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Temperate extinction in squamate reptiles and the roots of latitudinal diversity gradients

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ABSTRACT

Aim Many ecological and evolutionary hypotheses have been proposed to explain latitudinal diversity gradients. However, any mechanistic explanation must include factors that change at least one of the three processes that can directly affect species richness: speciation, extinction and dispersal. I hypothesize that higher extinction in temperate areas, higher speciation in tropical areas and reduced dispersal into temperate regions drives latitudinal diversity gradients in squamates, and that these processes may be common in other groups.

Location World-wide.

Methods I test for these processes using phylogenetic methods that can untangle speciation and extinction with respect to latitudinal position (GeoSSE), using a dated phylogeny containing *c.* 45% of all squamates (4161 species) with data on their geographic occurrence.

Results I find that lineages in the tropics have high speciation and low extinction, but that temperate lineages have even higher speciation and extinction, leading to lower net diversification and higher turnover in temperate areas, with much higher rates of dispersal into the tropics from temperate areas than the reverse.

Main conclusions Recent empirical studies using dated molecular phylogenies appear to be consistent in supporting a similar set of simple and intuitive results for processes driving latitudinal gradients in species richness: higher net diversification rates in the tropics, higher relative extinction fractions in temperate regions and reduced dispersal out of the tropics. I suggest that higher temperate extinction represents a dominant force for the origin and maintenance of latitudinal gradients, particularly in groups with ancient temperate clades.

Keywords

Extinction, latitudinal diversity gradients, speciation, species richness, squamate reptiles, tropical diversity.

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INTRODUCTION

The latitudinal gradient in diversity (LDG) remains one of the most well-known but least-understood patterns in ecology and evolution (Willig *et al.*, 2003; Hillebrand, 2004). A phylogenetic perspective is increasingly recognized as crucial for a mechanistic explanation (Wiens & Donoghue, 2004). In particular, dated molecular phylogenies are increasingly being used to test evolutionary hypotheses about the origin and maintenance of LDGs (Mittelbach *et al.*, 2007). Importantly, most recent studies (see Jansson *et al.*, 2013) have explicitly framed their phylogenetic

tests of LDG mechanisms in terms of the three fundamental processes that directly alter species richness: speciation, extinction and dispersal (Ricklefs, 1987). Any explanation for a LDG must incorporate factors that directly change at least one of these three processes.

There have been several formalizations of mechanistic, process-based explanations for LDGs. One is the evolutionary time hypothesis (ETH), which suggests that tropical areas have been occupied for longer than temperate regions, and thus have had more time to accumulate species (see Rohde, 1992). Related to this is the tropical conservatism hypothesis (TCH), which

suggests that the tropics have been occupied for longer, dispersal out of the tropics is rare and the greater past area of the tropics yielded more present-day tropical clades (Wiens & Donoghue, 2004). Somewhat contrastingly, the out of the tropics model (OTM) also suggests a tropical origin of clades, but with more frequent expansion to temperate latitudes (Jablonski *et al.*, 2006). These hypotheses do not posit latitudinal trends in diversification rates. Rather, the diversification rate hypothesis (DRH) suggests that net diversification rates (speciation–extinction) are higher at lower latitudes, yielding more species there over time (see Mittelbach *et al.*, 2007).

A recent meta-analysis of these models from 111 phylogenies claimed to generally support the OTM, with little evidence for the ETH, TCH or DRH (Jansson *et al.*, 2013). However, there are two major issues with both the results of that study in particular and the fundamental basis of the four models. First, those authors used only coarse summaries to test their major hypotheses, such as sister-clade contrasts in species richness to test for variation in diversification rates rather than the more powerful model-based estimators (Pyron & Burbrink, 2013). Second, as constructed, the four primary models are not mutually exclusive, and numerous mechanistic elements from each could interact to generate LDGs in any particular group. Length of occupancy in regions, frequency of dispersal between regions and differences in rates of diversification can all conceivably generate LDGs when combined in the right proportion, regardless of the area of origin or other rate differences.

In contrast to these findings, numerous recent studies using explicit model-based tests of hypotheses concerning rates of speciation, extinction and dispersal have supported two consistent results. First, net diversification rates are typically higher in tropical clades (Cardillo *et al.*, 2005; Jablonski *et al.*, 2006; Ricklefs, 2006; Weir & Schluter, 2007), a major prediction of the DRH. Second, dispersal out of the tropics seems to be limited (i.e. pole-ward range expansion), a major prediction of the TCH (Wiens *et al.*, 2006; Smith *et al.*, 2012). Large-scale phylogenetic studies of amphibians and mammals have found support for both of these results simultaneously (Pyron & Wiens, 2013; Rolland *et al.*, 2014). Increased diversification and limited dispersal thus combine to create and maintain LDGs. Furthermore, variation in these rates seems to be linked strongly to ecological factors such as temperature (Cardillo *et al.*, 2005; Pyron & Wiens, 2013).

