Costa Rica and Panama (with 10 of 39). In other words, given our intention to test whether nearby communities are sufficiently dissimilar, the distinctness of distant communities is irrelevant and potentially misleading.

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

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

$$C_s = 2a/(2a + b + c),$$

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

ANCESTRAL STATE ESTIMATION

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

We mapped biogeographic shifts and character evolution onto a hylid phylogeny based on combined Bayesian analyses of 10 nuclear and mitochondrial genes. The primary phylogeny used is based on a detailed phylogeny of the MAC (Smith et al. 2007). For other hylid clades, we used a composite chronogram from Moen and Wiens (2009), based primarily on data from Wiens et al. (2006b). Briefly, Wiens et al. (2006b) estimated phylogeny and divergence times for 124 hylid species, incorporating all relevant hylid fossils and geological calibration points. Moen and Wiens (2009) expanded taxon sampling within five individual clades (Phyllomedusinae, Cophomantini, Lophiohylini, *Scinax* clade, and *Dendropsophus* clade), and estimated the phylogeny and branch lengths using Bayesian analysis. Branch lengths were then converted into units of time using penalized likelihood analysis (Sanderson 2002) with r8s (Sanderson 2003), using the estimated ages of each clade from the 124-taxon chronogram of Wiens et al. (2006b) as root ages. Chronograms for individual clades were added to this “backbone” tree to produce an overall chronogram (see Figs. S1–S3). We used this overall

chronogram from Moen and Wiens (2009) and added the phylogeny of the MAC from Smith et al. (2007). This approach (from Wiens et al. 2006a) allowed us to obtain comparable branch lengths in units of time throughout the phylogeny, without estimating a chronogram for all 283 taxa simultaneously (large trees with heterogeneous branch lengths can be difficult for r8s). Further, preliminary results from an unpublished likelihood tree for 362 hylid taxa (from RAxML; Stamatakis 2006) with divergence dates (from BEAST; Drummond and Rambaut 2007) yields a very similar topology and age estimates ($r = 0.89$ with divergence dates in Table 4 and almost all dates within 3.5 million years [My] of those for each node).

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

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

We obtained data on larval habitat and body size from various literature sources (see Table S2), but most data on species from Middle America were obtained from Duellman (2001). Data were obtained for 278 of the species in our 283-taxon phylogeny (Figs. S1–S3) and for 32 additional Middle American hylids not included in the tree. We used snout-vent length (SVL) as an index of body size, which is standard in anuran studies. Given that body sizes generally are similar between males and females but are not necessarily identical (Duellman 2001), we analyzed data from males only (which are more commonly collected than females). We used maximum SVL within a species, to reduce potential confounding of mature and immature specimens when using average sizes. Geographic variation in male body size is generally limited. For example, Duellman (2001; vol. 1) presented data on geographic variation in male body size from 15 species of

hylid frogs in Middle America, and these data suggest limited size variation within species. However, we also conducted an analysis of variance (ANOVA) (Sokal and Rohlf 1995) on these data to examine the relative amount of within- versus among-species variation in body size. We found most variation to be among, rather than within, species ($n = 29\text{--}441$, mean $n = 139.5$; $F_{14,2077} = 4548$, $P < 0.0001$; $s^2_{\text{among}} = 0.1811$, proportion of total variation ($p_{\text{total}} = 97.2\%$; $s^2_{\text{within}} = 0.0053$, $p_{\text{total}} = 2.8\%$; analysis on \log_e -transformed data). Thus, overall variation in adult male body sizes within species is limited relative to variation across species, suggesting that use of mean, minimum, or maximum body size should have limited impact on the results. Furthermore, we focus here on very broad categories of body sizes (i.e., >20 mm). Table S2 lists raw data and specific literature sources for both larval habitat and body size.

Previous studies (e.g., Moen and Wiens 2009) suggest that body size should be the major axis of morphological variation in hylids. To test this hypothesis, we measured 135 museum specimens (numbers and data in Table S3) representing all genera of Hylidae. We measured 14 variables typically used to quantify morphometric variation in frogs (e.g., Duellman 2001): (1) SVL (tip of snout to anterior margin of cloaca); (2) tibia length (tip of knee to tip of heel); (3) foot length (proximal edge of inner metatarsal tubercle to tip of fourth toe); (4) head length (posterior corner of jaw to tip of snout); (5) head width (distance between posterior corners of jaw); (6) interorbital distance (width of bone between two orbits); (7) internarial distance (distance between narial openings); (8) eye-to-nostril distance (posterior tip of nostril to anterior corner of eye); (9) eye diameter (distance between anterior and posterior corners of eye); (10) hand length (proximal edge of outer palmar tubercle to tip of third finger); (11) thumb length (insertion point of thumb into hand to tip of thumb); (12) radioulnar length (elbow to distal edge of outer palmar tubercle); (13) maximum width of terminal digit of finger 3; and (14) tympanum width (anterior to posterior extent). All measurements were conducted on males.

We performed a principal components analysis (PCA; Manly 1994) on the correlation matrix of these variables. PC1 accounted for 91.2% of the variation, and represented overall size (sensu Jolicoeur 1963; i.e., all PC1 loadings on the original variables were nearly identical in sign and magnitude; Table S4). Other PC axes each accounted for less than 2.5% of the variation. Furthermore, when only Middle American hylids are included, PC1 accounted for 92.9% of the variation (Table S4). Thus, we used SVL as an overall measure of size, given that data on SVL are available for almost all hylid species (but data on PC1 are not), and that SVL and PC1 are strongly correlated among these 51 species ($r = 0.991$).

Ancestral values of larval habitat were estimated using parsimony and maximum likelihood in the program Mesquite

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

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

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

ESTIMATING THE ROLES OF ISE AND ECD

We first estimated the relative importance of ISE and ECD at the regional scale for each ecological character. Throughout the article, we use “origin” to describe the addition of a given

character state to a region or local community through either dispersal or ISE. For example, although two species may share the same character state (e.g., pond breeding), the state may have appeared (originated) in the region in two different ways, evolving within Middle America in one species and through dispersal from South America in the other. The same character state may be added to the region many different times through each process, and each instance of evolution or dispersal is counted as a separate origin in the region.

We used the ecological and biogeographic reconstructions to distinguish ISE and ECD events. If a state evolved after a biogeographic shift into Middle America, then this regional origin was considered to be through ISE (Fig. 1). If the state evolved before dispersal into Middle America, then the dispersal of that lineage into the region was considered to be an origin of that state through ECD (Fig. 1). In two cases (of 74 total origins), a shift in biogeography occurred on the same branch as a change in one of the characters. In such cases, it is not possible to distinguish between ISE and ECD. We arbitrarily lumped these few cases into the ISE category, given the assumption that these character-state changes most likely occurred in response to a new selective regime encountered in a new region. However, assigning them to the ECD category had negligible impact on the overall results (e.g., $r = 0.71$ between ROTIs [see below] of the four relevant communities when categorizing these as ISE vs. ECD). Finally, a limited number of species occur in both Middle America and North or South America; in all cases, biogeographic reconstruction allowed us to resolve the direction of colonization for these species. Figure 3 shows the inferred colonizations of Middle America, as well as character states for species and estimated character states at the internal nodes for Middle American hylid frogs.

