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Explaining Species Richness from Continents to Communities: The Time-for-Speciation Effect in Emydid Turtles

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ABSTRACT: Speciation is the process that ultimately generates species richness. However, the time required for speciation to build up diversity in a region is rarely considered as an explanation for patterns of species richness. We explored this "time-for-speciation effect" on patterns of species richness in emydid turtles. Emydids show a striking pattern of high species richness in eastern North America (especially the southeast) and low diversity in other regions. At the continental scale, species richness is positively correlated with the amount of time emydids have been present and speciating in each region, with eastern North America being the ancestral region. Within eastern North America, higher regional species richness in the southeast is associated with smaller geographic range sizes and not greater local species richness in southern communities. We suggest that these patterns of geographic range size variation and local and regional species richness in eastern North America are caused by glaciation, allopatric speciation, and the time-for-speciation effect. We propose that allopatric speciation can simultaneously decrease geographic range size and increase regional diversity without increasing local diversity and that geographic range size can determine the relationship between α, β, and γ diversity. The time-for-speciation effect may act through a variety of processes at different spatial scales to determine diverse patterns of species richness.

Keywords: species richness, macroecology, phylogeny, speciation, Emydidae.

Explaining patterns of species richness is a central problem in ecology and biogeography. Speciation is the process that ultimately generates species richness, but in the recent literature speciation is rarely invoked directly when explaining patterns of species diversity. The ability of speciation to build up species richness in a region may be constrained by two factors: space and time (Rosenzweig 1995). The extent to which speciation (and thereby species richness) is constrained by area has been demonstrated for *Anolis* lizards on Caribbean islands by Losos and Schluter (2000). Their results suggest that speciation can occur within relatively small areas (e.g., islands as small as approximately 3,000 km^2). Time may be as important as area in limiting species richness. For example, when members of a lineage first colonize an island or continental region, it may take hundreds of thousands or even millions of years for speciation to occur and build up species richness in situ (given that modern species are typically 300,000 to 7 million years old; Avise 2000). However, the constraints of time on speciation have been largely ignored in recent studies of species richness (but see Gaston and Blackburn 1996; Brown et al. 2000; McPeek and Brown 2000). We refer to disparity in species richness between regions or habitats that is caused by limited time for speciation as the time-for-speciation effect.

Despite its current neglect, the idea that patterns of species richness are related to how long members of a group have been present in a region has a long history. During most of the twentieth century, it was assumed that a group of organisms will be most diverse in the region where the group originated (Willis 1922), and this was a widely accepted explanation for the high species richness of many groups in tropical regions (e.g., Axelrod 1952; Darlington 1957; Cronquist 1968; Stebbins 1974). However, this hypothesis has become relatively neglected in recent years. For example, it is not mentioned in a recent community ecology textbook (Morin 1999) and is not presented as a current hypothesis in a recent biogeography textbook (Brown and Lomolino 1998). The importance of time to patterns of species richness has been discussed in some recent literature as the ecological and evolutionary

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time hypotheses (Pianka 1966, 2000; Gaston and Blackburn 2000). These hypotheses state that species richness in a region may be limited when there is too little time for either colonization (ecological time) or niche diversification and speciation (evolutionary time). The evolutionary time hypothesis, clearly related to the time-for-speciation effect, has only been discussed in relatively few recent studies (e.g., Rohde 1986, 1992; Bush et al. 1990; Gaston and Blackburn 1996; Andersen 1999). Conversely, despite the lack of interest in the general relationship between time and geographic patterns of species richness, there is intense research interest in groups that seem to be undergoing unusually rapid speciation (e.g., Baldwin and Sanderson 1998; Albertson et al. 1999; Lovette and Bermingham 2000; Schluter 2000; Magallón and Sanderson 2001; Richardson et al. 2001*a*, 2001*b*).

In this article we test the importance of the time-for-speciation effect on regional and local patterns of species richness in emydid turtles. The Emydidae is an excellent model system because the overall species richness and geographic distributions of individual species appear to be relatively well known (Iverson 1992). The Emydidae contains 40 currently recognized species in 10 genera (Ernst and Barbour 1989; Ernst et al. 1994; Vanzolini 1995) and includes many familiar North American turtles such as the painted turtles (*Chrysemys*), box turtles (*Terrapene*), and sliders (*Trachemys*). Although a few ambiguities remain in the species-level taxonomy of some emydids (Legler 1990; Seidel 1994; Lenk et al. 1999; P. R. Stephens and J. J. Wiens, unpublished manuscript), only a handful of species have been described in the last quarter century (Ward 1984; Lovich and McCoy 1992; Vanzolini 1995), which suggests that few species remain undescribed. Emydids are found in Europe, North America, Central America, South America, and the West Indies (Ernst and Barbour 1989). The family is ecologically diverse and includes herbivores, molluscivores, insectivores, and omnivores; species are found in brackish water, freshwater, and terrestrial habitats (Ernst et al. 1994). Emydids are a common and ecologically important group in North America and may be the major vertebrate component (in terms of biomass) of some freshwater communities due to large body size and high local abundance (Bury 1979).

There are two major patterns of emydid species richness to explain. First, eastern North America has much higher species richness than any other continental region, both at regional and local scales (fig. 1*A*). Regions of low emydid species richness are ecologically varied (temperate, tropical, arid, mesic), suggesting that no single environmental factor explains their low diversity. Furthermore, many emydid-poor regions are extremely large (e.g., Europe, South America), which suggests that speciation is not constrained by the size of these regions (Losos and Schluter 2000). Given these observations, the time-for-speciation effect is an obvious hypothesis to test.

Second, there is higher species richness in southeastern North America than in northeastern North America (fig. 1*B*). If the range of the Emydidae in eastern North America is divided at its latitudinal midpoint (37.5°), there are approximately twice as many species in the southern half as in the northern half (Iverson 1992; Ernst et al. 1994). Due to widespread species that occur in both southeastern and northeastern North America, the relative age of the family in each region is not easily determined, and the time-for-speciation effect could not be addressed directly. Patterns of species richness within eastern North America required an interconnected series of analyses to explain.

We first tested the hypothesis that regional patterns of species richness in eastern North America are related to differences in local species richness. Many studies have demonstrated that regional and local species richness tend to be correlated (e.g., Cornell 1985; Hawkins and Compton 1992; Caley and Schluter 1997; Shurin et al. 2000). Given that more species of emydids are found in southeastern than in northeastern North America (fig. 1*B*), we expected that more emydids would coexist locally in southeastern communities. This pattern would correspond to one of the most widespread trends in species richness: a negative correlation between latitude and species richness (i.e., increasing species richness from temperate to tropical regions; Fischer 1960; Pianka 1966; Brown and Lomolino 1998). Numerous hypotheses have been proposed to explain this pattern (Pianka 1966; Rohde 1992; Rosenzweig 1995; Brown and Lomolino 1998; Morin 1999), and many invoke local-scale ecological processes (e.g., abiotic "harshness," productivity). A negative correlation between local-scale species richness and latitude in eastern North America would support the hypothesis that local-scale ecological processes caused the higher emydid species richness of southeastern North America. Surprisingly, our results rejected this simple explanation, showing instead that local species richness is similar between southeastern and northeastern North America (fig. 1*B*).