Thus, recent empirical results seem to be converging on a set of simple and intuitive mechanisms for generating and maintaining LDGs: higher net diversification rates in the tropics, lower net diversification and higher turnover in temperate regions and limited dispersal out of the tropics. Temperate ecological factors seem to increase volatility in speciation and extinction, and limit colonization of temperate regions. Furthermore, at least one group (amphibians) exhibits a positive crown age/diversity relationship (Pyron & Wiens, 2013), suggesting that it is accumulating species richness under a relatively unbounded birth–death process (Rabosky, 2009; Cornell, 2013). A negative stem-age/diversity relationship, with older stem groups that are disproportionately depauperate (Wiens, 2007),

potentially indicates the action of high extinction over time pruning stem lineages (Pyron & Burbrink, 2012).

A major difference among studies that have untangled speciation and extinction rates is the exact pattern that yields higher net diversification rates in the tropics. Whether or not higher diversification rates at lower latitudes are attributable to increases or decreases in temperate or tropical speciation or extinction seems to vary among groups. In amphibians and most mammals, tropical clades show high speciation and low extinction, while temperate clades exhibit the reverse, with lower speciation and higher extinction (Pyron & Wiens, 2013; Rolland *et al.*, 2014). In birds and some mammals, recent sister-species pairs seem to exhibit the signature of higher temperate extinction but also higher temperate speciation (Weir & Schluter, 2007). The net effect is the same in both cases: lower net diversification at temperate latitudes and higher relative extinction fractions (extinction/speciation), indicating a faster turnover through time (Pyron & Burbrink, 2013).

In general, this should also be associated with clades exhibiting positive crown-age/diversity relationships and flat or negative stem-age/diversity relationships. Fewer clades will be present in temperate regions due to reduced temperate colonization, and will have fewer species than tropical clades. A positive crown age/diversity relationship indicates that diversification rates, rather than ecological limits, regulate species richness (Rabosky, 2009), while the flat or negative stem age/diversity relationship indicates the impact of higher extinction over time, pruning older temperate lineages (Pyron & Burbrink, 2012). For ancient groups, area of origin will be less important, as differences in the diversification rate will override temporal differences, as in amphibians and mammals, with depauperate clades with older stem-ages in temperate regions and younger, more diverse clades in the tropics (Pyron & Wiens, 2013; Rolland *et al.*, 2014).

Here, I test these predictions for squamate reptiles, a megadiverse (*c.* 9400 species) group of ectothermic terrestrial vertebrates that appear to exhibit a significant LDG. I use the GeoSSE algorithm (Goldberg *et al.*, 2011) to test for differences in speciation, extinction and dispersal between temperate and tropical regions. Furthermore, a recent study found that viviparous squamates had higher rates of speciation and extinction, and therefore lower net diversification and higher turnover, and that these taxa predominantly inhabited cooler climates (Pyron & Burbrink, 2014). This may provide a mechanistic link between ecological factors such as temperature and latitudinal differences in diversification rate, due to their effects on life history. Alternatively, turnover may be increased at temperate latitudes due to a decreased capacity for stable coexistence of many species in harsher or more unstable climates.

METHODS

Phylogeny and distribution data

A recent study presented a time-calibrated tree for Squamata containing 4161 species (Pyron & Burbrink, 2014) from a

maximum likelihood estimate based on 12 genes, 9 nuclear and 3 mitochondrial, totalling 12,896 bp (Pyron *et al.*, 2013). That chronogram is used here essentially as-is, including the outgroup *Sphenodon punctatus*. For the 67 squamate families and Sphenodontidae (Pyron *et al.*, 2013), I obtained the stem- and crown-group ages from the chronogram and the extant diversity of each family from published sources (Uetz, 2012).

Using published distributional data from the December 2012 update of the Reptile Database (Uetz, 2012), I classified 9416 species of squamate (*c.* 100% of known, extant species) as tropical, temperate or both. I classified species into 12 ecoregions, considering Tropical South America, Tropical Middle America, West Indies, the Afrotropics, Madagascar, South Asia, Southeast Asia and Oceania as tropical (excluding New Zealand, which I considered temperate) and Temperate South America, Nearctic, Western Palearctic, and Eastern Palearctic as temperate. This follows previous studies (Pyron & Wiens, 2013) and corresponds to commonly used definitions in herpetology and biogeography (Duellman, 1999; Vitt & Caldwell, 2009). This includes some tropical biomes (e.g. Atlantic Forest) that range into subtropical areas. There are 7955 tropical species, 1337 temperate species and 124 trans-tropical species.

I calculated the proportion of temperate taxa in each family as a basic metric of latitudinal position of the family (e.g. all species in the lizard family Opluridae are from Madagascar, and the family is thus 100% 'tropical'). I then used multiple regression to link species richness in clades to latitudinal position, stem-group age and crown-group age. Second, to evaluate the broad-scale signature of slowdowns in accumulation of diversity over time, I tested for the significance of a quadratic (curvilinear) relationship between crown-group age and diversity over a linear relationship (Rabosky, 2009; Cornell, 2013). Appendix S1 in Supporting Information gives the geographic range information and clade data.