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

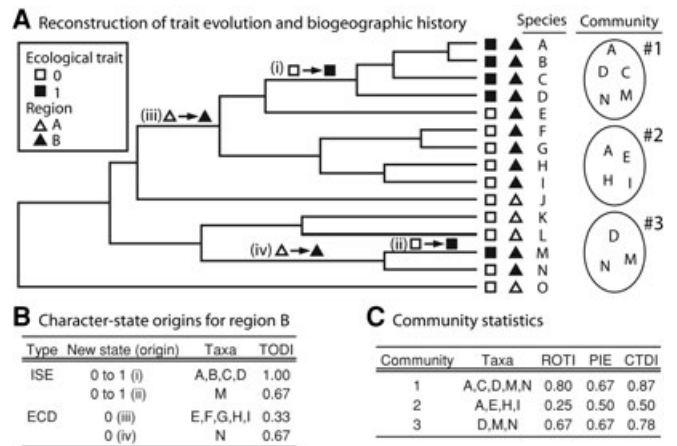


Figure 1. Diagrammatic example of our approach to quantifying the relative importance of in situ evolution (ISE) and ecologically conservative dispersal (ECD) in determining patterns of community structure within a region, based on hypothetical data. (A) First, we use ancestral-state estimation to examine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

Proportion of ISE Events (PIE). Although similar to the ROTI, the PIE reflects the relative importance of ISE in terms of the overall number of regional-scale dispersal and character evolution events represented in a given community, rather than the proportion of species that have a character-state whose origin was by ISE (as in the ROTI). For example, even though there may be 10 species in a community, their states may have originated through only two ISE events and one ECD event, given that speciation may occur after dispersal or character evolution. Although the PIE is distinct

from the ROTI in what it quantifies, we expect these two indices to be correlated (Fig. 1).

We also estimated the spread of each character-state origin among the surveyed communities within the region. We developed the Trait Origin Dispersal Index (TODI), which is the proportion of communities to which each origin (either through regional ISE or ECD) of each character state has spread among the included communities (Fig. 1). For example, a character state that has evolved in the common ancestor of two species that together occur in nine of the 39 communities would have a value of 0.23. We acknowledge that this is a relatively simplistic measure, because it only considers the number of sampled communities and not actual dispersal distances.

To identify communities having many character-state origins with limited dispersal, we also calculated the Community Trait Dispersal Index (CTDI). The CTDI is simply the average of TODI across species in a community for a given character (Fig. 1).

Finally, we note that one could develop probability models or a permutation procedure to examine whether a community's ROTI or CTDI was significantly small or large (i.e., close to 0.0 or 1.0, respectively). Because we are primarily interested in overall broad patterns (e.g., with elevation) and not the statistical significance of individual index values per se, we have not extensively explored such methods here. However, we examine one type of null model for the ROTI. We also examined the influences of species incidence across communities, community size, and regional pool size on the statistical significance of different ROTI values under this model.

In brief, we asked whether an individual community's ROTI was significantly different from the random expectation based on the total number of ISE and ECD events represented among all species in the region (Middle America). To assess significance, we used the hypergeometric probability distribution (Sokal and Rohlf 1995), a model of sampling without replacement. Under this distribution, one can assess the probability of obtaining a given community's ROTI value under the expectation based on random assembly from the regional pool of species and then compare this to the case when it is more likely that one type of event (i.e., ISE or ECD) is predominantly represented among the species within a community. The two models (random vs. nonrandom) are then compared using a likelihood-ratio test. This procedure is directly analogous to simulating community assembly from a regional pool but has the advantage of directly calculating the probabilities that a simulation would only approximate. See Appendix S1 for full model details, as well as our qualitative variations on the regional species pool (see above).

CORRELATION ANALYSES

If dispersal among high elevation communities is limited by climatic differences in intervening lowlands (see Introduction), we

expect to see significant relationships between elevation and our indices. First, we predict that higher elevations may be hot spots for diversification and may show more ISE (i.e., higher ROTIs in high elevation communities). Similarly, we predict that there will be a significant negative relationship between elevation and the CTDI, indicating relatively isolated ISE events and limited dispersal among communities. To address these predictions, we examined correlations between elevation and our community indices. All correlations presented are based on the Spearman's rank correlation coefficient (r_s), as many indices were not normally distributed. Rank correlations were calculated in JMP IN (Version 4.0.4, SAS Institute, Inc., Cary, NC, 2001). In many cases, the colonization of Holarctic *Hyla* into high elevation areas of northern Middle America resulted in outliers (statistically and biologically) in these elevation analyses, as this re-invasion into Middle America (Smith et al. 2005) represents the only high-elevation ECD event. In analyses in which these outliers had an impact on the results, we present results both including and excluding data from the three *Hyla*-dominated communities (localities 3, 6, 12; Table S1). Unless otherwise noted, the sample size for all correlation analyses is $n = 39$ (reflecting our 39 communities).

SIMILARITY OF CO-OCCURRING SPECIES

The principle of competitive exclusion predicts that establishment of a species in a new community may be limited by the similarity of the colonizing species to species already occurring there (Morin 1999). If competitive exclusion limits establishment in communities, we expect that species will not share identical states for characters that may affect competitive interactions, especially in cases in which South American lineages have recently invaded a community that contains ecologically similar incumbent species of the MAC. Thus, we tallied the number of species in each community that have the same states for the two characters under consideration. We considered pairs of species whose body size differs by less than 5 mm and with the same larval habitat to be ecologically similar. We consider this criterion as a conservative estimate of ecological similarity (i.e., we require that species be similar in both body size and larval habitat, and the body sizes must be very similar). That is, if the result of ECD is to add a species that is ecologically similar (by our conservative criterion) to another within the community, then it would appear that competitive exclusion does not necessarily prevent the co-occurrence of ecologically similar hylid species in the community. We also examined the impact of using different body-size similarity cut-offs, continuously varying the criterion from 0 mm to 10 mm.

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

larval habitat are likely the most important characters affecting ecological interactions among Middle American treefrogs.

CLIMATE AND COLONIZATION

We hypothesized that many of the colonizations of Middle America involved dispersal between regions with similar climatic regimes. Thus, we expected a general positive correlation between the climatic distribution of a given lineage in Middle America and its likely ancestral climatic distribution. For this analysis, we focused on the more recent invasions of the region and not the original invasion of Middle America by the MAC, as the ancestor of the MAC seemingly diversified to occupy every habitat and climatic zone inhabited by hylid frogs in the region.

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

To approximate the ancestral climatic distribution associated with each colonization event, we assumed that the ancestral climatic regime of the colonist was most likely to be represented by its closest relatives occurring in the ancestral region. Temperature seasonality shows strong phylogenetic signal in Hylidae (Wiens et al. 2006b), as does mean temperature of the coldest month within the MAC (Smith et al. 2005), so we expect this to be the case for other environmental variables. Therefore, we obtained average values of the same climatic variables for the sister species or clade of each colonizing lineage (given that the sister taxon occurred in the inferred ancestral region). Localities were obtained from literature and museum records. The sister species were inferred from the 283-taxon tree for all hylids (see above), and the ancestral region was determined by our biogeographic reconstructions (see above). Several cases involved species with populations both in Middle America and outside the region (typically South America), and we simply compared the two sets of populations as if they were different species. Finally, we used a Spearman's rank correlation (r_s) to estimate the relationship between the climatic regimes of each colonizing clade in Middle America and in the ancestral region.