We next tested the hypothesis that the higher species richness of southeastern North America is related to latitudinal variation in average geographic range size. Many authors have addressed the relationship between species richness and range size (e.g., Stevens 1989; Letcher and Harvey 1994; Brown 1995; Stone et al. 1996; Brown and Lomolino 1998; Gaston et al. 1998; Willig and Lyons 1998; Colwell and Lees 2000). A common pattern in temperate regions is for species at higher latitudes to have larger geographic ranges than those at lower latitudes (i.e., Rapoport's rule; Stevens 1989; Brown and Lomolino 1998; Gaston et al. 1998). If the average range size of southeastern emydid species is smaller (as implied by Hecnar

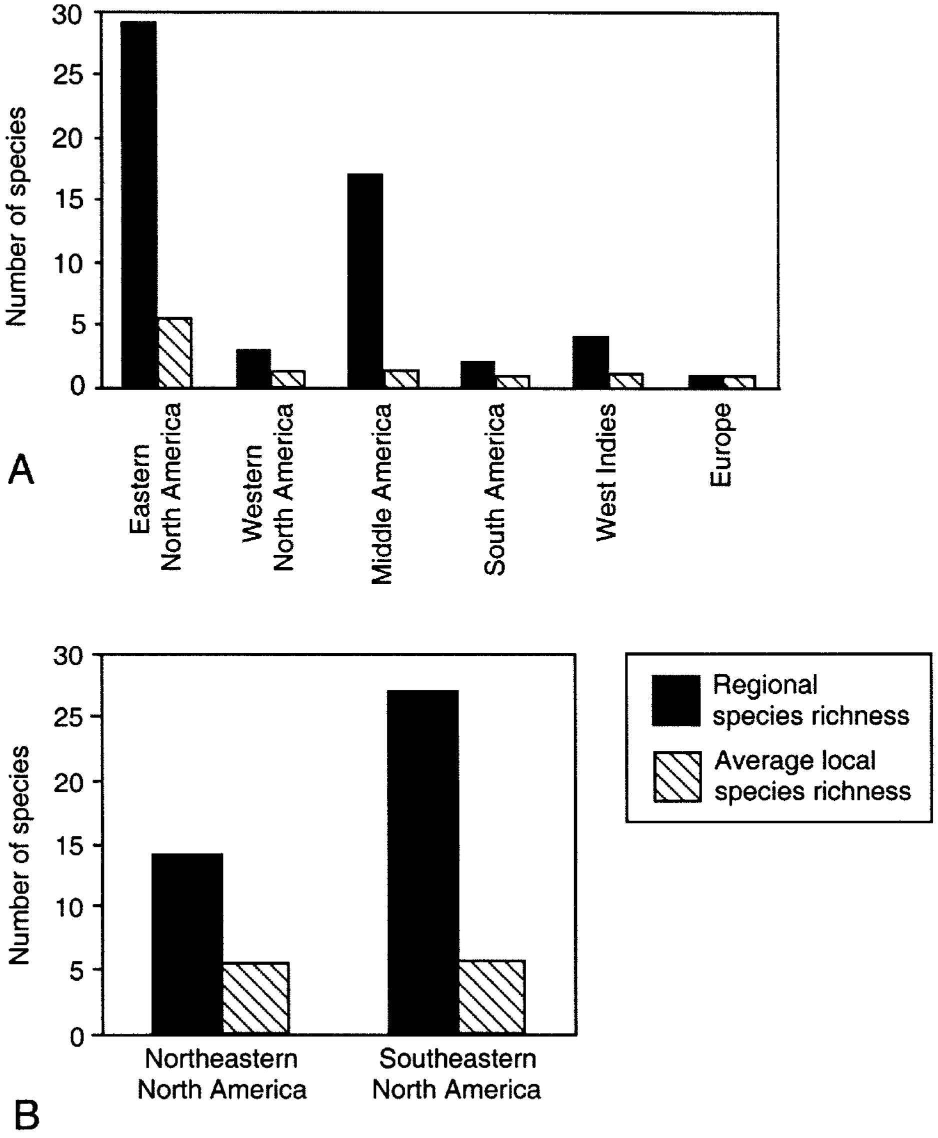

Figure 1: Patterns of local and regional species richness in emydid turtles between (*A*) continental regions and (*B*) southeastern and northeastern North America. Subspecies of *Trachemys scripta* endemic to Middle America are treated as species for this figure (the number of currently recognized species in Middle America is only four). Values of local species richness were calculated by averaging the maximum number of species estimated for each community across the communities in each region.

[1999]), it could allow more species to be "packed" into the region (Stevens 1989) without increasing local diversity.

We also investigated the mode of speciation in emydids. Mode of speciation (e.g., allopatric, sympatric) is rarely addressed in studies of species richness, but it can be important to the overall picture of species richness because different modes will affect diversity at different scales (i.e., regional vs. local). For example, a species generated by sympatric speciation will increase both local and regional species richness because it is added to existing communities. Conversely, a species generated by allopatric speciation is not "added" to a local community because it is a geographic fragment of an ancestral species. Such a species will increase regional species richness but will have no immediate effect on local species richness. Furthermore, species generated by allopatric speciation may often have smaller geographic ranges (at least initially) than the species they are descended from (Brown and Lomolino 1998). Allopatric speciation would provide a mechanism that could increase regional species richness and decrease average geographic range size in southeastern North America while maintaining similar local species richness between the southeast and the northeast.

In this article we show how the time-for-speciation effect has either directly or indirectly caused the two major trends in emydid species richness (fig. 1): the higher species richness of eastern North America compared to peripheral continental regions and the higher regional species richness of southeastern North America compared to northeastern North America. We also discuss the broader implications of our findings for latitudinal trends in species richness, geographic range size variation, and the relationship between regional and local species richness.

Material and Methods

For all analyses, data on species distributions were obtained from Smith and Smith (1979; Mexico), Seidel (1988; West Indies), Legler (1990; Mexico and Central America), Iverson (1992; Eastern Hemisphere and South America), and Ernst et al. (1994; North America). The phylogeny used was based on a combined analysis of morphological and molecular data that included all but one currently recognized species of emydid turtle (P. R. Stephens and J. J. Wiens, unpublished manuscript). Morphological data consisted of 237 parsimony-informative characters of osteology, external morphology, penial morphology, egg shell morphology, development, behavior, and allozymes. Molecular data included sequences from the cytochrome *b*, control region, ND4, and 16S mitochondrial gene regions (547 parsimony-informative characters; from the literature, e.g., Lamb et al. 1994; Lenk et al. 1999; Feldman and Parham 2002). Although some parts of this tree are weakly supported by bootstrapping (Felsenstein 1985*a*), this weak support was associated with including a few taxa with highly incomplete data. When these highly incomplete taxa are removed, the result is a "backbone" tree with generally high levels of bootstrap support (P. R. Stephens and J. J. Wiens, unpublished manuscript). This strongly supported tree is consistent with the comprehensive tree used in this study.

Patterns of Species Richness between Continental Regions

To address continental patterns of species richness, we examined the relationship between regional diversity and the estimated time when emydids colonized a region (based on levels of molecular and morphological divergence) using least squares linear regression. We first analyzed the relationship between the timing of each colonization event and the number of species of the dispersing lineage in the colonized region (i.e., we treated multiple invasions of the same region as separate data points). This analysis tested whether lineages that have been in a region for longer amounts of time will have more species in that region, as would be expected if there is a time-for-speciation effect in emydid turtles. We then examined the relationship between the species richness of each region and the relative age of the first emydid lineage to colonize that region. This analysis tested whether the time-for-speciation effect explains the relative species richness of each continent-scale region.

