Bridging the gap between community ecology and historical biogeography: niche conservatism and community structure in emydid turtles

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Abstract

Historical (phylogenetic) biogeography and community ecology were once integrated as part of the broader study of organismal diversity, but in recent decades have become largely separate disciplines. This is unfortunate because many patterns studied by community ecologists may originate through processes studied by historical biogeographers and vice versa. In this study, we explore the causes of a geographic pattern of community structure (habitat use) in the emydid turtle assemblages of eastern North America, with more semi-terrestrial species of the subfamily Emydinae in the north and more aquatic species of Deirochelyinae in the south. Specifically, we address the factors that prevent northern emydines from invading southern communities. We test for competitive exclusion by examining patterns of range overlap, and test for the role of niche conservatism using analyses of climatic and physiological data based on a multilocus molecular phylogeny. We find no support for competitive exclusion, whereas several lines of evidence support the idea that niche conservatism has prevented northern emydines from dispersing into southern communities. Our results show how understanding the causes of patterns of historical biogeography may help explain patterns of community structure.

Keywords: community ecology, Emydidae, historical biogeography, niche conservatism, phylogeny, turtles

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Introduction

Community ecology and historical (phylogenetic) biogeography were once part of a single discipline that addressed the factors responsible for the diversity and abundance of species in communities and regional biotas, as well as the factors responsible for the origin and spread of species and clades (reviewed in Wiens & Donoghue 2004; Lomolino *et al.* 2006). In recent years, they have become largely independent fields of study. This is unfortunate, because many patterns studied by community ecologists (i.e. community assembly, species richness, community structure; Morin 1999) involve processes typically studied by historical biogeographers

(e.g. buildup of regional biotas through speciation and large-scale dispersal). Conversely, many patterns studied by historical biogeographers (i.e. distributions of species and clades) arise through processes generally studied by ecologists (e.g. competition, dispersal, eco-physiological adaptation; Wiens & Donoghue 2004). One factor that may have contributed to the intellectual disconnect between these fields is the relative dearth of approaches that bridge the gap between the large-scale, long-term patterns with which historical biogeography is generally concerned (reviewed in Lomolino *et al.* 2006) and the shorter-term, local-scale processes that are often the focus of community ecology (reviewed in Morin 1999).

During the past two decades, phylogenetic studies have begun to relate the ecological diversification of lineages to patterns of community structure (reviewed in

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Webb *et al.* 2002; Emerson & Gillespie 2008; Vamosi *et al.* 2009; see also Chazdon *et al.* 2003; Vitt *et al.* 2003; Cavender-Bares *et al.* 2004a; Gillespie 2004), an important step in bridging the gap between historical biogeography and community ecology. There are now numerous published examples of convergence in community structure due to convergent adaptive evolution in different lineages in different regions (e.g. Winemiller 1991; Hertel 1994; Losos *et al.* 1998; Gillespie 2004; Melville *et al.* 2006; Wiens *et al.* 2006a), as well as geographic patterns of community structure related to phylogenetic trends in the geographic distribution and ecological characteristics of lineages (e.g. Cadle & Greene 1993; Price *et al.* 2000; Cavender-Bares *et al.* 2004a; Stephens & Wiens 2004). There is also a large literature concerned with the phylogenetic relatedness of species within communities, which is used to infer processes such as competition (e.g. Cavender-Bares *et al.* 2004b; Cooper *et al.* 2008; Webb *et al.* 2008). However, phylogenetic studies of community structure have not generally addressed the factors that limit the dispersal of lineages between communities (but see Tofts & Silvertown 2000; Cavender-Bares *et al.* 2004a; Prinzing *et al.* 2008). If species are able to disperse freely among all of the communities considered, geographic patterns of community structure that are related to phylogenetic trends in the ecological characteristics of lineages may be blurred or disappear entirely (e.g. Stephens & Wiens 2004). Similarly, without biogeographic isolation, there may be little selective pressure for convergent adaptive evolution, as any given niche may tend to be filled by the same species in each community (e.g. Schluter 2000; Wiens *et al.* 2006a; but see Kozak *et al.* 2009).

Numerous abiotic and biotic factors may set the geographic limits of species ranges, including limited physiological tolerances to stressful environmental conditions, competition with closely related species, limited food resources, predators or some combination of factors (Lomolino *et al.* 2006). One general factor that has been hypothesized to limit the distribution of species and clades is phylogenetic niche conservatism, the tendency of species to retain ancestral ecological characteristics (e.g. Peterson *et al.* 1999; Wiens & Graham 2005). This pattern can arise via several population-level processes (e.g. stabilizing selection, limited genetic variation, gene flow, pleiotropy) and can exist even when character evolution is stochastic (Blomberg *et al.* 2003). Niche conservatism can lead to closely related species having similar environmental tolerances (Wiens & Graham 2005). When this occurs, closely related species will be affected by similar dispersal barriers (Wiens 2004), which will tend to produce distinct patterns in the geographic distribution of lineages (Wiens & Graham 2005). In addition, because of phylogenetic

signal in other traits, geographic patterns in the distribution of clades may often be related to patterns of community structure because species of a given lineage have similar ecological characteristics (e.g. certain dietary and habitat specialists may be clustered within a particular clade, which will be restricted to a particular geographic area because of shared environmental tolerances). In other words, niche conservatism can be related to patterns of community structure both through phylogenetic trends in the major ecological characteristics of clades and in shared environmental tolerances that limit the geographic distribution of those clades (Webb *et al.* 2002).

Some disagreement exists over what patterns are evidence for niche conservatism (e.g. Peterson *et al.* 1999; Wiens & Graham 2005; Losos 2008a,b; Warren *et al.* 2008; Wiens 2008). Here, we are interested in whether geographic patterns of community structure are related to phylogenetic trends in traits that limit the distribution of species and clades. Such a pattern can occur regardless of whether ecological characteristics are less labile than expected under a Brownian motion model of character evolution (i.e. phylogenetically conserved *sensu* Losos 2008a). Showing that some ecological characters have phylogenetic signal (*sensu* Blomberg *et al.* 2003; Revell *et al.* 2008) or that sister species have environmental niches that are more similar than expected at random (i.e. Warren *et al.* 2008) potentially supports niche conservatism, but does not address whether niche conservatism affects geographic patterns of community structure. It is also necessary to show a relationship between conserved characters and patterns in the distribution of the species, and between species distributional patterns and patterns of community structure. Similarly, testing whether species in communities are phylogenetically 'clustered' or 'even' (*sensu* Webb *et al.* 2008) does not directly address the causes of large-scale patterns of community structure, unless coupled with analyses that explore the factors that limit species distributions (e.g. Cavender-Bares *et al.* 2004a).