We included 12 hylid lineages in this analysis, each representing a separate colonization of Middle America. Localities per species (or per species within a region) ranged from 2 to 83 (mean = 11.6). These lineages (and the sampled species) were (1) *Hyla eximia* group (Middle American lineage = *Hyla euphrobiacea*, *Hyla plicata*; North American = *H. wrightorum*), (2) *Hyla arenicolor* (it is unclear whether this species represents an independent colonization of Middle America [the biogeographic reconstruction of its most recent ancestor was ambiguous], but results were similar excluding it; Middle America (MA) and North America), (3) *Trachycephalus venulosus* (MA and South America [SA]), (4) *Dendropsophus microcephalus* (MA and SA), (5) *Dendropsophus ebraccatus* (MA; SA = *D. bifurcus*, *D. leucophyllatus*, *D. sarayacuensis*, *D. triangulum*), (6) *D. robertmertensi* and *D. sartori* (MA; SA = *D. leali*, *D. rhodopeplus*), (7) *Scinax boulengeri* (MA; SA = *S. garbei*, *S. sugillatus*), (8) *S. staufferi* and *S. elaeochrous* (MA; SA = *S. fuscovarius*, *S. nasicus*, *S. ruber*), (9) *S. ruber* (MA and SA), (10) *Hypsiboas rufitelus* (MA; SA = *H. pellucens*), (11) *Hypsiboas rosenbergi* (MA and SA), and (12) *Hypsiboas boans* (MA and SA). We did not include the two lineages of *Hyloscirtus* because our sample sizes of localities per species were very small (e.g., $n = 1$). We also excluded phyllomedusines, given the seemingly complex biogeographic relationships between Middle and South American lineages in the phylogenetic neighborhood of *Agalychnis* (Wiens et al. 2006b). Nevertheless, preliminary analyses including these three lineages gave qualitatively similar results to those using 12 lineages.

DATES OF COLONIZATION EVENTS

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

Unfortunately, estimating the ages of single-species invasions (i.e., one species occurs in the region and its sister species occurs in the ancestral region) is much more uncertain. For example, the timing of colonization could be much more recent than the timing of the split between these two species. Therefore, in these situations we present estimated ages of species that appear to have colonized Middle America as a single invasion, assuming that the colonization of Middle America did not occur before

the origin of those species. The ages of these species could also be overestimated because of incomplete taxon sampling of South American species within the relevant clades. In addition, many single-species invasions have populations in both regions. Colonization dates for these species are uncertain without detailed phylogeographic sampling, but we use the timing of their split from their sister species as a crude estimation of the maximum age of the colonization event.

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

RATES OF IN SITU EVOLUTION

Our interest in the ages of colonization events was related to their propensity for ISE. For example, are there lower rates of ISE in the lineages that colonized more recently? We first estimated the rate of ISE for each colonizing lineage for each character as the number of ISE events divided by the age of the colonizing lineage. For simplicity, we used the midpoint of the age of the branch on which the colonization event is inferred to have occurred (the average of the stem and crown group age estimates for the clade). We conducted these analyses using both the 100 and 160 Mya root ages. However, because results were qualitatively the same, we report only results using 100 Mya (given that we are interested in relative timing, not absolute timing). This comparison of rates is compromised somewhat by the many single-species colonization events (no body size or life-history differences expected); however, our results comparing the MAC only to multispecies colonizations were qualitatively similar (see below).

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

Results

A graphical summary of the distribution, ecological traits, and dispersal histories of hylid clades in Middle America is provided in Figure 2. Ancestral reconstructions of biogeographic history and trait evolution are presented for the MAC and non-MAC lineages in Middle America in Figure 3. A graphical summary

of the geographic location, clade composition, and ecological structure of each community is provided in Figure 4.

There have been 27 origins of larval habitat types among Middle American hylids, 10 through ISE and 17 through ECD (Table 1). Most origins through ECD represent colonization of lowland pond-dwelling lineages from South America (14 of 17; black circles on the lower bars in Fig. 2), many of which have spread throughout the Middle American lowlands (e.g., *Dendropsophus*, phyllomedusines, *Trachycephalus*, *Scinax*). There were also two invasions of highland stream-dwelling lineages into highland habitats in lower Central America (*Hyloscirtus colymba* and *H. palmeri*), and one invasion of a pond-dwelling lineage from temperate North America (*H. arenicolor* and the *H. eximia* group) into montane areas of Mexico and Guatemala (Fig. 2). Within the MAC, there was an early origin (ISE) of stream-dwelling (Fig. 3b), which spread to most montane communities in the region (Figs. 2 and 4). There has also been ISE of pond breeding (from stream-breeding ancestors; Fig. 3b) that spread into many low-elevation communities (i.e., *Diaglena*, *Isthmohyla*, *Smilisca*, *Tlalocohyla*, *Tripurion*). Two lineages within this pond-breeding clade have secondarily become stream breeding in lower Central America (*Isthmohyla*, *Smilisca*). There have been four origins of arboreally breeding hylids in the region (two from pond breeders, two from stream breeders), all representing ISE within the MAC.

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

There have been 44 origins of different body size classes in Middle America, most through ISE (29 of 44; Table 1) and a smaller number through ECD (15 of 44). Small, medium, large, and very large body sizes have each evolved repeatedly in situ. Within the MAC, a large range of body sizes is present within many clades (e.g., the *Charadrahyla*, *Plectrohyla*, and *Ptychohyla* clades all include species ranging in size from small to large or very large; Fig. 2). Most in situ changes are within the MAC, but seven of 29 in situ changes involve species from South American lineages, including species of small, medium, and very large body sizes.

The relative importance of regional ECD and ISE for the assembly of individual communities differs considerably among characters and communities. The ROTI ranges between 0.0 and 1.0 for both characters across different communities (Table 2).

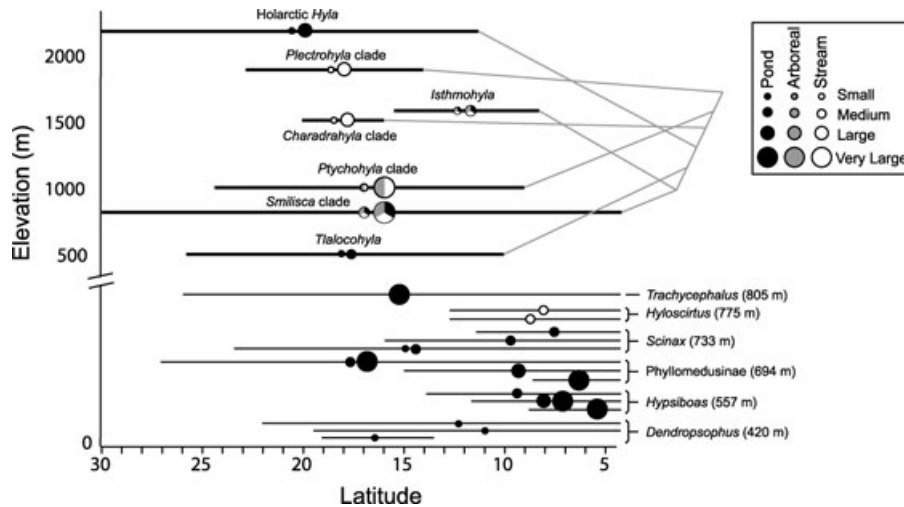


Figure 2. Elevational and latitudinal distribution of hylid clades in Middle America, including a summary for each clade of the range in maximum male body size among species (circle size) and types of larval habitat use (circle color; note that different colors only indicate the presence of different character states, and not their relative frequencies). Widths of horizontal lines indicate latitudinal ranges, and the height of the line indicates the elevational midpoint of the clade (i.e., mean of the elevational midpoints of the species in each clade; Smith et al. 2007). Heavy lines indicate subclades within the Middle American clade, and phylogenetic relationships among these subclades are shown in gray. The *Charadrahyla* clade includes *Charadrahyla* and *Megastomatohyla*, the *Plectrohyla* clade is *Exerodonta* and *Plectrohyla*, the *Ptychohyla* clade is *Bromeliohyla*, *Ecnomiohyla*, *Duellmanohyla*, and *Ptychohyla*, and the *Smilisca* clade is *Anotheca*, *Diaglena*, *Smilisca*, and *Triprior*. Thin lines indicate lineages of the predominately South American clades, where each line represents a separate hypothesized dispersal event into Middle America. Note that these latter lines are not positioned based on their elevational midpoints; rather, these lines are clustered by the larger clade to which they belong. Elevational midpoints of the Middle American species of these predominately South American clades are indicated in parentheses.