Dispersal between regions was localized on specific branches of the phylogeny using parsimony reconstruction (see below), and the relative timing of these events was estimated based on the depth of those branches in the tree (i.e., summing branch lengths). Our approach assumes that the relative timing of a colonization event approximates the relative age (divergence time) of the branch on which the colonization event is inferred (i.e., the branch on which a change between continental regions is reconstructed). Relative divergence times were estimated independently based on morphological and molecular branch lengths.

Molecular branch lengths were estimated using maximum likelihood analyses of mitochondrial cytochrome *b* sequences, the molecular data set that was the most thoroughly sampled for emydid taxa (Lamb et al. 1994; Lenk et al. 1999; Feldman and Parham 2002). Likelihood parameters were estimated using the best-fitting model of sequence evolution (GTR + G; Rodriguez et al. 1990), using PAUP* version 4.0b8a (Swofford 2002). MODELTEST version 3.06 (Posada and Crandall 1998) was used to select the model of sequence evolution that best fit the cytochrome *b* data via a hierarchical likelihood ratio test. Note that the topology used to estimate branch lengths was based on all the molecular and morphological data, not on a separate analysis of the cytochrome *b* data alone. Estimating divergence times directly from branch lengths assumes a constant rate of evolution between lineages over time (i.e., clocklike behavior; Hillis et al. 1996). To test this assumption with cytochrome *b* sequences, a likelihood-ratio test was performed comparing the likelihood of our best-fitting model to that of the same model with a molecular clock enforced (Goldman 1993; Huelsenbeck and Crandall 1997). This test rejected strict rate constancy between lineages (likelihood-ratio test statistic $= 33.3$, $df = 31$, $P > .20$). We therefore used Sanderson's nonparametric rate smoothing method (NPRS; Sanderson 1997), which is robust to violations of rate constancy, to determine relative divergence times. The NPRS method was performed using TreeEdit version 1.0α8 (Rambaut and Charleston 2001).

No sequence data were available for Neotropical *Trachemys*. However, based on the topology of the combined-data tree, invasions of Mexico and the West Indies by *Trachemys* seemingly occurred after the origin of the North American clade of *Trachemys scripta* and before the origin of the *Graptemys* + *Malaclemys* clade (P. R. Stephens and J. J. Wiens, unpublished manuscript). These "bracketing" divergences were used to obtain molecular estimates of the minimum and maximum ages for the colonization of Mexico and the West Indies by *Trachemys*, and analyses were repeated using both estimates for the age of each invasion. Results were similar using both estimates, and only those using maximum ages are reported.

Due to the lack of molecular data for some taxa, the relative ages of several colonization events could not be estimated from molecular data. We therefore repeated these analyses using branch lengths based on parsimony analysis of the external morphological data (109 characters, available for all but two of 64 taxa) using ACCTRAN character optimization (DELTRAN gave similar results in other analyses; see "Results"). The NPRS method, which can be applied to any set of nonzero branch lengths, was used to estimate relative divergence times from morphological branch lengths.

To account for ambiguities in the species-level taxonomy of emydids, the preceding analyses were repeated using both minimum and maximum estimates of emydid species richness in each region. The minimum estimate used only currently recognized species whereas the maximum estimate counted geographically isolated subspecies as distinct species. Regression analyses were performed using Statview version 4.51 (Roth et al. 1995). Relative age and species richness were significantly correlated ($P < .05$) in all analyses, with one exception. An analysis that compared the minimum number of emydid species in each region to the age of the oldest emydid lineage in each region based on molecular data, and using the minimum age estimate for West Indian *Trachemys*, did not show a significant correlation ($r^2 = 0.711$, $P = .073$). However, there is abundant evidence that many currently recognized emydid species are polytypic (Legler 1990; Lenk et al. 1999; P. R. Stephens and J. J. Wiens, unpublished manuscript), and all results using these higher estimates of regional species richness were significant. Only results using the maximum number of species and estimated lineage age in each region are reported. All analyses of age and species richness were repeated using natural log transformed estimates of species richness, because many models of diversification predict an exponential relationship between lineage age and species richness (Sanderson and Donoghue 1996; Schluter 2000). Results were similar to those using untransformed estimates of species richness and are not reported.

Colonization events were inferred by coding the regional distribution of each species as a character state and reconstructing changes on the phylogeny with parsimony. We used the following character states: (0) eastern North America, (1) western North America, (2) Middle America, (3) South America, (4) the West Indies, and (5) Europe. These regions are of sufficient size that each contains a largely unique emydid fauna. Species distributions were first mapped onto the tree as unordered characters and coding polymorphisms in distribution (i.e., a single taxa that occurred in more than one region) using the "polymorphic" method (sensu Wiens 1995, 1999). Thus, species found in two regions were treated as occurring in only one during reconstructions (with the state chosen to maximize global parsimony). Although this coding method is widely used, it is potentially problematic for ancestral state reconstructions (Wiens 1999), and so an analysis was also performed in which polymorphisms were coded with step matrices using the scaled method (see Mabee and Humphries 1993 for a detailed description and Wiens 1999 for justification of the use of this method in ancestral state reconstructions). A third analysis was performed in which polymorphisms were coded using step matrices and in which transitions between states were also weighted based on the simplified proximity of the six areas (e.g., a change from Middle America to South America is easier than a change from South America to North America). Analyses were performed with MacClade version 3.04 (Maddison and Maddison 1992).

Relationship between Regional and Local Species Richness

Based on regional trends in emydid species richness (i.e., higher species richness in eastern North America relative to other regions and higher species richness in the southeast than in the northeast), we expected local species richness to be positively correlated with latitude in the Western Hemisphere and negatively correlated with latitude in eastern North America. We tested these hypotheses by regressing community species richness against community latitude in two separate analyses. One analysis used communities from throughout the range of the Emydidae in the Western Hemisphere ($n = 65$), whereas the other used only communities from eastern North America ($n = 46$). River drainages and islands were used as units to estimate local species richness (fig. 2). For each drainage or island, local species composition was tabulated where the maximum number of species overlapped, based on the geographic references listed above. For most of the range of the Emydidae, individual drainages and islands were chosen to represent unique assemblages of species (areas of geographic-range overlap between species). In cases where a particular assemblage covered a wide geographic area, a