Relatively new Geographic Information Systems (GIS)-based methods, particularly niche modelling, are beginning to revolutionize our understanding of the factors that control the distribution of species over large spatial scales (e.g. Peterson *et al.* 1999; Peterson & Holt 2003; Martinez-Meyer *et al.* 2004; Smith *et al.* 2005; reviewed by Graham *et al.* 2004a). However, to date these approaches have not been used to address the origins of large-scale geographic patterns of community structure. Using GIS-based climatic data to explore the distribution of clades assumes that the climatic distribution of species is related to phylogenetically heritable traits that they possess (e.g. physiological tolerances). This underlying assumption also has yet to be directly

tested. However, an interesting study by Edwards & Still (2008) did examine the climatic distribution of introduced plants on the Hawaiian Islands, and found that C4 grasses were confined to warmer areas due largely to phylogenetically inherited traits. Here, we use GIS-based methods to test the causes of geographic patterns of community structure in emydid turtles in eastern North America.

Emydid turtle community structure

Emydids contain 41–47 currently recognized species (reviewed in Stephens & Wiens 2003; Bickham *et al.* 2007; Uetz 2009) and are geographically widespread and ecologically diverse (Ernst & Barbour 1989). Emydidae is the most species-rich turtle family in North America, and contains many familiar species such as the painted turtle (*Chrysemys picta*), red-eared slider (*Trachemys scripta*) and eastern box turtle (*Terrapene carolina*). In eastern North America, southern assemblages of emydids have a greater proportion of strictly aquatic species than northern assemblages, whereas northern assemblages have a greater proportion of semi-terrestrial species (Stephens & Wiens 2004). This pattern seems to be related to phylogenetic trends in the ecological characteristics of the two basal emydid clades (Deirochelyinae, Emydinae; Fig. 1), along with patterns of endemism in those lineages (Fig. 1, see also Stephens & Wiens 2004). Deirochelyines (*Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Trachemys*) are aquatic, and in eastern North America species either occur in both northern and southern communities or are restricted to southern communities. Emydines that occur in eastern North America are terrestrial or semi-terrestrial (i.e. habitat generalists that utilize both aquatic and terrestrial habitats extensively), and are either widespread in both southern and northern communities (*Terrapene*, *Clemmys*) or largely restricted to northern communities (*Emydoidea*, *Glyptemys*).

The latitudinal pattern in emydid habitat use occurs because most aquatic deirochelyine species do not disperse into northern communities and because most semi-terrestrial emydine species do not disperse into southern communities. It is generally accepted that the northern range limits of most emydids are related to freeze tolerance or lack of it and whether the potential active season (i.e. the warm season) is long enough for a given species to reproduce (reviewed in Ernst *et al.* 1994; Ultsch 2006). The failure of northern endemic species to disperse into southern communities is more puzzling. There are no obvious dispersal barriers between northern and southern communities, and the warm conditions of southern communities would intuitively seem

to be more hospitable for large ectotherms than northern communities.

Two factors that may be most important in setting geographic range limits are competition and physiological tolerances. Here we explore the factors that may prevent northern semi-terrestrial emydines from dispersing into southern communities, using a GIS-based approach to look for evidence of competitive exclusion and niche conservatism. We also test for a correlation between climatic conditions where species occur and a seemingly relevant physiological variable (critical thermal maximum, CTM) that has been measured in a number of emydid species.

Methods

Testing for competitive exclusion

We predict that if competition with southern emydid species limits the southward dispersal of northern species, pairs of southern and northern species should be closely abutting rather than broadly sympatric or allopatric. We tested for this pattern by comparing locality data from northern semi-terrestrial emydines to locality data from the remaining emydids. Locality data (latitude/longitude coordinates) were obtained from Iverson (1992). They include all museum localities and literature records available when his survey was published, and contain an average of 292 localities for each of the three northern endemics. The possibility that some presence localities were excluded cannot be ruled out. However, such omissions are likely to be minor, given that the geographic extent of localities reported by Iverson (1992) are consistent with estimates of the overall geographic range of species, which have been stable for >40 years (e.g. Conant 1958; Ernst *et al.* 1994; Conant & Collins 1998).

The range of each northern species was divided into 10 bins of equal longitudinal width. Within each bin, the southernmost locality of each northern species was compared to the northernmost locality of each emydid species that occurred in the same longitudinal band. Species that occurred >100 km south or north of the southern range limit of the focal species (averaged across all 10 bins) were considered unlikely to be important as agents of competitive exclusion. Species that occurred on average >100 km north of the southern range limit of a given species were considered broadly sympatric, whereas those that occurred on average >100 km south were considered allopatric. We also repeated this analysis after pooling all locality data for species that were not broadly sympatric, to see if the remaining species when considered as a group might determine the southern range limits of each northern
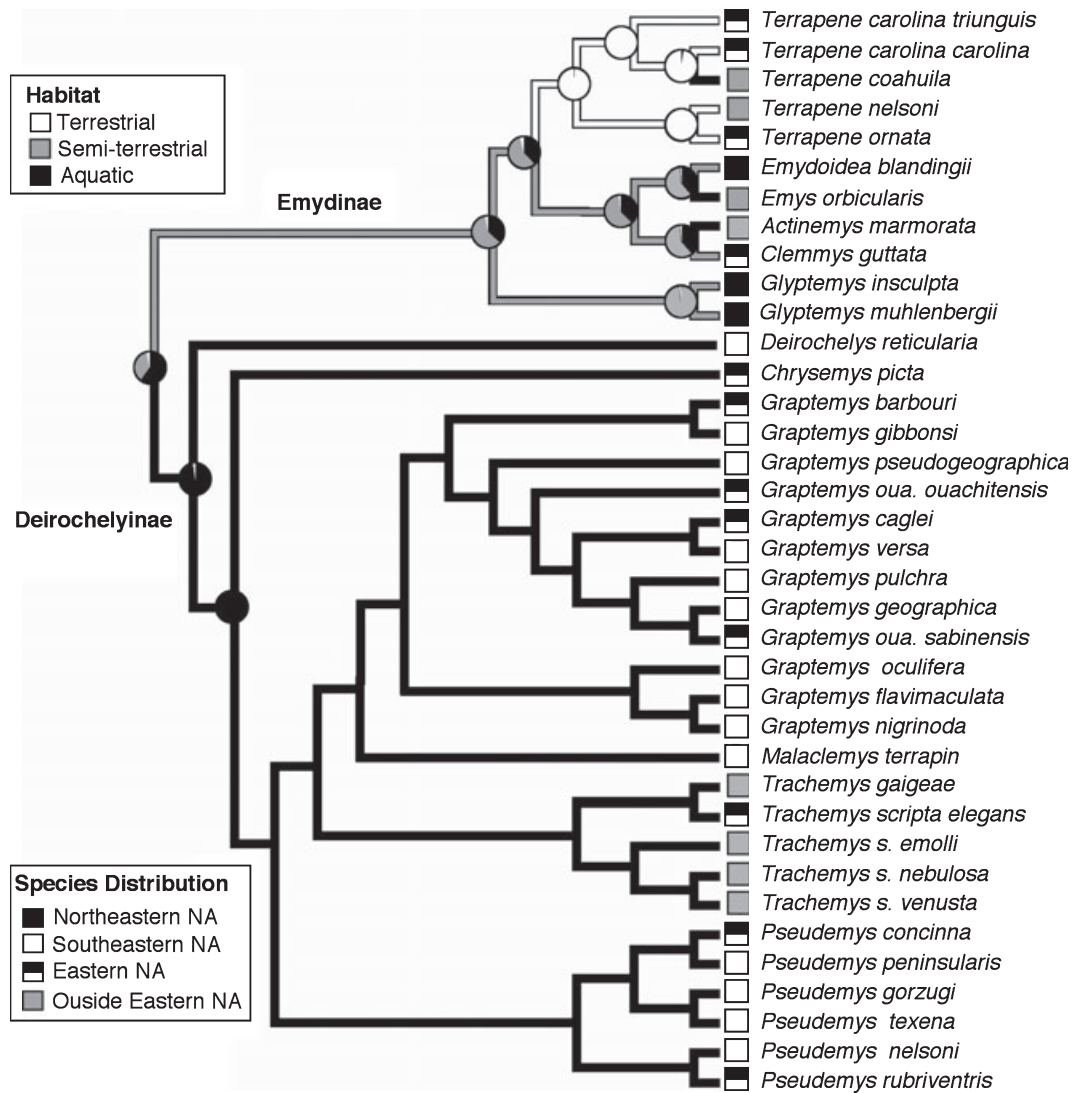
Fig. 1 Ancestral character reconstruction of habitat and region of occurrence in emydids. Boxes to the right of the tree indicate regions of occurrence for each species: black is northern endemic (in eastern North America), white is southern endemic, black and white is widespread, and grey is outside of eastern North America. Shading on branches indicates parsimony reconstruction of habitat, white is terrestrial, black is aquatic, and grey is semi-terrestrial. The area of shading in pie charts indicates the relative likelihoods of the same three character states in a maximum likelihood reconstruction of habitat. Likelihood reconstructions where the likelihood of 'aquatic' was >0.99 are not shown. Parsimony and likelihood reconstructions were performed with MESQUITE, using the phylogeny based on combined Bayesian analysis of six nuclear genes.