Across all 39 communities, the average ROTI is 0.574 for body size and 0.579 for larval habitat (i.e., on average slightly more than half of the species within a given community trace their character states to ISE within Middle America). The PIE was very similar to the ROTI (Table 2; correlation between ROTI and PIE for body size: $r_s = 0.808$, $P < 0.001$; larval habitat: $r_s = 0.901$, $P < 0.001$). Thus, further analyses were only conducted on the ROTI.

There is a weak relationship between the ROTI for larval habitat and that for body size, but this relationship is primarily due to the influence of the three *Hyla*-dominated communities (all data: $r_s = 0.315$; $P = 0.051$; *Hyla* excluded: $r_s = 0.170$; $P = 0.322$). Elevation shows a positive correlation with the ROTI for larval habitat (all data: $r_s = 0.403$; $P = 0.011$; *Hyla* excluded: $r_s = 0.693$; $P < 0.001$) and a negative correlation with the ROTI for body size ($r_s = -0.401$; $P = 0.012$), indicating that higher-elevation communities are dominated by larval habitat character states that evolved within Middle America and by body-size character states that evolved outside of Middle America. Most body-size evolution in the MAC occurred in clades that secondarily invaded the low elevations, whereas montane communities have many species of medium body size, a trait that originated through ECD in the ancestor of the MAC (Fig. 3b).

The trait-origin dispersal index (TODI) for body size ranges between 0.00 and 0.74, with an average of 0.110 (i.e., a single

character-state origin is represented in an average of 4.29 of the 39 local communities; Table 1). Origins of body-size classes through ISE have spread to an average of 10.1% of sampled communities, whereas origins of size classes through ECD have spread to an average of 12.6% of sampled communities. Origins of larval habitat through ISE and ECD have each spread on average to 16.7% and 13.4% of communities, respectively (overall average 14.6%, Table 1). The community trait-dispersal indices (CTDIs) for body size range between 0.103 and 0.615 and for larval habitat between 0.128 and 0.697. The body size CTDI is not correlated with elevation ($r_s = 0.056$, $P = 0.736$). In contrast, community elevation is strongly but negatively correlated with the CTDI for larval habitat ($r_s = -0.486$, $P = 0.002$), indicating limited dispersal of larval habitat character-state origins at higher elevations.

Twenty-nine of the 39 communities (74%) include pairs of ecologically similar species (same larval habitat and body size within 5 mm). Of the total of 77 ecologically similar species pairs, 31 pairs (40%) consist of species from lineages that independently invaded Middle America (e.g., an MAC species and a species from a South American clade). For example, many lowland communities contain both small, pond-breeding species of the MAC (e.g., *Tlalocohyla picta*) and small, pond-breeding species from South America (e.g., *D. microcephalus*, *S. staufferi*), and we have observed them in microsympatry in many localities in Mexico

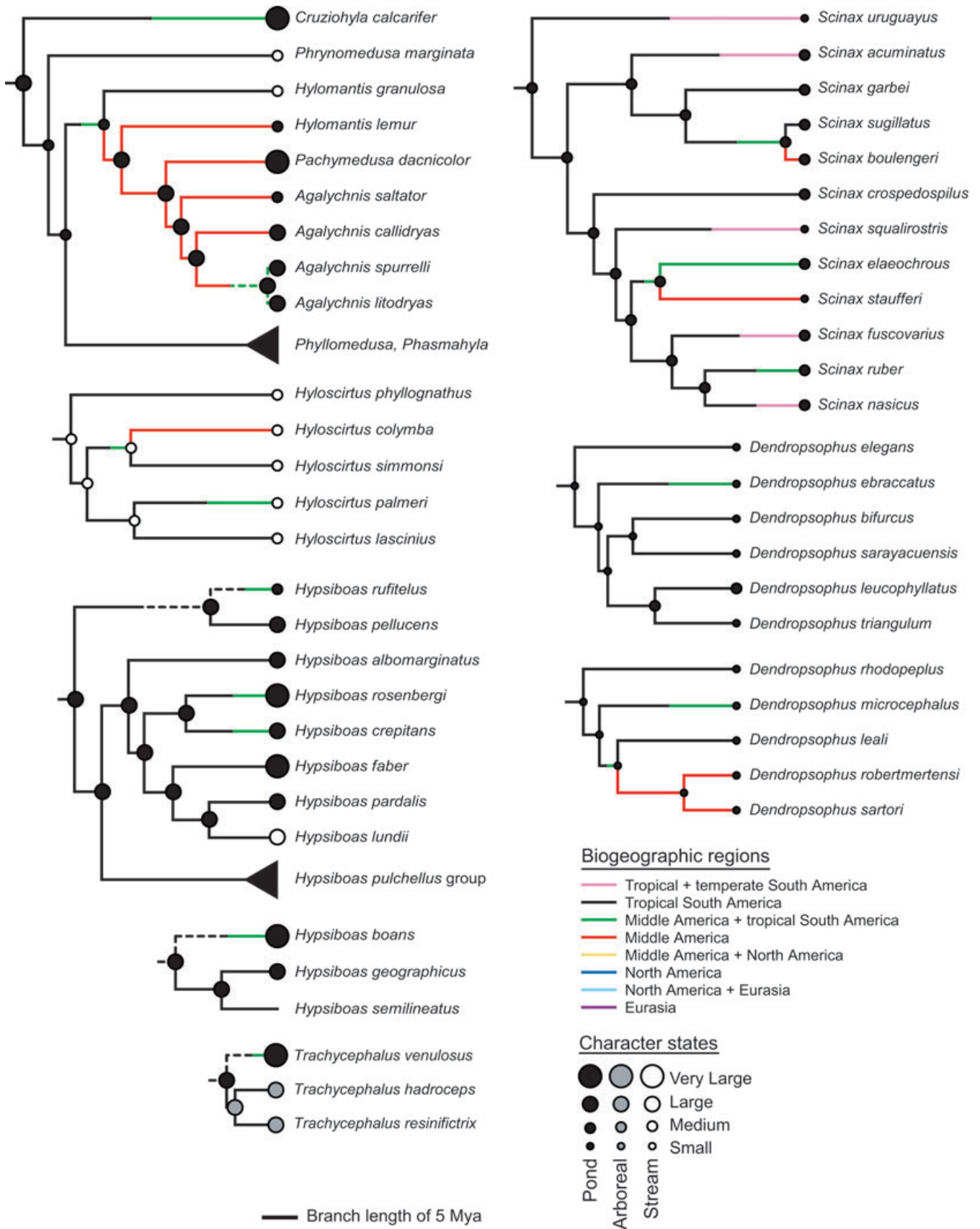


Figure 3a.