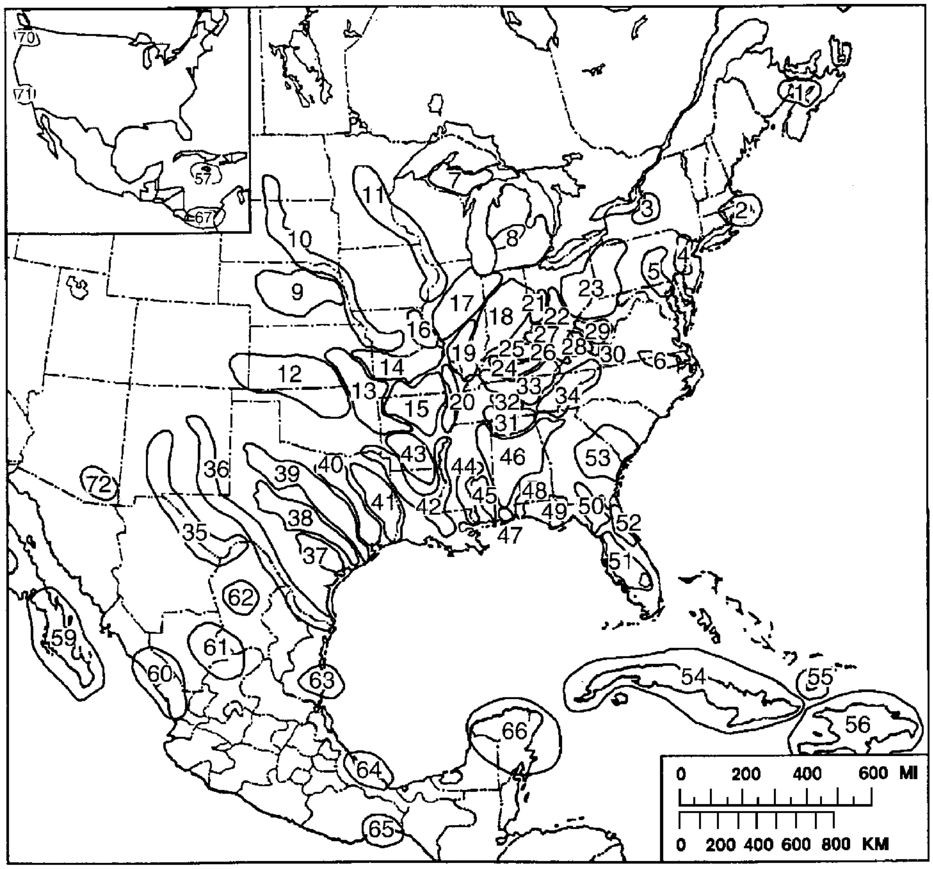

Figure 2: Drainages, islands, and other areas used to estimate the maximum number of species in local communities. Numbers indicate the following areas (all names indicate river drainages unless stated otherwise): central and eastern North America: (1) Nova Scotia between Bay of Fundy and Northumberland Strait; (2) Sakonnet; (3) Oswego and other drainages connected to southeast Lake Ontario; (4) Delaware; (5) Susquehanna; (6) Roanoke; (7) western state of Michigan; (8) Muskegon; (9) central Nebraskan drainages including Platte, Loupe, North Loupe, South Loupe, Cedar, Elkhorn; (10) upper Missouri; (11) upper Mississippi; (12) upper Arkansas; (13) middle Arkansas (in eastern Kansas and Oklahoma); (14) Osage, Gasconade, and Meremec; (15) White, Eleven Point, Current, Black; (16) Salt; (17) Illinois; (18) Wabash; (19) Kaskaskia, Big Muddy; (20) Saint Francis; (21) Miami; (22) Scioto; (23) upper Ohio; (24) Green; (25) Salt (in state of Kentucky); (26) Kentucky; (27) Licking; (28) Big Sandy; (29) lower Kanawha; (30) upper Kanawha; (31) lower Tennessee; (32) Duck; (33) Cumberland; (34) upper Tennessee; (35) upper Grande; (36) Pecos; (37) San Antonio, Guadalupe; (38) Colorado; (39) Brazos; (40) Trinity; (41) Neches, Sabine; (42) lower Mississippi; (43) Ouachita; (44) Pearl; (45) Pascagoula; (46) Alabama, Tombigbee; (47) Mobile Bay; (48) Escambia; (49) Apilachicola; (50) Suwannee; (51) Withlacoochee, Peace, Caloosahatche; (52) St. John's; (53) southeast North American Atlantic coastal drainages (from Edisto south to Altamaha). West Indies: (54) island of Cuba; (55) Great Inagua island; (56) island of Hispaniola; (57) island of Jamaica; (58) island of Puerto Rico (not depicted). Middle America: (59) southern peninsula of Baja California; (60) regions of Culiacán and Sinaloa (to Cabo Corientes); (61) Nazas; (62) basin of Cuatro Cienegas in Coahuila; (63) San Fernando; (64) southern state of Veracruz; (65) coast of Oaxaca; (66) Yucatan peninsula; (67) Republic of Panama. South America: (68) northern Republic of Venezuela (not depicted); (69) Uruguay (not depicted). Western North America: (70) Columbia; (71) central state of California; (72) southeastern Arizona.

drainage was chosen to represent the assemblage from near the latitudinal center. In much of central eastern North America, patterns of range overlap were so complex that picking out all unique assemblages by eye became problematic. Therefore, within this area, the drainages from Mayden's (1988) study of the historical biogeography of the fish fauna were used. Drainages with identical emydid species composition and similar vicariant histories were collapsed into a single unit. A few groups of drainages had dissimilar vicariant histories but identical species compositions. From each of these groups of drainages, only one (chosen at random) was used in any analysis. In summary, each data point represented a different combination of species, and each unique assemblage of emydids in eastern North America was represented by a single data point. The latitudinal midpoints of all drainages and islands were determined by reference to a world atlas (Christie et al. 1991).

Drainages and islands represent a scale larger than what some might consider to be good units of local species richness. The number of species found in each drainage or on each island should indicate the maximum number of species that may occur sympatrically in any community but may not reflect the minimum (i.e., a given pond, river, or meadow could have fewer species of emydids than the number we infer for a given "community" but could not have more). However, because each drainage or island (hereafter referred to as a community) was chosen to represent a unique assemblage, subdividing them would presumably have produced similar results only with more nonindependent data points. Raw data on the species composition and latitude of these communities are available from the authors.

In order to more directly investigate the relationship between local and regional species richness, the number of species in each community was regressed against the number of species in the region in which the community occurs (using the continent-scale regions defined above). The communities were the same as in the previous analysis, although three communities were added to represent Europe and northern Africa ($n = 68$). A similar analysis was performed using only communities in eastern North America ($n = 46$) and dividing eastern North America into southern and northern regions at 37.5° north latitude (the latitudinal midpoint of the range of the Emydidae in North America). The preceding analyses violated an assumption of regression analysis in that many data points could be sampled from a given region, and thus the values of the independent variable (regional species richness) were not independent for all data points. Sampling multiple communities from the same region is also problematic because it inflates the number of regional-local data points (Caley and Schluter 1997), which leads to a P value that is not sufficiently conservative. We therefore repeated these analyses using regions as data points and averaging local species richness across the communities in each region. We also repeated all analyses using minimum and maximum estimates of the number of species in each region as described above. Results were similar using both estimates, and only those using the maximum number of species for each region are reported.

Geographic Range Size Variation

To investigate latitudinal trends in geographic range sizes, range maps of species that occur in eastern North America were digitized and fitted onto an Alber's equal area projection map of the continental United States. The latitudinal midpoint and the area of each species' geographic range were then calculated using the public domain NIH Image program (developed at the National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). Because characteristics that determine geographic range size may be inherited phylogenetically (e.g., Jablonski 1987; Price et al. 1997), we tested the relationship between range size and latitude in a phylogenetic framework using Felsenstein's (1985*b*) independent contrasts method. Analyses used a pruned version of the combined-data tree used elsewhere but included only the 30 taxa that occur in eastern North America.

The use of independent contrasts requires specification of branch lengths, and this was dealt with in two ways. First, branch lengths were estimated from the external morphological data using parsimony (PAUP* 4.0b8a). These data were available for the largest number of relevant taxa. This analysis assumes that the extent of morphological divergence generally reflects the relative amounts of time between speciation events (gradual model, sensu Martins and Garland 1991). Because branch lengths estimated using parsimony may vary depending on character optimization, we used both ACCTRAN and DELTRAN optimizations (Swofford and Maddison 1987) to assess the sensitivity of the results. Second, all branch lengths were assumed to be equal and were arbitrarily set at 1 (the punctuational model of Martins and Garland [1991]).