semi-terrestrial species. Ten bins was chosen somewhat arbitrarily, but it was the greatest number of bins that the ranges of *Emydoidea* and *Glyptemys muhlenbergii* could be divided into without producing some bins that contained three or fewer localities.

This method is equivalent to the 'natural experiments' observational approach that has often been used to infer competitive exclusion in past studies (reviewed in Diamond 1986; Lomolino *et al.* 2006). Showing a pattern of range overlap consistent with competitive exclusion (i.e. closely abutting ranges or parapatry) would not prove

that such interactions occur (Diamond 1986; Morin 1999), but the absence of such a pattern would seemingly preclude the importance of competition in preventing semi-terrestrial emydines from dispersing into southern communities (particularly in the case of allopatry). One limitation of our approach is that it cannot detect the effects competitive interactions that change along a gradient. For example, if the strength of competition varies along an abiotic gradient (e.g. temperature, rainfall), the limit of a species distribution might result from the interaction between competition and climate.

However, even in the latter case, competition is not the sole cause of a species range limits. Potential competitors besides emydids were also considered (e.g. non-emydid turtles, omnivorous mammals). However, none showed a pattern of range overlap consistent with our predictions for competitive exclusion, and we do not report these results in detail (see Discussion).

Testing correlations with environmental variables

Using BIOCLIM (Busby 1991), an extension of ArcView GIS v3.3 (Environmental Systems Research Institute), we determined the values of climatic variables at localities where the three northern semi-terrestrial species occur. For these analyses we used the WorldClim bioclimatic (Bio) variables (Hijmans *et al.* 2004, 2005), which consist of 19 GIS 'layers' (Table 1) based on monthly temperature and rainfall data at 2.5 s resolution (roughly 5 km^2). Many of these variables are highly correlated, given that they are derived from the same underlying temperature and precipitation data. To

Table 1 Climatic variables in the WorldClim data set

Abbreviation	Group	Variable
Bio 1	A	Annual mean temperature
Bio 2	*Neither*	*Mean diurnal range [mean of monthly (max temp − min temp)]*
Bio 3	A	Isothermality (Bio 2/Bio 7) (×100)
Bio 4	A	Temperature seasonality (standard deviation × 100)
Bio 5	*A*	*Maximum temperature of warmest month*
Bio 6	A	Minimum temperature of coldest month
Bio 7	A	Temperature annual range (Bio 5–Bio 6)
Bio 8	*Neither*	*Mean temperature of wettest quarter*
Bio 9	A	Mean temperature of driest quarter
Bio 10	A	Mean temperature of warmest quarter
Bio 11	A	Mean temperature of coldest quarter
Bio 12	*B*	*Annual precipitation*
Bio 13	A, B	Precipitation of wettest month
Bio 14	B	Precipitation of driest month
Bio 15	*B*	*Precipitation seasonality (coefficient of variation)*
Bio 16	B	Precipitation of wettest quarter
Bio 17	B	Precipitation of driest quarter
Bio 18	B	Precipitation of warmest quarter
Bio 19	B	Precipitation of coldest quarter

Variables in italics were used for analyses of species southern range limits. Group refers to which of two sets of highly correlated variables (see Methods) each climate variable fell into. A quarter equals 3 months.

identify independent sets of climatic variables, all possible two-way comparisons of the 19 variables (across all localities where the northern emydines occur) were made using Spearman's rank correlation (implemented in JMP™ v. 3.2.1). Sets of variables with $|r_s| > 0.70$ were considered 'strongly correlated'. This somewhat arbitrary cut-off was chosen because with so many localities (a total of 876) even correlations that would generally be considered weak ($r_s < 0.08$) were statistically significant at α = 0.05.

These comparisons identified two groups of variables that were strongly correlated, one corresponding to temperature and another to rainfall (Table 1). One exemplar variable was chosen to represent each of these sets for further analyses. Exemplars were chosen that represented the same data throughout the range of species considered (for example, mean temperature during the driest quarter was not chosen because it might indicate summer temperatures in some places and winter temperatures in others), and that seemed likely to be biologically meaningful in influencing range limits based on previous emydid physiological literature (reviewed in Ernst *et al.* 1994). We also assumed that extreme temperatures (e.g. maximum temperature during the warmest month) are more likely to determine range limits than average temperatures (e.g. mean annual temperature). Two environmental variables (mean diurnal temperature range and mean temperature of wettest quarter) did not show strong correlations with any other variables. Precipitation seasonality (i.e. coefficient of monthly variation) was also included, even though it showed a strong correlation with annual precipitation, because variance in precipitation was not a component of any other variable we included. For analyses that included all emydid species (see below), we also considered minimum temperature of the coldest month, even though it is inversely correlated with the warmest temperature of the hottest month. This variable was included because it is generally believed to determine the northern range limit of many emydid species (Ernst *et al.* 1994; but see Ultsch 2006).