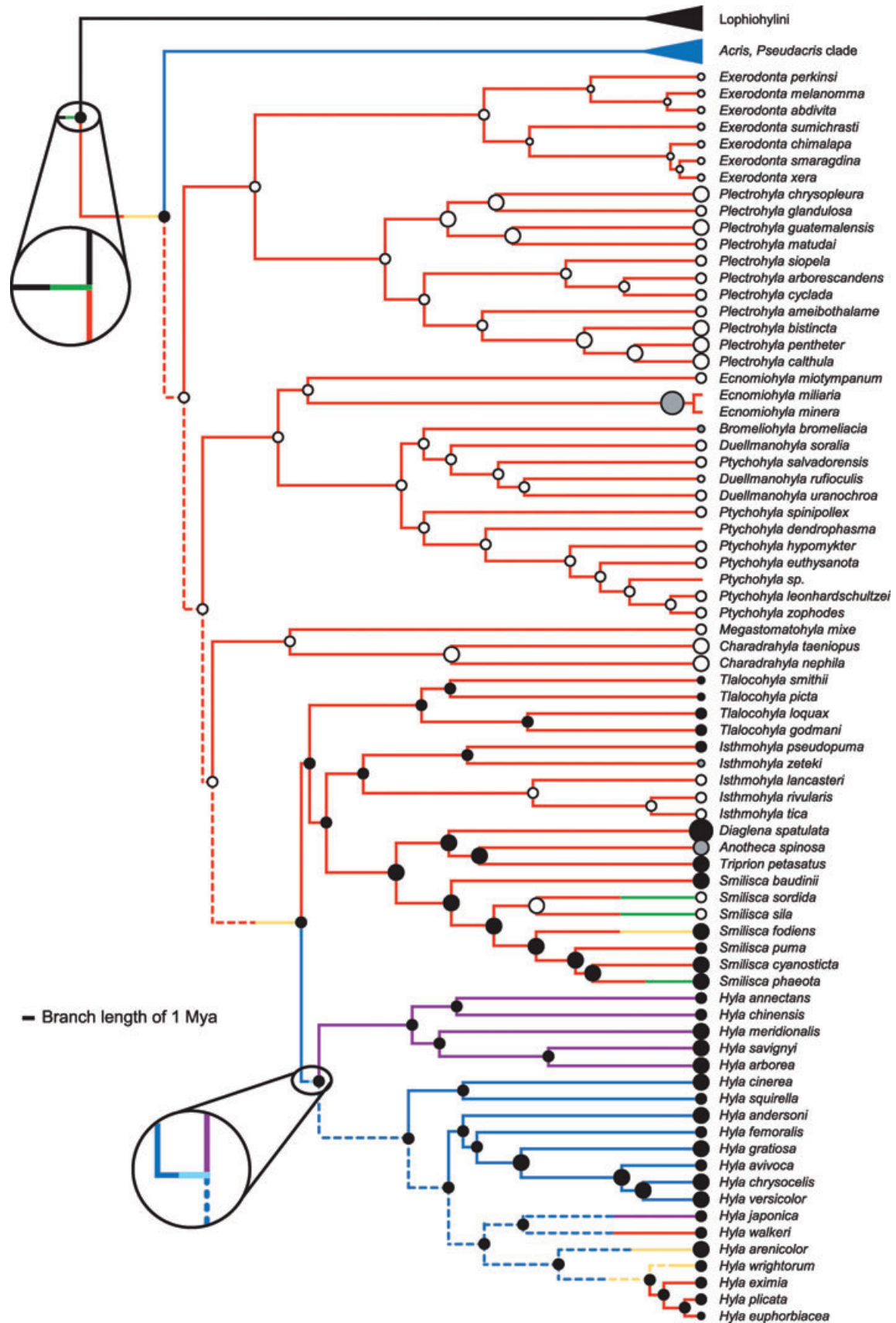


Figure 3b.

(J. J. Wiens, unpubl. data). Even when we increased the stringency for ecological similarity by reducing the body-size similarity cut-off, we still found many examples of co-occurring species that were very similar (e.g., in 15 of the 39 communities, there are 26 instances of co-occurrence of species that have the same larval habitat and adult body size within 2 mm of each other; Fig. S5).

There is a mixed relationship between the climatic distribution of lineages in Middle America and the climatic distribution of conspecific populations and closely related species in the inferred ancestral region. A strong positive correlation exists for precipitation ($r_s = 0.755$; $P = 0.005$; $n = 12$) but not temperature ($r_s = 0.406$; $P = 0.191$; $n = 12$). Note, however, that the lack of strong temperature correlation is mostly a consequence of the similarity in temperature values among most colonizing lineages, with limited variation between lineages that colonized warm areas and those that colonized cooler areas (Table 3). Most of the colonizing lineages dispersed from lowland tropical habitats in South America into similar habitats in Middle America, but biogeographic reconstruction indicated one invasion of relatively cool, dry montane habitats in Middle America from temperate montane habitats in semiarid western North America.

The estimated ages of species and clades show that the MAC is by far the oldest invasion of Middle America, and that all other invasions are considerably younger (Table 4). The MAC has undergone extensive in situ diversification since its colonization of the region, with 20 and nine ISE events in body size and larval habitat, respectively, within Middle America. The other 17 hyliid colonizations of Middle America have only resulted in a total of nine body-size and one larval habitat ISE events. Additionally, the rate of ISE is 0.355 body-size and 0.160 larval-habitat ISE events/My for the MAC. The average rate of ISE for all other

colonizations is 0.039 and 0.003 events/My (range: 0–0.222 and 0–0.051) for body size and larval habitat, respectively. When the MAC rates are statistically compared to those of the 16 subsequent colonizations, the former are significantly higher (body size: $t_s = 17.82$, $P < 0.0001$; larval habitat: $t_s = 44.44$, $P < 0.0001$). Although these comparisons are compromised by the many single-species colonization events (for which dates are uncertain and ISE unlikely), the rates for the MAC are still substantially higher than for all six other multispecies colonization events (body-size ISE: mean = 0.055, range = 0–0.153; larval habitat ISE: mean = 0.009, range = 0–0.051), a difference that is also statistically significant (body size: $t_s = 10.50$, $P = 0.0001$; larval habitat: $t_s = 16.41$, $P < 0.0001$). Overall, these results suggest that rates of ISE are lower in the lineages that colonized Middle America more recently.

However, when we estimated the rate of ISE per unit branch length, we did not find the MAC to be different when compared to the six more recent colonizations for rate of ISE in both body size (MAC = 0.023 ISEs/My; Others_{mean} = 0.019, SE = 0.009; $t_s = 0.329$, $P = 0.755$) and larval habitat (MAC = 0.010; Others_{mean} = 0.003, SE = 0.003; $t_s = 2.069$, $P = 0.093$). This result suggests that the rate of ISE in the MAC may not be exceptional, but the greater number of ISEs within that clade (relative to more recent colonizations) is due to its longer residence within the region and greater number of species.