To verify that independent contrasts were adequately standardized by their estimated branch lengths, the absolute values of each independent contrast for each node were regressed on their standard deviations (the square root of the sum of the branch lengths for that contrast), following Garland et al. (1992). Most contrasts were adequately standardized ($P > .100$), and no further transformation of the data or branch lengths was considered necessary. However, contrasts in geographic range area were positively correlated with their standard deviation when using ACCTRAN optimization to estimate branch lengths. Contrasts were recalculated in this case using squared branch lengths (following Garland et al. 1992). This transformation adequately standardized the ACCTRAN-based contrasts in geographic range area ($r^2 = 0.027$, $P = .391$).

Independent contrasts and standard deviations for each branch and character were obtained using COMPARE version 4.4 (Martins 2001). The relationship between contrasts for each pair of variables was examined using least squares linear regression, which forced the model through the origin (as recommended by Garland et al. 1992), with significance levels based on the regression coefficients.

Mode of Speciation

We used Lynch's (1989) method to determine which geographic mode of speciation predominates in emydids. Using this method, sister taxa generated by allopatric speciation are assumed to have little overlap in their geographic ranges, whereas sister taxa generated by sympatric speciation are expected to have extensive overlap. Range maps for sister species (based on P. R. Stephens and J. J. Wiens, unpublished manuscript) were superimposed graphically, and the area of overlap in geographic ranges was calculated using NIH Image. Because dispersal is expected to obscure patterns of distribution indicative of different modes of speciation given enough time (Lynch 1989; Chesser and Zink 1994; Barraclough and Vogler 2000), only the most recent speciation events were considered (i.e., only sister species). This restriction is a conservative modification of Lynch's method and is intended to minimize the effects of dispersal. All subspecies of *Trachemys scripta* endemic to Middle America were treated as separate species in this analysis because of evidence that at least some are distinct species (Smith and Smith 1979; Ernst and Barbour 1989). Areas of overlap were transformed into percentage overlap by dividing the area of overlap in geographic ranges by the geographic range area of the species having the smaller range (Lynch 1989). According to Lynch's (1989) criterion, species with less than 10% overlap are "obvious" cases of allopatric speciation, and we used this as our cutoff. Although this cutoff is controversial (Chesser and Zink 1994), our results are unambiguous (i.e., no overlap in almost all cases; see "Results").

Results

Mapping regional distributions onto the phylogeny suggests that species richness is lower in regions peripheral to eastern North America because emydids have not been present in these regions for as long. Regression of the relative age of each colonizing lineage against the number of species of that lineage in the colonized region showed a positive correlation using both molecular (fig. 3*A*; $r^2 = 0.665$, $P = .014$) and morphological (fig. 3*B*; $r^2 = 0.599$, $P = .002$) data. Regression analysis also showed a correlation between the age of the oldest emydid lineage in each region and the overall number of emydid species in each region regardless of whether relative age was estimated based on molecular (fig. 3*C*; $r^2 = 0.988$, $P = .001$) or morphological (fig. 3*D*; $r^2 = 0.895$, $P = .004$) branch lengths.

Communities in eastern North America showed no relationship between local species richness and latitude (fig. 4*A*; $r^2 = 0.005$, $P = .635$). However, in the Western Hemisphere overall, there is a strong positive relationship between latitude and species richness (fig. 4*B*; $r^2 = 0.232$, $P < .001$), with species richness of local communities decreasing from temperate to tropical regions (mirroring regional patterns of species richness).

Among continental regions, local species richness is correlated with regional species richness ($r^2 = 0.573$, $P < .001$). Average local species richness of each region was also strongly correlated with regional species richness ($r^2 = 0.909$, $P = .003$). Thus, low local diversity in regions peripheral to eastern North America is seemingly related to the small size of the regional species pool. However, local and regional species richness are not correlated when eastern North America is divided into northern and southern regions and communities of southeastern North America are compared to those of the northeast ($r^2 = 0.005$, $P = .603$; fig. 1*B*). Communities in the northeast have local species richness similar to communities in the southeast despite higher regional species richness in the southeast ($P = .808$ for unpaired two-sample *t*-test comparing local species richness in the southeast to the northeast).

Within eastern North America, range size is positively correlated with latitude (fig. 5*A*; $r^2 = 0.200$, $P = .013$) such that species in the northeast tend to have larger geographic ranges. Phylogenetically independent contrasts in geographic range size and latitude show the same trend (fig. 5*B*), using both the gradual model (ACCTRAN: $r^2 = 0.205$, $P = .012$; DELTRAN: $r^2 = 0.194$, $P = .015$) and the punctuational model ($r^2 = 0.164$, $P = .026$) to estimate branch lengths.

Allopatric speciation has predominated in the Emydidae, at least recently. Nine of 10 pairs of sister taxa show no overlap in their geographic ranges (table 1). The only sister species with any overlap in their geographic ranges are *Clemmys insculpta* and *Clemmys muhlenbergii*, with 60.7% overlap. Regardless of whether this is considered sufficient evidence for sympatric speciation or not, allopatric speciation accounts for at least 90% of recent speciation events in the Emydidae.

Discussion

In this article, we argue that the time-for-speciation effect explains two major patterns of species richness in emydid turtles: (1) the high regional and local species richness of eastern North America compared to other continental regions and (2) the greater regional species richness of southeastern North America compared to northeastern North America (despite the lack of differences in local species richness). We suggest that the time-for-speciation effect has the potential to explain patterns of richness in a variety of systems. Our results also have implications for