We used logistic regression to determine which climatic variables were most strongly correlated with the presence and absence of a given species across localities, and thus might set the southern range limits of the three northern emydine species. Identifying the importance of specific variables would be more difficult using the composite variables created by principal components analysis, and so this approach was not used. Absence localities were selected immediately south of the southern range limits of each of the three northern emydine species. Rather than randomly selecting absence localities, we used localities where two other widespread emydines have been collected (*Terrapene*

carolina and *Terrapene ornata*), but the northern semi-terrestrial emydines have not. Absence localities included all *Terrapene* localities between 50 and 400 km south of the southernmost range limit of each emydine species at any given longitude that it occurred. It seems unlikely that the true range limit of any species was more than 50 km away from the known southernmost locality, and 50 to 400 km covered a band similar in latitudinal extent to the presence localities for each species. *Terrapene* was chosen because it occurs throughout the range of the northern semi-terrestrial emydines, as well as far to the south of them.

Logistic regression (implemented in JMP) was then used to quantify the strength of the correlation between each of the five climate variables and the presence and absence of a given species along its southern range limit. After performing separate analyses of each climate variable, we investigated more complex models incorporating multiple climate variables. Models using all possible combinations of the five climate variables were compared using Akaike's Information Criterion (AIC, Akaike 1973) implemented in R (R Development Core Team 2008). The minimum sample size (452) greatly exceeded the maximum number of model parameters (five) in these comparisons, so no adjustment to raw AIC scores was needed (Burnham & Anderson 1998). The model with the lowest AIC score was used for subsequent analyses. The spatial density of localities varies considerably from one region to another. To correct for this sampling bias, analyses were repeated using one random locality per species per county that it occurred in (for both presence and absence data). These analyses had qualitatively identical results to analyses using all data and are not reported.

Finally, we compared the extent to which niche models based on each of the five bioclimatic variables successfully predicted the presence and absence of each species along their southern range limit (following Smith *et al.* 2005; Wiens *et al.* 2006b). Niche models for each climatic variable were constructed for each species in Maxent (http://www.cs.princeton.edu/~schapire/maxent/). The general procedure followed Phillips *et al.* (2006), with all settings in Maxent set to default save that 80% of localities were used for training models and 20% were used to test models. Preliminary analyses showed that this latter procedure greatly increased the precision of models compared to the default setting, which does not use any localities to test models. We examined a range of cut-offs for 'predicted occurrence'; $r = 0.10, 0.20, 0.30, 0.40, 0.50$ and 0.60 (few models had values of $r > 0.69$ in any presence or absence locality). Using each cut-off, we calculated the percentage of presence localities excluded (i.e. the extent to which the model underpredicted) and the

percentage of absence localities included (i.e. the extent to which the model overpredicted). We then averaged these two values to come up with a 'percentage error' for each niche model and cut-off. We repeated this analysis using niche models estimated from each climate variable separately, as well as niche models estimated from all variables selected by AIC from models of presence and absence localities. Note that both logistic regression and niche modelling analyses are intended to illustrate correlations between climate variables and species southern range limits, so no correction for multiple comparisons was applied.

Testing environmental variables for phylogenetic conservatism

If phylogenetically conserved climatic tolerances are important in limiting the distribution of the northern semi-terrestrial species, then we predict three patterns. First, relevant climatic variables should show statistically significant phylogenetic signal across the phylogeny of emydids (i.e. λ significantly different from 0, see below), particularly variables that seem to set the range limits of species based on niche modelling and logistic regression. Second, the variables that are correlated with the southern range limits of the northern semi-terrestrial emydines should be correlated with the range limits of close relatives that occur in other continental regions outside eastern North America. Finally, reconstructions of environmental variables on the phylogeny should show that the ancestors of the northern endemic emydids occurred in cooler climates than the southern endemic emydids (i.e. that the differing climatic regimes of these clades are phylogenetically inherited). These results would support the hypothesis that phylogenetic niche conservatism has limited the ability of the three northern semi-terrestrial species to disperse into southern communities.

Phylogenetic analyses utilized two Bayesian trees: one based on combined nuclear DNA (six genes), mitochondrial DNA (two genes) and morphology; and one based only on nuclear genes (Appendix S1; online at the journal website). Both trees are very similar and gave identical results for the tests of phylogenetic conservatism. We report results using the nuclear DNA tree as the branch lengths of this tree are likely the most accurate. For detailed information on the data and methods used to estimate these phylogenies, see Appendix S1. These phylogenies were generally strongly supported and congruent with previous phylogenies (e.g. Stephens & Wiens 2003, 2008, 2009). For example, the generic-level topology based on combined data is almost identical to that of Stephens & Wiens (2009), and the nuclear DNA tree is congruent except

for minor differences in the placement of *Actinemys* and *Chrysemys*.

Phylogenetic signal was assessed using λ (Pagel 1999; Freckleton *et al.* 2002), with Continuous (M. Pagel; http://www.evolution.reading.ac.uk/Files/Continuous Manual.pdf). λ varies between 0 (no phylogenetic signal) and 1 (expected pattern under a Brownian motion model given the observed branch lengths and tree topology). Measures of 'phylogenetic signal' such as λ and Blomberg's *K* (Blomberg *et al.* 2003) have been criticized because they reveal little about the process or rate of trait evolution (Revell *et al.* 2008). However, high λ should indicate that trait variation is distributed primarily among major clades rather than within them (Freckleton *et al.* 2002; Revell *et al.* 2008). This is the expected pattern if niche conservatism in climatic tolerances determines the large-scale distribution of emydid species and clades.

For all six environmental variables (i.e. the five used for logistic regression plus Bio 6, lowest temperature of the coldest month, see Table 1), we determined the average, minimum value, and maximum value for each species and subspecies in the phylogeny based on locality data from Iverson (1992). Localities ranged from 7 to 2423 per species (average 305.94). Raw climatic data for localities where species occur were extracted from the WORDCLIM data set using BIOCLIM as described above. We then determined λ and its 95% confidence interval for each of these variables in emydids. Variables with a 95% confidence interval that did not include 0 were considered to have statistically significant phylogenetic signal.

We also repeated all of the analyses described above under 'Testing Correlations with Environmental Variables' using *Emys orbicularis* (which occurs in Europe, the Middle East and Northern Africa). This species is the closest living relative of the northern semi-terrestrial endemic *Emydoidea blandingii* (Stephens & Wiens 2003). No species of emydid (or any other turtle in most of the range) occurs between 50 and 400 km of the southern range limits of *E. orbicularis*. We therefore sampled environmental data using a grid of evenly spaced latitude and longitude coordinates for absence localities (every 0.25°). Absence localities in water (e.g. the Mediterranean Sea) were excluded.