Discussion

To what extent is local community structure determined by ISE or ECD of character states from outside the region? In this article, we address this question quantitatively for the first time, by developing new indices and applying them to the hyliid frogs of Middle

Figures 3. Cropped phylogeny figures showing ancestral character-state estimates for (1) body size, (2) larval habitat, and (3) biogeographic region, estimated by maximum likelihood (for the first two) and the DEC likelihood model (for the third). Phylogenies shown were chosen to illustrate the ISE and ECD events for Middle American treefrogs, but the entire phylogeny (Figs. S1–S3) was used to estimate ancestral states. Branch lengths indicate estimated ages of lineages based on penalized likelihood analysis using the younger set of calibration dates (see Materials and Methods for details). Branch colors reflect biogeographic designations (for species at tips) and ancestral-state estimates (for internal nodes), estimated under the DEC model of Ree and Smith (2008). This model distinguishes between range evolution along branches and changes that occur at cladogenesis events; thus, we show changes as occurring mid-branch (for changes along branches) or as vertical branches differing from their common ancestor (for changes at cladogenesis). Note that the position of changes along branches is arbitrary and was chosen for visual clarity. Branch colors reflect maximum-likelihood estimates (MLEs) of states, and dashed branches represent cases in which alternative reconstructions fell within two \log_e -likelihood units of the MLE (Ree and Smith 2008). In most of these latter cases the displayed resolution still had a much higher likelihood than all other possible resolutions, with the exception of the nodes in the vicinity of the Middle American *Hyla* in Figure 3b. Because of the extreme amount of ambiguity in this case (no potential resolution had a normalized likelihood higher than 0.44 and 3–5 alternative resolutions were possible), we considered it most likely that *Hyla* recolonized Middle America only once. However, considering this clade as representing multiple colonization events did not influence our results (not shown). In Figure 3b, we magnify two changes in ancestral range simply because they may be difficult to visualize at the original scale of the figure. Tips with no circles indicate taxa for which either body size, larval habitat, or both types of data were unavailable. The two colors of *H. arenicolor* represent both pond and stream breeding in this species. Finally, the circle left of *Ecnomihyla miliaria* and *E. minera* is for both taxa and their common ancestor (all the same states), but has been moved to facilitate visualization of the terminal branch lengths for these taxa.

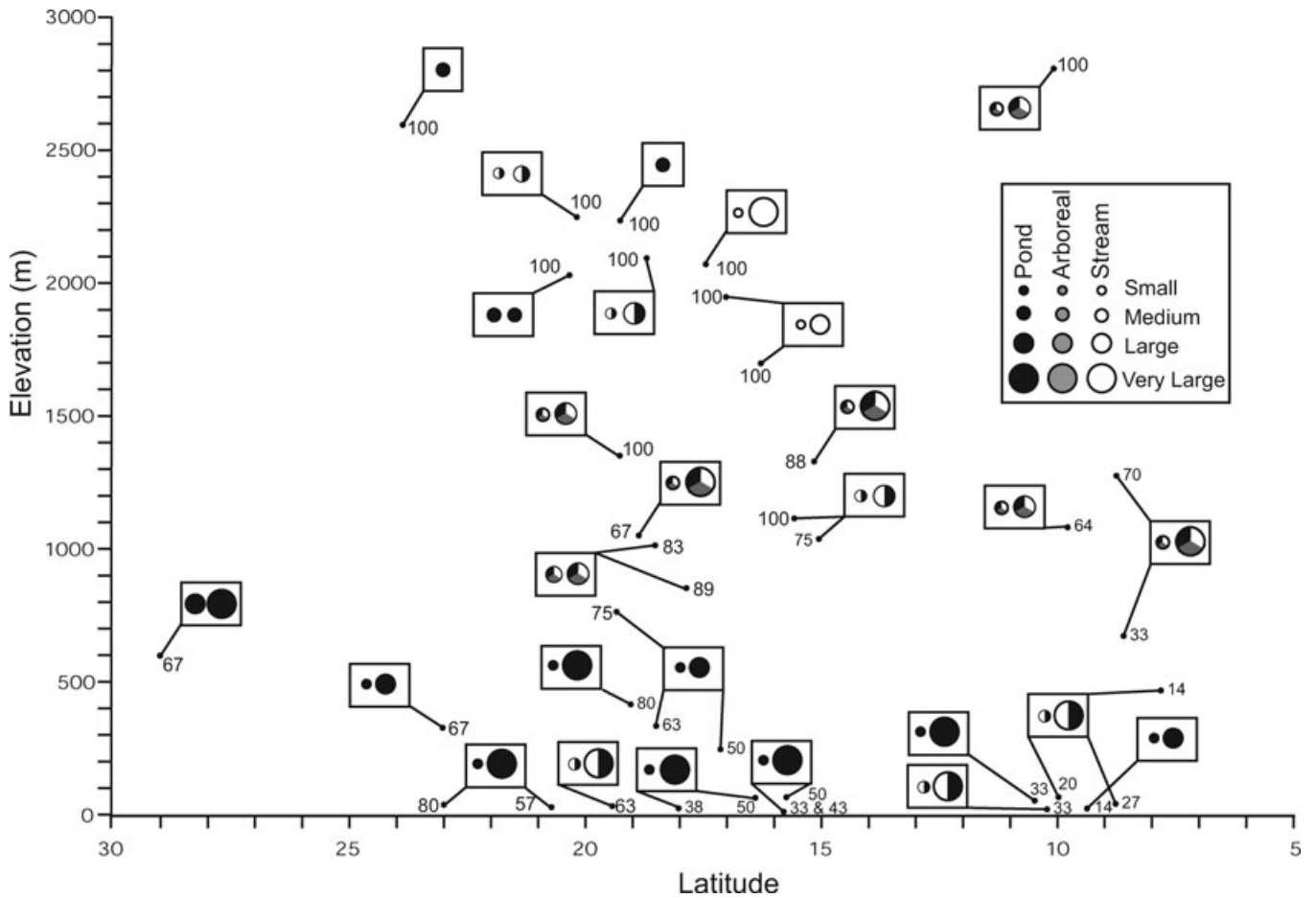


Figure 4. Simplified summary of the structure of 39 hylid frog communities in Middle America. Points indicate the latitude and elevation of each community, circles in boxes indicate the range of maximum male body sizes among species (circle size) and range of larval habitats (circle color) in each community. Boxes with only one circle indicate sites with only one species. The numbers next to each point indicate the percentage of species in the community belonging to the Middle American clade. In some cases, one box (summarizing body size and larval habitat) summarizes the ecological traits of two or more communities with similar trait ranges, as indicated by boxes connected to multiple points.

America. We find that the average ROTI among communities is 0.574 for body size and 0.579 for larval habitat, indicating that on average just over half of the species present in each community can trace their character states to ISE within the region. However, the proportion of character states in each community originating through each process varies considerably between characters and communities, with the proportion varying from 0 to 1 for each character, depending upon the community. We also found that patterns of ISE and ECD at the regional scale may not predict patterns at the local scale. For example, even though more origins of larval habitat in the region are through ECD (Table 1), within the local communities sampled, more communities are dominated by character-state origins through ISE. This disparity arises because many origins of larval habitat through ECD are somewhat limited in geographic extent, whereas two of those arising through ISE are widespread within the region.