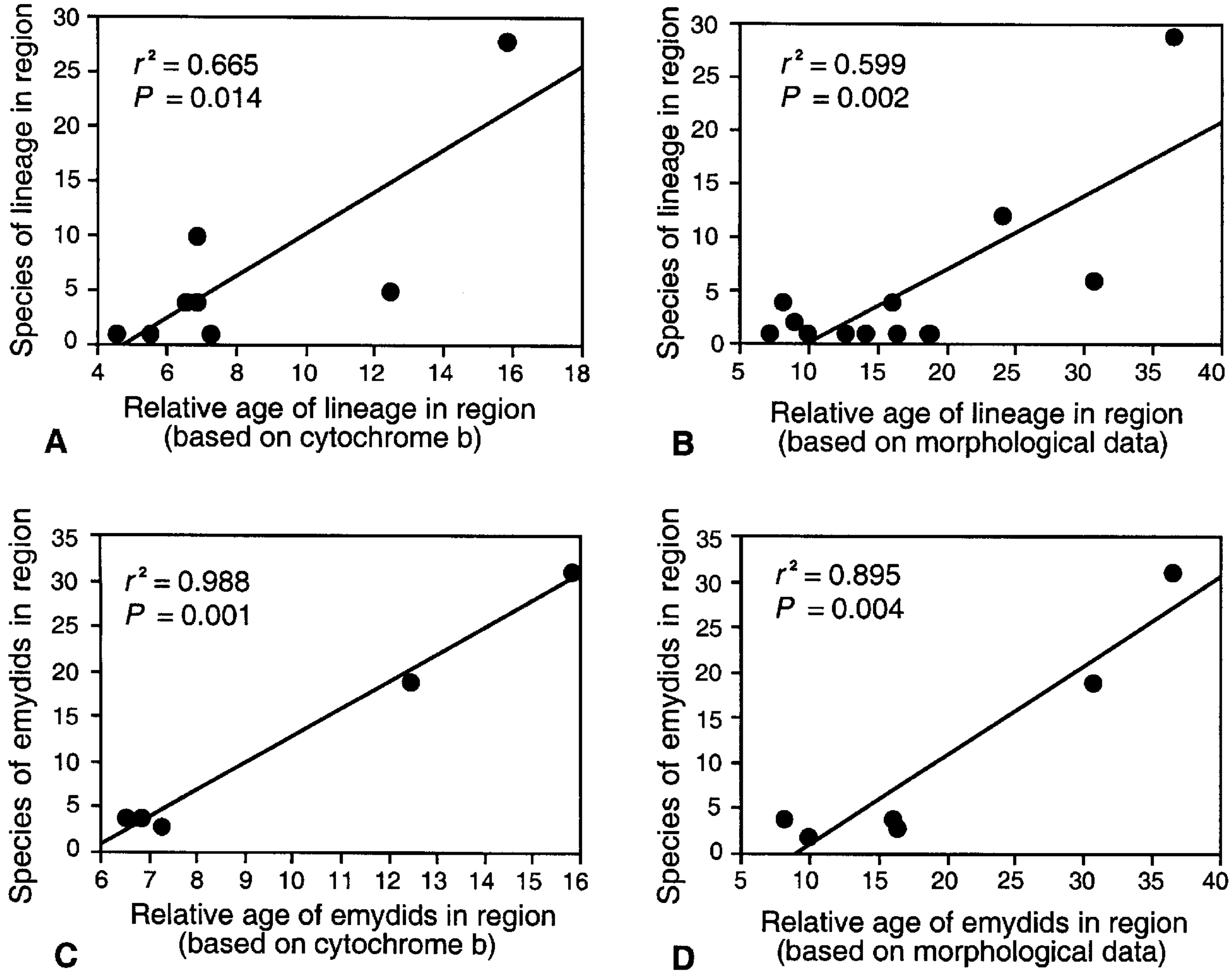

Figure 3: The time-for-speciation effect explains continent-scale patterns of species richness in emydid turtles. The top two graphs (*A*, *B*) show regressions of the timing of each colonization event versus the number of species in the dispersing lineage in the colonized region, with relative ages of lineages estimated from cytochrome *b* sequences using maximum likelihood (*A*) or from morphological data using parsimony (*B*). The bottom graphs (*C*, *D*) show regressions of emydid species richness in a region versus the relative age of emydids in that region (based on the first emydid lineage to colonize the region), with relative age estimated from cytochrome *b* sequences using maximum likelihood (*C*) or from morphological data using parsimony (*D*). Units of relative age are based on summed branch lengths (as described in the text) using either substitutions per site (× 100) for *A* and *C* or estimated evolutionary change (number and weight of character state changes) for *B* and *D*.

the relationship between geographic range size and different measures of diversity as well as for studies of "saturation" in communities.

Continent-Level Patterns of Emydid Species Richness

The time-for-speciation effect seems to provide the simplest explanation for patterns of emydid species richness at the regional, continent-level scale. No single environmental factor seems to explain these patterns, especially given the extreme environmental heterogeneity of emydid-poor regions (e.g., arid, mesic, tropical, temperate) and the ecological similarity of some of these regions (e.g., temperate Europe, northwestern North America) to eastern North America, where emydids are most speciose. The possibility that there was limited open "niche space" in regions of low emydid diversity also seems unlikely. If emydid species richness had been limited by competition, we would expect the number of emydid species to be inversely correlated with the number of non-emydid turtle species in each continental region. Regression analysis of the number of emydid versus non-emydid turtle species in each continental region confirms that there is no such pattern ($r^2 = 0.063$, $P = .631$; non-emydid distribution

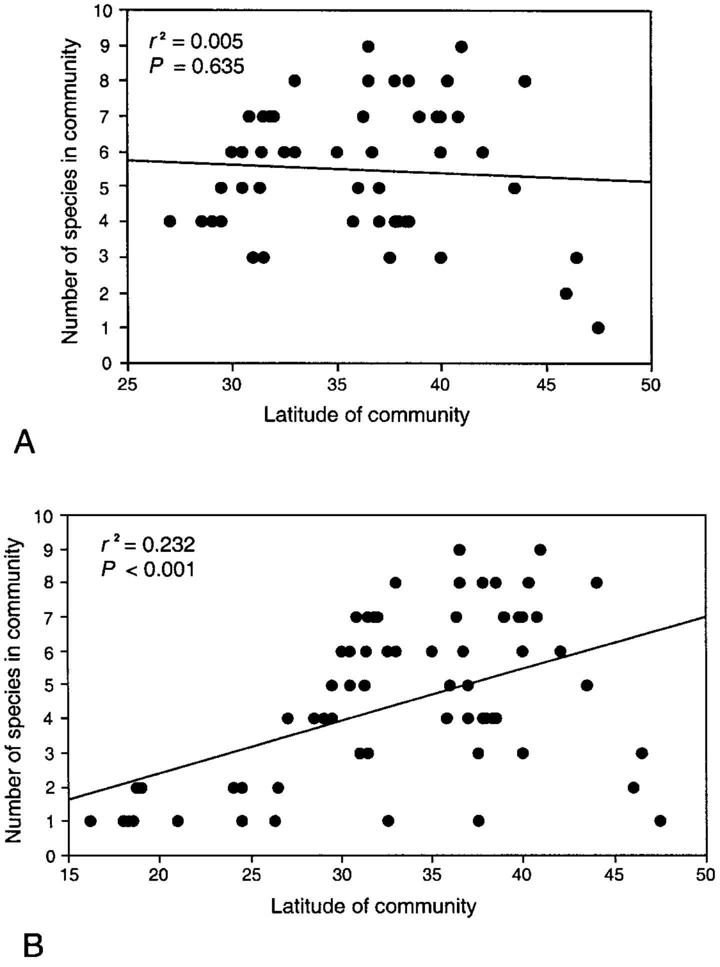

Figure 4: Regression of community latitude versus community species richness in (*A*) eastern North America and (*B*) the Western Hemisphere

data from Iverson 1992). Most regions outside of eastern North America contain few non-emydid turtle species: there is only one each in western North America and the West Indies and only six in Europe. The number of non-emydid species is similar in both emydid-poor Middle America (22 species overlap with emydids) and emydid-rich eastern North America (18 overlapping species). Among emydid-poor regions, only South America has many more non-emydid turtle species (38 species) than eastern North America.

In contrast to many groups of organisms (Brown and Lomolino 1998; Gaston and Blackburn 2000), emydids show lower species richness in tropical regions than temperate regions. This unusual pattern suggests the possibility that some ecological factor makes the tropics a "harsher" environment for emydids than temperate regions. However, emydids are among the most abundant vertebrates (in terms of biomass) in some tropical communities, and some tropical emydids grow to larger sizes and are more fecund than their close temperate zone relatives (Moll and Legler 1971; Moll and Moll 1990). The reverse latitudinal gradient in species richness seen in emydid turtles, combined with their ability to thrive in tropical regions, makes a compelling "natural experiment" that suggests that phylogenetic history (i.e., the time-for-speciation effect) can be more important than local ecological processes in determining latitudinal patterns of species richness. If local ecological conditions were more important than time, emydids should have higher species richness in tropical regions despite their recent arrival. These observations imply that the pattern of high tropical species richness observed in many organisms might be caused by those groups originating in tropical regions and having been present and speciating in tropical regions for longer periods of time (the museum hypothesis; Gaston and Blackburn 1996), as was widely believed during the