Result of all the analyses described above indicated that temperature variables were most likely to be important to patterns of clade distribution, niche conservatism and community structure in emydids. To assess phylogenetic patterns of variation in climatic distribution of emydids, we reconstructed the maximum temperature of the warmest month (Bio 5) and the minimum temperature of the coolest month (Bio 6) for all emydid species included in the phylogeny. If niche conservatism in temperature tolerance sets the southern

distributional limits of the northern emydines, they should be members of clades in which Bio 5 and Bio 6 are ancestrally lower than in most emydids. These climatic variables were reconstructed as continuous variables using the generalized least-squares method (Martins & Hansen 1997), implemented in COMPARE version 4.6b (Martins 2004). Reconstructions were repeated using both averages of climate variables for each species (i.e. an average across all localities) and the highest and lowest temperatures observed in each species (i.e. maximum Bio 5 and minimum Bio 6), and overall phylogenetic patterns were similar. However, a subsequent analysis showed the highest temperature where a species occurs (max Bio 5) rather than the average across each species range is more strongly correlated with a physiological variable (i.e. CTM) that has been measured across several species of emydids. This is the pattern that would be expected if Bio 5 and CTM are primarily important in determining species southern range limits. As we are primarily interested in range limits, we only report the results of reconstruction of temperature extremes (i.e. coldest and warmest temperatures) for each species.

Finally, we wished to visualize the match between the southern range limits that would be predicted based on the temperature tolerances of the northern semi-terrestrial emydines and those of other emydines occurring outside northeastern North America. If climatic niches have been conserved between the northern endemic species and their relatives, we would expect that the southern range limits predicted by the climate envelopes of the northern semi-terrestrial species should match the southern range limits observed in closely related emydines. First, we constructed a niche model from the combined point localities of *E. blandingii*, *Glyptemys insculpta* and *Glyptemys muhlenbergii* based on maximum temperature of the warmest month (Bio 5) using Maxent. We compared this to the southern range limits observed in other emydines that are semi-terrestrial or whose most recent ancestor seems to have been semi-terrestrial: *Emys orbicularis* in Europe and the Mediterranean region of Africa and the Middle East, *Actinemys marmorata* in western North America and *Clemmys guttata* in southeastern North America. Although we made only a qualitative assessment of whether a given species 'matched' its predicted southern range limit, the results were sufficiently dichotomous that we felt a quantitative assessment of the trend was unnecessary (see Results).

Correlations with physiology

The analyses described above suggest that emydid species distributions may be related to their physiological

tolerances to cold and/or heat. Cold tolerance has been directly quantified in only six emydid species (Costanzo *et al.* 2006), and in adults of only four (Storey & Storey 1992; see Ultsch 2006 for qualitative reports of freeze tolerance in additional species). However, heat tolerance has been more widely assessed, and is potentially more relevant to understanding the southern range limits of the northern emydines. Hutchison *et al.* (1966) measured CTM, the thermal point at which individuals lose the ability to locomote effectively, for a total of 12 emydids.

To investigate the relationship between climatic distribution and physiological tolerances, we regressed maximum values of Bio 5 (max. temp.) against the average and maximum CTM. Hutchison *et al.* (1966) measured CTM of some species across several populations, and we used CTM from the population with the highest average CTM. Hutchison *et al.* (1966) characterized their results as 'preliminary', presumably because the number of individuals sampled varied widely among species ($n = 1$–43). To adjust for possible sampling error in species with extremely small sample sizes, we only included the eight species with $n \geq 5$. Five was chosen because a higher threshold would exclude at least half the species sampled by Hutchison *et al.* (1966). Correlations including all 12 species were in the same direction, but were roughly halved and only marginally significant (P-values ranged from 0.04 to 0.08), presumably due to measurement error in poorly characterized species.

Regression analyses were performed using phylogenetically independent contrasts (PIC) of Bio 5 and CTM, implemented in MESQUITE version 1.12 (Maddison & Maddison 2006). Species-level (i.e. tips) analyses were not performed because we wished to test for an evolutionary correlation between CTM and Bio 5 (Freckleton 2009). The tree and branch lengths used to estimate contrasts were from a Bayesian analysis of six nuclear genes, given that branch lengths from mitochondrial DNA alone seem to be distorted in some genera (Appendix S1). Contrasts were estimated across all nodes of the phylogeny, which was pruned to include only the eight species having adequate CTM data. We plotted the absolute value of standardized contrasts against their standard deviations using MESQUITE and confirmed that contrasts were adequately standardized by the branch lengths they were estimated from. This analysis was also repeated using phylogenetic generalized least squares (Martins & Hansen 1997) implemented in COMPARE. The results were identical to PIC analyses with respect to direction and statistical significance of correlations.

Results

Testing for competitive exclusion

None of the three northern semi-terrestrial species showed a pattern of range overlap with other emydids that is consistent with our predictions assuming competitive exclusion (Table 2). Instead of being parapatrically distributed, other emydid species were either broadly allopatric or broadly sympatric with the northern emydines.

Correlations with environmental variables

All correlations between environmental variables and the southern range limits (presence and absence) of the

Table 2 Patterns of range overlap between northern emydines and other species of emydids that occur in the same longitudinal range

	Number of localities	Broadly sympatric	Parapatric	Broadly allopatric
Emydoidea blandingii	420	1, 8, 12, 14, 25*, 26, 27*	None	3, 4, 5, 6, 7, 9, 10, 11, 13, 15, 16, 17, 18, 19, 20, 21, 22, 23*, 24, Combined
Glyptemys insculpta	331	1, 2, 8, 14*, 23*, 25	None	3, 4, 6, 7, 10, 11, 13*, 15, 17*, 18, 19, 21, 22, 26, 27, Combined
Glyptemys muhlenbergii	125	1, 2*, 8, 19*,25, 27*	None	3, 4, 17*, 21, 22, 23*, Combined

*A species that is allopatric throughout most of its range but broadly sympatric in some part of its range or vice versa. Species (and subspecies likely to represent species, see Stephens & Wiens 2003) are as follows, the number in parentheses is the number of localities for each species: 1. *Chrysemys picta* (1939), 2. *Clemmys guttata* (505), 3. *Deirochelys reticularia* (461), 4. *Graptemys barbouri* (69), 5. *Graptemys caglei* (15), 6. *Graptemys ernsti* (13), 7. *Graptemys flavimaculata* (13), 8. *Graptemys geographica* (433), 9. *Graptemys gibbonsi* (46), 10. *Graptemys nigrinoda* (65), 11. *Graptemys oculifera* (22), 12. *G. ouachitensis ouachitensis* (177), 13. *G. ouachitensis sabinensis* (9), 14. *Graptemys pseudogeographica* (256), 15. *Graptemys pulchra* (52), 16. *Graptemys versa* (20), 17. *Malaclemys terrapin* (259), 18. *Pseudemys alabamensis* (32), 19. *Pseudemys concinna* (520), 20. *Pseudemys gorzugi* (19), 21. *Pseudemys nelsoni* (149), 22. *Pseudemys peninsularis* (220), 23. *Pseudemys rubriventris* (93), 24. *Pseudemys texana* (210), 25. *Terrapene carolina* (2424), 26. *Terrapene ornate* (549), 27. *Trachemys scripta* (1550). 'Combined' indicates the results when data from all species that are not broadly sympatric with each species are combined.

northern emydines were significant at α = 0.05. However, the maximum temperature of the warmest month (Bio 5) consistently showed stronger correlations with presence and absence along the southern range limits of these species than the other environmental variables (Table 3). Niche models based on this variable also had consistently lower percentage error (averaged across thresholds; Table 4). The multivariate model that included all five environmental variables had the lowest AIC score in all three species and explained roughly twice as much variation in presence and absence as bivariate analyses (Table 3). See Appendix S1 for AIC scores, delta AIC values and r^2 for all 30 models that were assessed for each species. Multivariate niche models also had lower percentage error (averaged across all

six thresholds for 'predicted occurrence') than models based on individual climate variables (Table 4).