Variation among communities in the proportion of character-state origins by ECD and ISE (i.e., the ROTI) is seemingly explained by complex patterns of trait evolution and dispersal. Biogeographic analysis suggests that the MAC of hylids were the first hylid treefrogs to enter Middle America, ~55–80 Mya (Table 4). This lineage then diversified into three montane stream-breeding clades (Fig. 3b), which have spread to many communities and diversified considerably in body size (Fig. 2). One clade within this montane, stream-breeding lineage evolved to use lowland ponds (*Isthmohyla*, *Smilisca* clade, *Tlalocohyla*; Fig. 3b) and also diversified considerably in body size (Figs. 2 and 3b). The pond-breeding clade then secondarily invaded streams in lower Central America (*Isthmohyla*, *Smilisca*), where most other stream-breeding clades are absent. The lowland clade also invaded temperate North America, Europe, and Asia, and then re-invaded the Middle

Table 1. Summary of the origins of each character state in Middle America (through in situ evolution or dispersal). The trait-origin dispersal index (TODI) indicates the spread of each trait origin among the sampled communities.

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

American highlands, likely from the western North American highlands (Smith et al. 2005). More recently (~20–30 Mya or later), the lowlands of Middle America were invaded by various South American hylid clades. These invasions consisted mostly of lowland pond breeders and included a broad range of body sizes. Some of these invasions spread throughout the Middle American lowlands (*Dendropsophus*, phyllomedusines, *Trachycephalus*, *Scinax*), whereas others remained in lower Central America (most *Hypsiboas*, some *Scinax*). There were also two invasions of Middle American highlands from a lineage of South American montane stream breeders (*Hyloscirtus*), but these two invasions were limited in their biogeographic extent, and are only represented in one of the 39 sampled communities. These recent invasions from South America show relatively little ISE, apart from some minor shifts in body size.

PRINCIPLES OF COMMUNITY ASSEMBLY

Despite this complexity, we suggest that a limited number of general principles may explain many of these patterns and that these principles may apply to many other organisms and regions. First, the temporal staggering of colonizations may explain which lineages have undergone extensive ISE and which have not. The MAC almost certainly was the first lineage to invade Middle America (Table 4), and it underwent extensive ISE in both body size and larval habitat. Other lineages invaded more recently, and most have undergone relatively limited diversification in body size and larval habitats within Middle America. Because rates of ISE were not higher for the MAC when we calculated ISE per unit branch length (see Results), our results suggest that the time available for speciation and ecological diversification within a colonizing group may be more important for ISE than ecological opportunity per se. The temporal staggering of hylid invasions was likely caused by the separation of Middle and South America during most of the Tertiary, and their more recent reconnection (Lomolino et al. 2006). We note that some of our estimated clade ages (Table 4) imply that treefrogs dispersed prior to the terrestrial reconnection of Middle and South America, but overwater dispersal of frogs no longer seems implausible (e.g., Evans et al. 2003; Vences et al. 2003).

Second, elevation seems to play an important role in driving patterns of community assembly, even though the relationship between elevation and the ROTI is not simple. Most highland communities are dominated by species of the in situ radiation (MAC), but both ECD and ISE contribute to both lowland and highland communities. For example, some species of the MAC are present in many lowland communities. Conversely, some South American clades extend into lower montane communities (e.g., 1000 m). Furthermore, a clade from North America (*Hyla*) has dispersed into many communities in northern Middle America, and these are the only hylids present in some high-montane communities.

Ecological differences between lineages inhabiting different elevations also play a role in driving patterns of community structure. For example, stream-breeding lineages dominate mid-elevation cloud forest habitats (where ponds may be rare) and pond-breeding lineages dominate lower-elevation communities (where high-gradient streams may be rare). There is also a trend for higher-elevation communities to lack species of the largest body sizes (maximum male size of the largest species in each community decreases with elevation; $r_s = -0.677$, $P < 0.001$; see also Fig. 4). This is associated with the negative correlation between elevation and the body-size ROTI, because most body-size evolution in the endemic MAC occurred at low elevations. High-elevation communities are dominated by moderate-sized species, which was the ancestral body size category of the MAC. We note that high latitude hylid communities also lack very large species (Moen and Wiens 2009), suggesting selection against large body

Table 2. Properties of communities included in this study. The regional trait origin index (ROTI), proportion of ISE events (PIE), and community trait dispersal index (CTDI) are defined in the text.

Locality number	Elevation (m)	Number of species in community	Latitude	Longitude	Body size			Larval habitat		
					ROTI	PIE	CTDI	ROTI	PIE	CTDI
1	597	3	29.217	-110.133	1.00	1.00	0.547	0.66	0.50	0.684
2	9	5	23.217	-106.417	1.00	1.00	0.369	0.80	0.50	0.697
3	2603	1	23.800	-105.400	0.00	0.00	0.103	0.00	0.00	0.179
4	11	8	19.533	-105.083	0.75	0.71	0.279	0.63	0.40	0.519
5	412	5	19.020	-102.100	1.00	1.00	0.369	0.80	0.50	0.697
6	2240	1	19.300	-99.117	0.00	0.00	0.103	0.00	0.00	0.179
7	2078	8	17.474	-100.196	0.50	0.50	0.333	1.00	1.00	0.359
8	2	6	15.850	-97.070	0.66	0.67	0.158	0.33	0.20	0.449
9	1768	8	16.204	-97.129	0.75	0.75	0.212	1.00	1.00	0.359
10	53	4	16.333	-95.233	1.00	1.00	0.481	0.50	0.33	0.596
11	361	3	23.050	-99.150	0.66	0.67	0.376	0.33	0.33	0.410
12	2007	3	20.367	-98.733	0.00	0.00	0.274	0.33	0.33	0.128
13	2253	4	20.183	-98.250	0.25	0.50	0.474	0.75	0.50	0.314
14	767	4	19.208	-96.808	0.75	0.75	0.468	0.75	0.50	0.622
15	1369	7	19.141	-96.991	0.43	0.75	0.487	1.00	1.00	0.374
16	2093	4	18.700	-97.317	0.50	0.67	0.340	0.75	0.50	0.314
17	1041	9	18.870	-97.030	0.56	0.57	0.447	0.55	0.50	0.382
18	1015	6	18.572	-95.169	0.83	0.80	0.462	0.83	0.75	0.441
19	350	8	18.583	-95.100	0.63	0.57	0.420	0.63	0.40	0.571
20	876	9	17.850	-96.333	0.44	0.80	0.499	0.88	0.75	0.330
21	30	8	18.090	-96.120	0.50	0.50	0.385	0.38	0.17	0.484
22	1942	6	17.149	-93.007	0.67	0.75	0.269	1.00	1.00	0.359
23	30	7	20.700	-88.467	0.57	0.50	0.469	0.57	0.25	0.571
24	254	8	17.225	-89.613	0.63	0.57	0.446	0.50	0.20	0.542
25	1324	8	15.083	-88.917	0.75	0.86	0.330	0.88	0.80	0.369
26	1085	8	15.083	-88.933	0.63	0.80	0.468	0.75	0.66	0.558
27	2	7	15.800	-84.300	0.57	0.57	0.403	0.43	0.80	0.516
28	1132	4	15.633	-86.792	0.75	0.75	0.365	1.00	1.00	0.449
29	10	6	15.783	-86.783	0.50	0.50	0.397	0.50	0.25	0.500
30	2802	5	10.133	-84.100	0.00	0.00	0.615	1.00	1.00	0.323
31	1172	11	9.850	-83.433	0.36	0.50	0.485	0.63	0.50	0.420
32	54	12	10.417	-83.950	0.58	0.60	0.289	0.33	0.14	0.452
33	38	11	8.700	-83.483	0.73	0.67	0.238	0.27	0.22	0.303
34	13	6	10.333	-85.200	0.50	0.50	0.291	0.33	0.33	0.303
35	1349	10	8.800	-83.000	0.40	0.57	0.431	0.70	0.67	0.300
36	27	7	9.223	-80.019	0.43	0.50	0.282	0.14	0.17	0.308
37	643	9	8.600	-80.133	0.56	0.57	0.221	0.33	0.38	0.231
38	490	7	7.700	-77.583	0.57	0.50	0.282	0.14	0.17	0.330
39	31	10	9.167	-79.833	0.60	0.63	0.276	0.20	0.25	0.319

sizes in cooler climates (but see Ashton 2002). The causes of these patterns in body-size evolution and distribution are unclear and deserve further study.