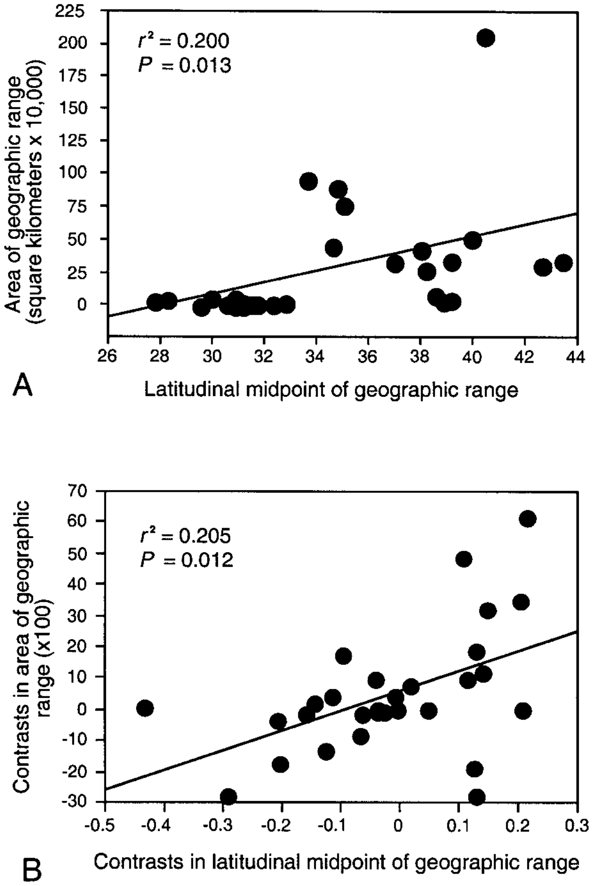

Figure 5: Regression of geographic range size and midpoint of geographic range using (*A*) raw data and (*B*) independent contrasts using a gradual model of character evolution and ACCTRAN optimization of the morphological data.

first half of the twentieth century (Stebbins 1974; Nelson 1978).

Patterns of Species Richness within Eastern North America

We hypothesize that the differences in regional diversity and average geographic range size between northeastern and southeastern North America may also reflect the time-for-speciation effect, in this case acting through local extinction or emigration of northern emydid populations caused by glaciation. If speciation is primarily allopatric (table 1), then we would expect species with large geographic ranges to be broken up over time into descendant species with smaller geographic ranges by vicariant speciation events (even though the range size of descendant species may eventually increase after speciation). Because the northern regions of North America were scoured by glaciers that reached their maximum extent only 20,000 yr ago (Holman 1995; Brown and Lomolino 1998), emydids in northeastern North America must be relatively recent immigrants to the region, with little time to be split into new species by vicariance. Conversely, in the southeast, there has been more time for vicariant speciation events to simultaneously fragment range sizes and increase regional species diversity. This hypothesis is also consistent with the similarity in local species richness between northeastern and southeastern North America.

Another possibility is that the disparity in regional species richness between southeastern and northeastern North America reflects greater rates of extinction in the northeast or higher rates of speciation in certain lineages in the southeast. Based on fossil evidence, Holman (1995) suggested that most (if not all) of the present-day northeastern emydid fauna was present before Pleistocene glaciation (beginning 1.9 million years ago) and that these species responded to glaciation by shifting their distributions southward or contracting their ranges to southern refugia and then reinvading northern regions after glaciers retreated. (Note: The presence of emydids in the northeast before glaciation explains how northeastern North America has high species richness relative to other continent-scale regions despite being recolonized quite recently.) The fossil record reveals only one extinct emydid species in all of North America (Holman 1995). However, even if there were many northeastern species that went extinct and were not recorded in the fossil record (which seems unlikely), the failure of the northeast to catch up to the southeast in species richness might still reflect the time-for-speciation effect. Similarly, molecular studies of North American birds (Zink and Slowinski 1995) suggest that glaciation slowed the rate of speciation in the Pleistocene by reducing or displacing habitats rather than causing extinction. Given that the southeast and northeast may have been inhabited by emydids for a similar period of time before glaciation, the higher species richness in the southeast may be explained largely by southeastern taxa that speciated during the Pleistocene (when much of the northeast was periodically rendered uninhabitable for emydids).

Although heightened rates of species extinctions in the northeast are unlikely, it is possible that greater rates of speciation related to habitat specificity in some southeastern emydids increased species richness in southeastern North America. The southeastern emydid fauna includes several river specialists (e.g., *Graptemys flavimaculata*, *Graptemys gibbonsi*, *Graptemys ernsti*, *Graptemys oculifera*) that seem to make overland migrations between drainages much less frequently than other species of aquatic emydids (Ernst et al. 1994). Because of their reduced propensity for terrestrial dispersal, these southeastern *Graptemys* may have experienced increased rates of allopatric speciation

Table 1: Modes of speciation in emydid turtles as inferred from overlap in the geographic ranges of sister species

Sister species pair	% overlap
Clemmys insculpta + *Clemmys muhlenbergii*	60.7
Graptemys ernsti + *Graptemys gibbonsi*	0
Graptemys flavimaculata + *Graptemys oculifera*	0
Graptemys ouachitensis sabinensis + *Graptemys versa*	0
Pseudemys nelsoni + *Pseudemys rubriventris*	0
Terrapene carolina + *Terrapene coahuila*	0
Terrapene nelsoni + *Terrapene ornata*	0
Trachemys decorata + *Trachemys decussata*	0
Trachemys scripta callistrosis + *Trachemys scripta venusta*	0
Trachemys scripta grayi + *Trachemys scripta nebulosa*	0

Note: The absence of overlap in the ranges of most sister species indicates a preponderance of allopatric speciation.

caused by vicariant events that affected riverine habitats (e.g., separation of previously connected drainages) during the Pleistocene (Lamb et al. 1994). Low levels of divergence in cytochrome *b* sequences also indicate that these *Graptemys* have speciated relatively recently (Lamb et al. 1994). Thus, high rates of speciation in certain southeastern taxa (associated with habitat specificity) and limited time for speciation in the northeast both may have contributed to the higher species richness in southeastern North America.

The Time-for-Speciation Effect versus Variation in Rates of Speciation and Extinction

A potential criticism of using the time-for-speciation effect to explain geographic patterns of species richness is that this hypothesis assumes that rates of speciation and extinction are generally similar between regions and lineages. In fact, these rates can vary extensively over space, time, and taxa (e.g., Sanderson and Donoghue 1994, 1996; Schluter 2000). For example, many recent studies have postulated that certain groups have undergone recent rapid diversification and thus have greater species richness than expected given their age (e.g., Baldwin and Sanderson 1998; Albertson et al. 1999; Magallón and Sanderson 2001; Richardson et al. 2001*a*, 2001*b*). However, the fact that rates of speciation in these groups are considered unusual suggests that they are deviations from a more general relationship between time and species richness. We suggest that the time-for-speciation effect may be important in explaining patterns of species richness generally but not universally. This study may be the first to use phylogenetic methods to test whether time alone can explain patterns of species richness between geographic regions rather than variation in rates of speciation or extinction (but see Gaston and Blackburn 1996). Our results show that time explains most of the variation in emydid species richness at the continental scale (fig. 3).