Testing environmental variables for phylogenetic conservatism

Three temperature variables [maximum temperature of the warmest month (Bio 5), minimum temperature of the coldest month (Bio 6) and mean temperature of the wettest quarter (Bio 8)] showed higher values of λ than other environmental variables tested (Table 5), indicating greater phylogenetic signal. Logistic regression showed that mean diurnal temperature range (Bio 2) and maximum temperature (Bio 5) were most strongly correlated with the southern range limits of the

Table 3 Correlations (r^2) between environmental variable and presence or absence of species along southern range limit based on logistic regression

	Presence localities/ absence localities	Mean diurnal temperature range (Bio 2)	Maximum temperature of the warmest month (Bio 5)	Mean temperature of the wettest quarter (Bio 8)	Annual precipitation (Bio 12)	Precipitation seasonality (Bio 15)	Multivariate model
Emydoidea blandingii	420/771	0.220	0.345	0.011	0.242	0.041	0.667
Glyptemys insculpta	331/463	0.019	0.266	0.187	0.113	0.016	0.434
Glyptemys muhlenbergii	125/327	0.089	0.299	0.053	0.034	0.177	0.441

All correlations are significant at $P < 0.001$.

Table 4 Percentage error (see Methods) of climatic niche models, averaged across six thresholds for 'predicted occurrence'

	Mean diurnal temperature range (Bio 2)	Maximum temperature of the warmest month (Bio 5)	Mean temperature of the wettest quarter (Bio 8)	Annual precipitation (Bio 12)	Precipitation seasonality (Bio 15)	Multivariate model
Emydoidea blandingii	37.57	28.62	37.13	30.63	46.68	24.52
Glyptemys insculpta	41.38	39.12	42.68	63.25	52.59	36.02
Glyptemys muhlenbergii	45.92	24.52	29.83	46.52	25.37	12.90

Table 5 Values of λ for the mean, maximum and minimum of six environmental variables across 37 species and subspecies of emydids

	Mean diurnal temperature range (Bio 2)	Maximum temperature of the warmest month (Bio 5)	Minimum temperature of the coldest month (Bio 6)	Mean temperature of the wettest quarter (Bio 8)	Annual precipitation (Bio 12)	Precipitation seasonality (Bio 15)
Minimum	0.116	1.00*	0.340	0.426*	0.915*	0.000
Maximum	0.452	1.00*	0.630	0.978*	0.000	0.986*
Mean	0.380	1.00*	0.688	0.745	0.000	0.620

*Values that showed statistically significant phylogenetic signal (i.e. values for which the 95% confidence interval did not include zero).

	Correlation with presence and absence	Average percentage error
Mean diurnal temperature range (Bio 2)	0.542	17.00
Maximum temperature of the warmest month (Bio 5)	0.452	24.94
Mean temperature of the wettest quarter (Bio 8)	0.106	43.79
Annual precipitation (Bio 12)	0.286	36.81
Precipitation seasonality (Bio 15)	0.209	43.62
Multivariate model	0.693	39.02

Numbers in the middle column indicate correlations (r^2) between environmental variables (listed in the left column) and presence or absence of this species along its southern range limits, based on logistic regression. Numbers in the right column indicate percentage error (see Methods) of climatic niche models, averaged across six thresholds for 'predicted occurrence'.

European emydine *Emys orbicularis* (the sister taxon to the northern semi-terrestrial species *Emydoidea blandingii*), and models based on these variables overpredicted into fewer localities than those based on other climate variables (Table 6). The multivariate model that included all five environmental variables had the lowest AIC score, and multivariate regression analyses explained more variation in presence and absence than bivariate analyses. However, multivariate niche models had higher percentage error than several models based on single variables.

Phylogenetic reconstruction of maximum temperature (Bio 5) and minimum temperature (Bio 6) showed that the northern, semi-terrestrial emydines are members of clades for which both variables are ancestrally lower than in most emydids (Fig. 2). The clades that contained the semi-terrestrial emydids generally showed reconstructed values of Bio 5 of ≤34.3 °C and of Bio 6 of ≤−12.35 °C. In contrast, within Deirochelyinae and *Terrapene*, reconstructed values were nearly always ≥35.3 °C for Bio 5 and ≥−8.36 °C for Bio 6. Finally, a niche model based on the values of Bio 5 from presence localities for the three northern endemic semi-terrestrial emydines predicted overall southern range limits that are similar to those observed in *Actinemys marmorata* and *Emys orbicularis*, but not *Clemmys guttata* (Fig. 3). Predicted southern range limits match those observed for *Emys orbicularis* with the exception of northern Tunisia (Fig. 3B), and only one locality occurred further south than the overall predicted southern range limit of *Actinemys marmorata* in the Baja peninsula (Fig. 3C). In

contrast, *Clemmys guttata* in eastern North America occurs far to the south of the predicted range limits based on Bio 5 (Fig. 3D).

Correlations with physiology

Although only eight species were sufficiently characterized to be included, contrasts of the highest value of maximum temperature of the warmest month (i.e. maximum Bio 5) in each species were strongly and positively correlated with contrasts of both average and maximum CTM ($r^2 = 0.652$, $P = 0.015$ for average CTM; $r^2 = 0.646$, $P = 0.016$ for maximum CTM).

Discussion

This study illustrates how using a GIS approach in a phylogenetic context can help bridge the gap between historical biogeography and community ecology. Our results suggest that niche conservatism, rather than competitive exclusion, seems to explain patterns of endemism in three semi-terrestrial emydines. This pattern of endemism is in turn related to a latitudinal pattern of community structure (Stephens & Wiens 2004), with more semi-terrestrial species in northern communities (dominated by emydines) and more aquatic species in southern communities (dominated by deirochelyines). Thus, historical biogeography of emydid clades influences geographic patterns of community structure, and phylogenetic niche conservatism in climatic tolerances seems to explain the pattern of historical biogeography.