Elevation may also strongly influence community assembly through its effects on dispersal. The larval habitat CTDI is strongly negatively correlated with elevation, indicating that montane origins of larval habitat are not generally widespread, in contrast to

larval habitat origins at low elevations. This result suggests that a dispersal gradient may exist across elevations, with the most dispersal in the lowlands and the least dispersal in the highlands.

Third, limited climatic tolerances (i.e., niche conservatism) may help explain many patterns of dispersal and community assembly. Most cases of ECD involve invasion from climatically similar regions, such as the multiple invasions of tropical lowlands

Table 3. Summary of selected climatic niche characteristics of hylid lineages that have colonized Middle America and of their close relatives (or conspecific populations) that occur in their inferred ancestral geographic range.

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

in Middle America from tropical lowlands of South America, the invasion of cool, dry montane habitats (e.g., pine forest) from temperate North America (*Hyla*), and two invasions of tropical montane Central America from tropical montane South America (*Hyloscirtus*). Conversely, there were no invasions from the temperate lowlands of North America into tropical lowlands of Middle America, and only two invasions of temperate North America from Middle America (Smith et al. 2005; Wiens et al. 2006b). Furthermore, the general distinctness of lowland and highland communities may reflect specialization to different climatic regimes (although the different life-history modes of lowland and montane species may also be important). The climatic insularity of high elevation habitats may also explain why there seems to be more limited dispersal of character-state origins among montane communities relative to lowland communities, based on the CTDI.

Fourth, ECD of lineages into communities is not precluded by the presence of ecologically similar species in those communities. Instead, we find many cases in which species with similar body size and larval habitat co-occur. Of course, these species pairs may be differentiated in other characters besides these two, and more precise measurements of even these two characters might reveal important differences (but see Materials and Methods). We simply point out that overlap in these two characters does not seem to prevent co-occurrence, contrary to our initial expectations based on the principle of competitive exclusion (Morin 1999). In fact, some ecological theory suggests that ecological similarity among sympatric species may facilitate their co-occurrence under some conditions (e.g., Leibold and McPeck 2006; Scheffer and van Nes 2006). Additionally, previous research on ecologically similar frog species suggests that competition may affect abundance, but

need not preclude co-occurrence (Inger and Greenburg 1966). Finally, our results are consistent with those of Ernst and Rödel (2008), who suggested that similarity in breeding habitat did not influence community assembly in a South American hylid frog assemblage.

THE POTENTIAL ROLE OF COMPETITION

We see three major roles that competition might play in the assembly of Middle American hylid communities that should be addressed in future studies. First, competition may limit dispersal between different communities and different climatic regimes. For example, lineages invading from lowland South America may not extend into higher elevation communities because these communities are already occupied by hylid species, and resources may be too limited to support additional species (or simply too limited to favor niche expansion). We note that the majority of communities have 5–10 species (Table 2), and that most species belong to the MAC in higher elevation communities but less than half do in many lower elevation communities (Fig. 4). However, as mentioned above, limited climatic tolerances and differences in larval habitat may also constrain elevational shifts.

Second, in a similar vein, competition may limit niche shifts within communities. For example, stream breeding evolved in *Isthmohyla* and *Smilisca* only in lower Central America, where many other stream-breeding lineages are absent (e.g., *Charadrahyla* clade, *Plectrohyla* clade). Furthermore, we found that recently invading lineages showed reduced amounts of ISE, possibly because species of the MAC already evolved to occupy much of the available niche space, reducing selection for divergence in the more recent colonists (for other possible examples

Table 4. Estimated ages of dispersal events for hylid frogs colonizing Middle America from North and South America, showing that the Middle American clade colonized the region far earlier than any other hylid clade. Estimates are based on two potential root ages for Neobatrachia (100 Mya and 160 Mya). We present an interval of ages for each clade, with the more recent date indicating the crown-group age of the clade and the earlier date indicating the stem-group age. Thus, these intervals potentially bracket the date of colonization of Middle America, as inferred from our ancestral area reconstructions. Single species are those that either occur in both Middle and South America or are Middle American-endemic species that are nested within South American clades. Each represents a separate colonization event. The dates for these species merely indicate the estimated age of these species (i.e., the split from their putative sister species), and suggests only the earliest date at which they are likely to have colonized Middle America. See Methods for various caveats associated with these dates. Note that the date associated with *Cruziohyala calcarifer* is likely grossly overestimated, given that this species seemingly has a close relative in South America and only a limited distribution in Middle America.

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

see Losos et al. 1998; Wiens et al. 2006a; but see Kozak et al. 2009). However, this might also be a consequence of less time for speciation and ecological diversification in these more recently colonizing clades (i.e., rates of ISE are not higher in younger lineages when summed branch lengths are used).

Third, competition may drive trait divergence within communities, as suggested by the ecological theory of adaptive radiation (Schluter 2000). The repeated evolution of extreme body sizes within major lineages of the MAC may reflect divergence driven by competition (e.g., Moen and Wiens 2009), coupled with the general separation of highland and lowland faunas and the shifting mosaic of lineages present in different highland communities (see Table S1). Intriguingly, despite the potential role of competition in causing and/or constraining evolutionary changes in these characters, we found little evidence that competition prevents the co-occurrence of species having similar values for these traits.

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Supporting Information

The following supporting information is available for this article:

- Table S1.** Estimates of local species composition at 39 sites in Middle America based on data summarized by Duellman (2001).
- Table S2.** Data on body size and larval habitat and original literature sources.
- Table S3.** Morphometric data for hylid frogs.
- Table S4.** Results of principal components analysis (PCA) on the hylid morphometric data (Table S3), showing the loadings of each original variable on PC1 (left) and the proportion of the total variation represented by each PC axis (right).
- Table S5.** Results of ROTI null model analyses for body size, showing ROTI value for each community, and its associated *P*-value under different regional pools.
- Table S6.** Results of ROTI null model analyses for larval habitat, showing ROTI value for each community, and its associated *P*-value under different regional pools.
- Figure S1–S3.** Phylogeny of Hylidae that was used for all analyses, estimated by (1) separate Bayesian analyses of each major South American clade (from Moen and Wiens 2009) and the Middle American clade (Smith et al. 2007), (2) converting branch lengths into units of time using the program r8s, and (3) connecting these clades together by placing on an ultrametric phylogeny (with branch lengths in units of time) of Hylidae, as estimated by Wiens et al. (2006b).
- Figure S4.** Effect of community size on the power of ROTI null model analyses.
- Figure S5.** Results of varying the body-size cutoff for our ecological similarity analyses.
- Appendix S1.**

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

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

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