Range Size and Species Richness

Many authors have discussed the relationship between species richness and average geographic range size, specifically, the idea that smaller range sizes allow more species to be "packed" into a region (e.g., Stevens 1989; Gaston 1996). However, few have addressed the effects of geographic range size on different measures of species richness (sensu Whittaker 1972); namely, α diversity (local species richness), β diversity (turnover in species composition between communities or habitats), and γ diversity (regional species richness). Brown and Lomolino (1998) stated that one implication of Rapoport's rule is that "alpha and beta diversity appear to be positively correlated" (Brown and Lomolino 1998, p. 470) in the Northern Hemisphere due to smaller geographic ranges causing greater species turnover in areas that have higher α diversity (i.e., the tropics). We have shown that in emydid turtles, Rapoport's rule is supported (smaller ranges in the south) and yet α and β diversity appear to be uncoupled: β and γ diversity are higher in southeastern North America than they are in northeastern North America, but α diversity is similar between these regions (figs. 1*B*, 4*A*). We suggest that this pattern is caused by the effects of allopatric speciation on species diversity and average geographic range size.

The effect of allopatric speciation on range size and different types of diversity can be illustrated with a simple example (fig. 6). Consider three wide-ranging, closely related species (A, B, C) that occur sympatrically throughout the same geographic region. In this region, γ diversity is 3, α diversity in each community is 3, and β diversity is 0. A vicariant event then divides the region in half so that three pairs of descendant sister species (A_1 and A_2, B_1 and B_2, C_1 and C_2) are generated by allopatric speciation. The average geographic range size of species in the region will decrease, γ diversity of the region will increase to 6, α diversity will remain 3 in any community, and species

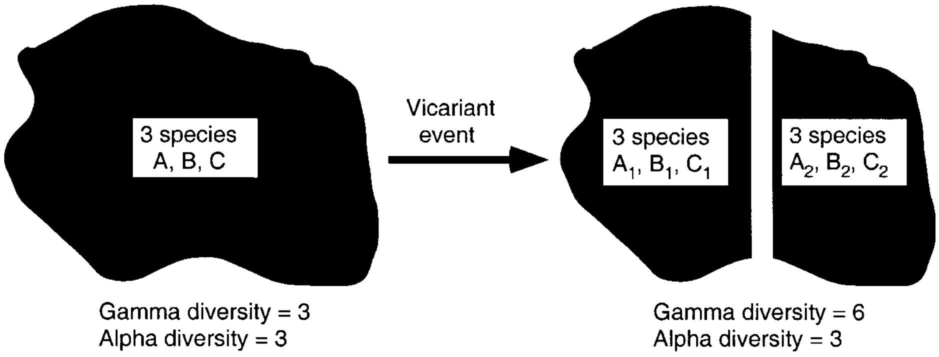

Figure 6: Effect of vicariant events and allopatric speciation on patterns of geographic range size variation and α, β, and γ diversity. Before the vicariant event (*region on the left*), species turnover between any two communities is zero. After the vicariant event, turnover in species composition between any two communities in the region is 100% or zero, depending on which communities are sampled.

turnover between any two communities will be either 100% or 0, depending on which two communities are sampled. Thus, allopatric speciation can increase γ and β diversity without increasing α diversity, and it will tend to reduce the average geographic range size of species in a region.

These observations imply a general relationship between range size and species richness. When average geographic range size is very large, species will tend to overlap with more of the other species in the regional species pool, which makes α diversity a greater proportion of γ diversity and β diversity small. Conversely, when average geographic range size is small, species will tend to overlap with few other species in the region, leading to high β diversity and to γ diversity that is many times α diversity. This relationship can be summarized with the following equation:

$$\gamma = \frac{A_t}{\bar{R}} \times \bar{\alpha},$$

where γ equals the number of species in a region, $\bar{\alpha}$ equals the average number of species at any locality in the region, A_t equals the area of the entire region, and $\bar{R}$ equals the average geographic range area of an organism within the region (this assumes that portions of the range of any species that lie outside the region are ignored). In fact, this equation is a simple derivation of the relationships that Whittaker (1972, p. 232) originally used to define β diversity.

Based on these general relationships and our results from emydid turtles, we suggest that species richness will accumulate in a region in a predictable series of stages, each typified by different patterns of regional and local species richness and geographic range size. The first species in the group to colonize a region (e.g., after glaciation) will often spread throughout the region and come to inhabit a large area. This pattern corresponds to the large average range sizes of emydids in postglacial northeastern North America. In time, the ranges of some species will be reduced by vicariance and allopatric speciation, producing a variety of range sizes. This will increase β and γ diversity but have no initial effect on α diversity (fig. 6). This pattern corresponds to southeastern North America, with high regional species richness and species that exhibit a variety of range sizes (from single drainages to the entire region) despite local species richness that is no higher than in the northeast. Eventually some of these new species will disperse and invade the ranges of other species, raising average α diversity and increasing average geographic range size. This situation might correspond to the pattern seen in many tropical lineages with high local and regional diversity. In support of this hypothesis, Hecnar (1999) analyzed latitudinal patterns of geographic range size across almost all turtles and continents and found that large geographic range sizes in temperate regions may be a localized effect of recent glaciation, whereas large geographic ranges are a general pattern in tropical regions. Thus, according to this scenario, latitudinal patterns of geographic range size distributions and species richness may reflect a temporal progression of events that has gone further in tropical regions than temperate ones.

Local and Regional Species Richness and Saturation of Communities

Many studies have tried to determine whether the species richness of communities tends to be limited more by the size of the regional species pool or by the niche space available in communities (e.g., Terborgh and Faaborgh

1980; Cornell 1985; Tonn et al. 1990; Cornell and Lawton 1992; Hawkins and Compton 1992; Caley and Schluter 1997; Shurin et al. 2000). A common approach to this problem is to examine the relationship between local and regional species richness for a set of communities (reviewed in Cornell and Lawton 1992; Cornell 1993). In some cases, a plot of regional versus local species richness bears an asymptote such that local species richness no longer increases, regardless of regional species richness (i.e., "Type II" communities; Cornell and Lawton 1992). Communities along such an asymptote are said to be "saturated" with species, and the number of species in these communities are assumed to be limited by competition (Terborgh and Faaborg 1980; Cornell and Lawton 1992; Aho and Bush 1993; Caley and Schluter 1997). In this study, we have shown that regional species richness increases from northeastern to southeastern North America but that local species richness does not. This pattern could be interpreted as evidence that communities in southeastern North America are saturated with emydids. However, we have described how allopatric speciation can increase regional species richness without affecting local species richness (fig. 6). This mechanism would produce a pattern resembling saturation even in the absence of competition. This mechanism seems to explain patterns of regional and local species richness in emydids in eastern North America and may explain patterns resembling saturation in other systems as well.

Local Processes and the Time-for-Speciation Effect

At the largest spatial scale, patterns of emydid species richness seem to have been determined directly by the time-for-speciation effect, with species richness in various regions being tightly correlated with how long emydids have been present in each region (fig. 3). At a smaller scale, within eastern North America, the impact of the time-for-speciation effect is more indirect and is seemingly mediated through temporary local extinction caused by glaciation. We suggest that the time-for-speciation effect may often influence patterns of species richness at smaller spatial scales by acting through a variety of local ecological processes, such as extinction, competition, adaptation, and predation. For example, Brown et al. (2000) and McPeek and Brown (2000) recently used a phylogenetic approach to explore patterns of species richness in lakes containing damselfly larvae (genus *Enallagma*). They found that lakes where dragonflies are the top predator have much lower diversity than lakes where fish are the top predator. Mapping habitat type onto the phylogeny suggests that the dragonfly lake habitat has only recently been invaded by damselflies. Thus, the low diversity in dragonfly lakes can be attributed to the limited time for speciation within this habitat (although McPeek and Brown [2000] allowed that unusually high extinction rates in dragonfly lakes was also possible). It is easy to imagine similar scenarios in which the time-for-speciation effect is mediated through other local-scale processes.

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