Patterns of endemism in northern endemic semi-terrestrial emydids

Phylogenetic niche conservatism with respect to climatic temperature regime seems to be the major factor preventing *Emydoidea blandingii*, *Glyptemys insculpta* and *Glyptemys muhlenbergii* from invading communities in southeastern North America. The clade that contains these three species consists primarily of species that occur at cooler temperatures than most emydid species (Fig. 2), and temperature variables were also correlated with the southern range limits of the European sister species to *Emydoidea* (i.e. *Emys orbicularis*; Table 6). Maximum temperatures of the warmest month (Bio 5) were strongly correlated with the southern range limit of each species (Table 3), niche models based on this variable were the most accurate at predicting the southern range limits of each species (Table 4), and this variable has a strong phylogenetic signal in emydids in general (Table 5). A niche model based on values of Bio 5 from the three northeastern endemics was also
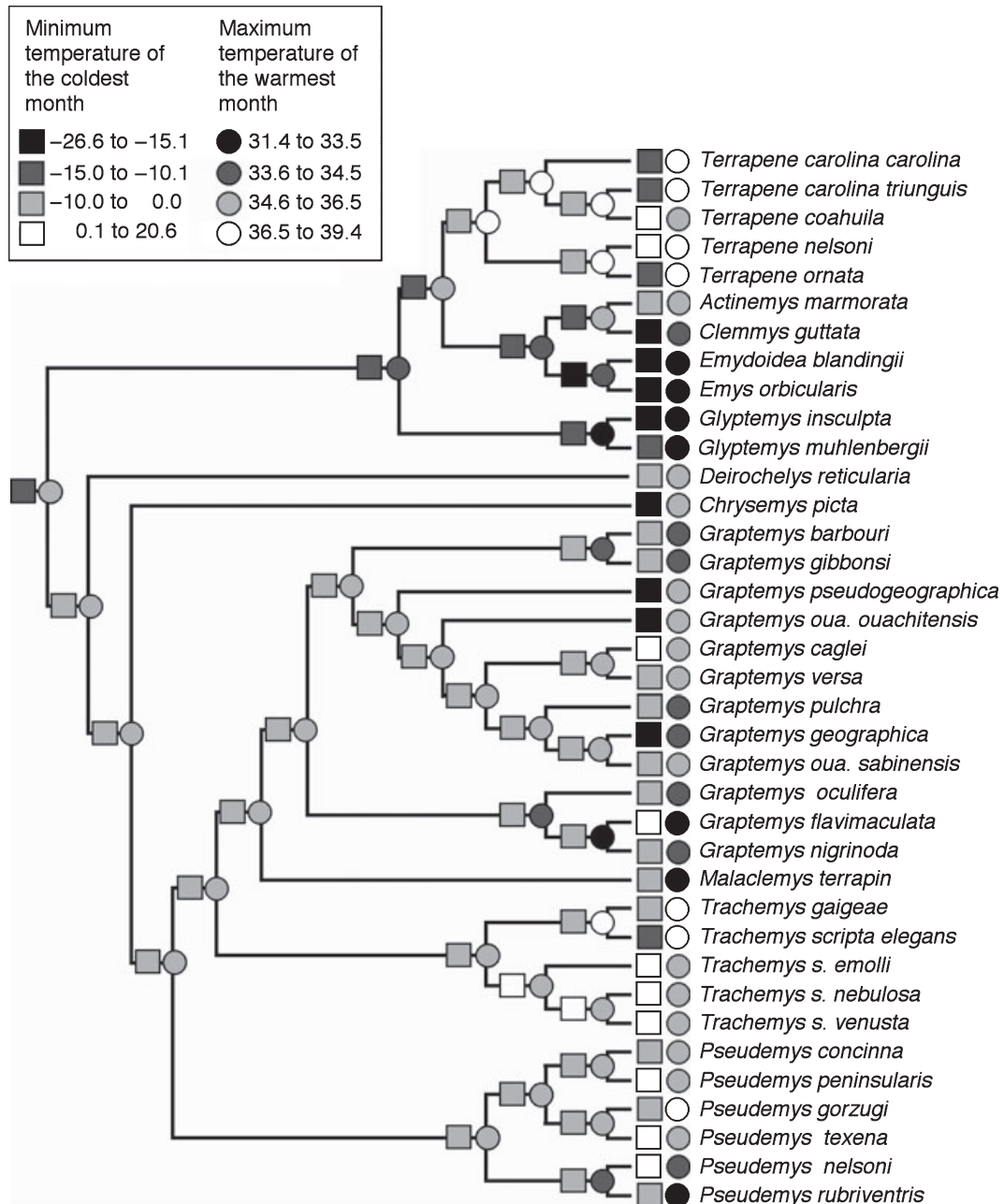
Fig. 2 Ancestral character reconstruction of maximum Bio 5 (maximum temperature of the warmest month) and minimum Bio 6 (minimum temperature of the coolest month) in degrees Celsius. Note that the scale for each variable is somewhat arbitrary, and intended to illustrate a 'breakpoint' in each variable between the two basal lineages of emydids. Phylogeny is based on combined Bayesian analysis of six nuclear genes.

able to predict the southern range limits of related emydines in Europe and western North America.

We acknowledge that there is considerable error in niche models based on these climatic variables, and that the correlations between putatively limiting climatic variables and species absences are significant but not perfect (Tables 3 and 4). However, there is no direct evidence for other obvious factors that could explain the failure of these species to disperse into southern communities. Our results show little evidence for competitive exclusion from other emydids (Table 2). Turtle species in other families also fail to show geographic ranges that abut those of these northern endemics (Iverson 1992; Ernst *et al.* 1994). We assume that much larger or much smaller species are unlikely to strongly compete for the same resources utilized by the northern

Fig. 3 Niche model based on maximum temperature of the warmest month (Bio 5) at for the northern semi-terrestrial emydines, compared to localities for (A) *Glyptemys insculpta*, *Glyptemys muhlenbergii* and *Emydoidea blandingii*; (B) *Emys orbicularis*; (C) *Actinemys marmorata* and (D) *Clemmys guttata*.
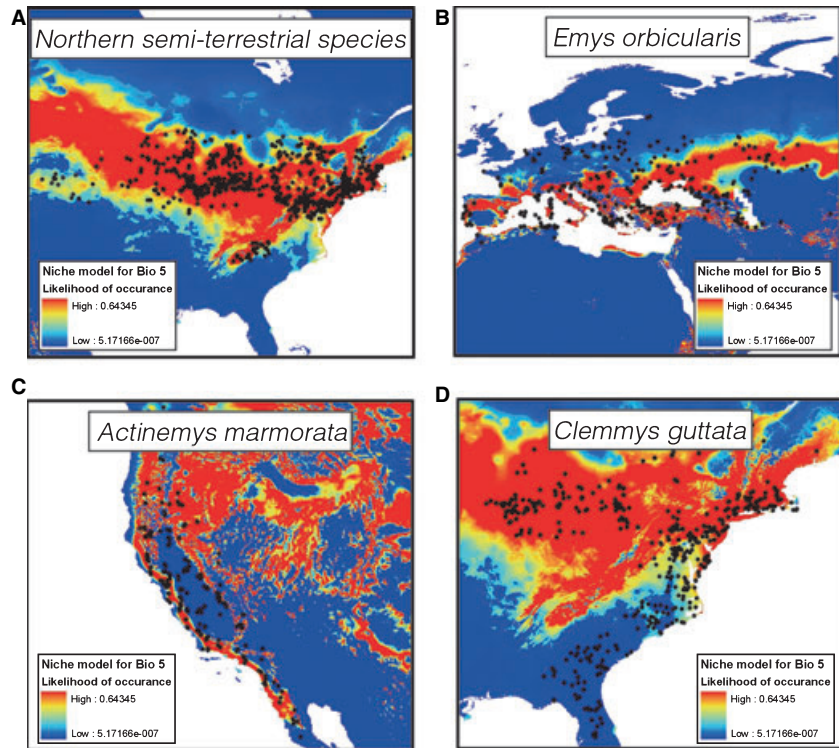
semi-terrestrial emydines. However, apart from the turtle species mentioned above, there are no other omnivorous ectotherms of similar body size in eastern North America. Even if we consider omnivorous mammals, species of similar size (e.g. skunks, raccoons, opossums) are broadly sympatric with each of the three semi-terrestrial emydines (Hall 1981). However, we acknowledge that our approach does not preclude the possibility that the range limits of the northern semi-terrestrial species are related to competitive interactions that vary along a climatic gradient.

Predation and resource limitation also seem unlikely. Adult turtles of most species are little affected by predation, and the predators that attack adults of a few species and nestlings (coyotes, river otters, foxes, raccoons, opossums, reviewed in Ernst *et al*. 1994; Ultsch 2006) occur widely in North America (Hall 1981). The sole exception is the American Alligator (*Alligator mississippiensis*) which occurs far to the south of any of the northern semi-terrestrial emydines (Conant & Collins 1998). Given that all three species are omnivores (Ernst *et al*. 1994), it also seems unlikely that their distributions are tracking the distribution of a specific food resource. Parasite loads are known to be heavy in both southern and northern populations of some turtle species (Ernst & Ernst 1977). However, parasites have not been thoroughly studied in the three northern endemics. The possibility that the distribution of a parasite species or some interaction with climate and parasite

abundance limits the southern distribution of these species cannot be completely ruled out, although there is no evidence for it. In contrast, we find several lines of evidence for the influence of climatic variables on the southern range limits of these species, particularly the highest summer temperatures.

Given the assumption that climatic variables are the primary factor setting the range limits of these species, what proximate factors might explain the failure of these species to disperse further south? Most turtle species exhibit temperature-dependent sex determination (Ernst & Barbour 1989), and the effects of temperature on eggs might therefore set the southern range limits of the northern endemics (i.e. a nest laid outside of the normal thermal niche of a species might produce all males or all females). However, this cannot be a factor for *G. insculpta* or *G. muhlenbergii*, because they have chromosomal sex determination (Ewert & Nelson 1991). Limited overall thermal tolerances of eggs (i.e. eggs laid in southern communities might fail to hatch at all) cannot be ruled out.

Another possibility is limited tolerance of adults to high temperatures. Intriguingly, only one semi-terrestrial emydine (*Clemmys guttata*) extends farther south than would be predicted based on a niche model for the three northern endemics (Fig. 3). But unlike other semi-terrestrial emydines, *C. guttata* aestivates during most of the summer (Ernst *et al*. 1994), and so is inactive during the time of year that it would

experience the high temperatures that seemingly limit the distribution of its close relatives. The shift in activity patterns in *C. guttata* may represent a behavioural adaptation to circumvent the physiological limitations that potentially determine the southern range limits of other semi-terrestrial emydines. Similarly, *G. muhlenbergii* extends further south than the other two northern endemics, but at the southern edge of its range it occurs in the Appalachian mountains (Ernst *et al.* 1994) where summer temperatures are cooler than in the surrounding lowlands. The fossil record also implicates climate in the case of *E. blandingii*. During glacial maxima, it occurred far to the south of its current range, and existed in local assemblages with a southern species (*Pseudemys nelsoni*) that it does not encounter under modern climatic conditions (Holman 1995).

The limited physiological data that are available for emydids also support the importance of temperature in setting species range limits. CTM showed a correlation with the maximum summer temperatures (Bio 5) at which emydids occur in the eight species in which it has been well characterized. The correlation between CTM and maximum Bio 5 was somewhat weaker when all 12 emydid species that Hutchison *et al.* (1966) sampled were considered (P. R. Stephens, unpublished). This could reflect sampling error due to including poorly characterized species. However, it is also possible that the correlation between maximum summer temperatures and CTM is indirect. If species range limits are determined by the optimum temperature range for each species rather than the maximum temperature a species can tolerate, the correlation between maximum Bio 5 and CTM can be no stronger than the correlation between the CTM and the thermal optimum across species. Turtles are known to maintain body temperatures well below CTM both from voluntary temperature selection experiments and temperature measurements of wild specimens (Brattstrom 1965). Unfortunately maximum voluntary temperature has not been measured in a sufficient number of emydid species to allow us to directly test this hypothesis at present (reviewed in Brattstrom 1965; Ernst *et al.* 1994; see also Plummer 2003). It would be interesting to determine if voluntary temperature preferences or peaks in species temperature performance curves are more strongly correlated with temperatures at species range limits than CTM.

Phylogenetic niche conservatism

Past studies of phylogenetic patterns of community structure have rarely addressed the factors that prevent lineages from dispersing among communities (but see Tofts & Silvertown 2000; Cavender-Bares *et al.* 2004a).

Yet, such limitations are essential for creating geographic patterns of community structure (Stephens & Wiens 2004). Stephens & Wiens (2004) identified a latitudinal gradient in community structure and the key lineages that cause this pattern. Here, we investigated the factors that limited the ability of these lineages to disperse among communities. Niche conservatism with respect to high temperature tolerances seems to explain the patterns of endemism in several semi-terrestrial emydines. We do not mean to imply that temperature tolerance is static in emydids. Our results suggest that the climatic distribution changes (Fig. 2), even among the closely related semi-terrestrial emydines (i.e. *Clemmys guttata*; Fig. 3). We mean only that there are strong phylogenetic trends, which may help explain the predominately northern distribution of emydines and the predominately southern distribution of deirochelyines (Fig. 2). Combined with phylogenetic trends in their patterns of habitat use (Fig. 1), these patterns of endemism in the major emydid clades seem to produce a geographic trend in community structure.

This study illustrates how a GIS approach can be used to help bridge the gap between historical biogeography and community ecology. GIS methods have been used with great success to predict potential distributions in studies of single species (reviewed in Graham *et al.* 2004b), but few past studies have used them to try and understand the historical biogeography of larger clades (e.g. Smith *et al.* 2005; Wiens *et al.* 2006b). This is also among the first phylogenetic studies to attempt to link GIS-based climatic envelopes to physiological data (but see Kozak & Wiens 2007; Edwards & Still 2008). Given the wide use of GIS methods to characterize species climatic niches in disciplines ranging from historical biogeography to conservation biology (e.g. Wiens & Graham 2005), additional studies testing the relationship between the physiology of species and environmental conditions where they occur are badly needed.

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Details of phylogeny estimation.

Appendix S2. AIC scores from model selection.

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