Geographic diversification

I tested for differences in rates of speciation, extinction, and dispersal between temperate and tropical areas using the GeoSSE (geographic-state speciation and extinction) model (Goldberg *et al.*, 2011) implemented in the R package 'diversitree' (Fitzjohn, 2010). The GeoSSE model is an extension of the BiSSE (binary-state speciation and extinction) model (Maddison *et al.*, 2007), and tests whether speciation and extinction rates vary as a function of a binary character. In contrast to BiSSE, GeoSSE interprets the binary character in a geographic context, where a species can occur in tropical (A), temperate (B) or both (AB) regions. Thus, there are parameters for speciation rate in states A, B and AB (s_A , s_B and s_{AB}), extinction rate in states A and B (x_A and x_B), and dispersal from A to B and vice versa (d_A and d_B). Some, all or none of these parameters may differ between regions.

I tested a set of 10 distinct models using the time-calibrated tree described above. I first tested a model in which all parameters were free to vary (seven parameters). I then compared this

model with a set of constrained submodels in which one or more parameters were set to be equal between regions. This yields a total of 10 models.

1. s_A , s_B , s_{AB} , x_A , x_B , d_A , d_B (full model).
2. $s_{AB} = 0$ (no intermediate speciation).
3. $s_A = s_B$ (speciation equal between regions).
4. $x_A = x_B$ (extinction equal between regions).
5. $d_A = d_B$ (dispersal symmetric between areas).
6. $s_A = s_B$, $x_A = x_B$ (speciation and extinction equal between areas).
7. $s_A = s_B$, $d_A = d_B$ (speciation and dispersal equal between areas).
8. $d_A = d_B$, $x_A = x_B$ (dispersal and extinction equal between areas).
9. $s_A = s_B$, $x_A = x_B$, $d_A = d_B$ (equal speciation, extinction, and dispersal).
10. $s_A = s_B$, $x_A = x_B$, $d_A = d_B$, $s_{AB} = 0$ (9 with no intermediate speciation).

The GeoSSE model also accounts for incomplete taxon sampling by taking into account the proportion of taxa in each state (e.g. A, B or AB) included in the phylogeny, using essentially the same algorithm as BiSSE (Fitzjohn, 2012). The 4161-species phylogeny contains 73% of species that occur in both areas (90 of 124), 41% of tropical species (3269 of 7955) and 60% of temperate species (803 of 1337). I used the Akaike information criterion (AIC) to discriminate between models, choosing the lowest delta AIC score ($\Delta AIC = 0$). To account for model uncertainty, I sampled the posterior probability distribution of the parameters for the best-fit model using Markov chain Monte Carlo (MCMC), with a broad exponential prior (mean of 0.5) on all parameters as recommended (Fitzjohn, 2012), run for 100 generations. While the proportion of tropical taxa included is sub-optimal (59% are missing), including these species (i.e. adding more branches) would only serve to increase estimates of tropical speciation, which would only reinforce the results (see below). If more branches are added to a phylogeny with a constant root age this decreases the average branch length, increasing speciation and decreasing extinction estimates (Pyron & Burbrink, 2013).

In addition to absolute speciation and extinction rates, I calculated net diversification rates and relative extinction fractions taken as the per-sample difference or quotient. Importantly, simulation studies of the SSE models and others using phylogenetic branch-length information show a relatively high power to detect differential rates of both speciation and extinction using large phylogenies such as this one (Fitzjohn, 2010; Etienne *et al.*, 2012; Pyron & Burbrink, 2013; Rolland *et al.*, 2014). This allays concerns raised by recent studies suggesting that such inferences (particularly of extinction) are unreliable, as these were based primarily on small trees using clade-based (i.e. age and diversity) estimators and not the branch lengths of the phylogenies themselves (Rabosky, 2010).

Location and life history

A previous analysis of this tree indicated that viviparity as a life-history strategy was linked to higher speciation and

extinction, and thus reduced net diversification rates and higher turnover (Pyron & Burbrink, 2014). Viviparous taxa are commonly, but not exclusively, found in temperate regions (Shine, 1985). The previous study was unable to sort out the causative effects of climate versus parity mode per se on diversification rates. Thus, parity mode may be a covariate of an underlying relationship between climate and diversification (Lynch, 2009; Pincheira-Donoso *et al.*, 2013). As both the BiSSE algorithm (Pyron & Burbrink, 2014) and the GeoSSE algorithm measure a binary trait with similar states in many taxa, it is possible that the same phylogenetic signal is being reflected in both analyses.

The relationship between geographic area, parity mode and diversification rates can possibly be sorted out by examining the direction and magnitude of parity–diversification and area–diversification relationships, and the correspondence of states among taxa. For example, if most viviparous taxa (i.e. with higher speciation and extinction yielding lower net diversification and higher turnover) are temperate, but temperate taxa are found here by GeoSSE to have lower speciation and extinction (yielding lower net diversification but lower turnover), this would suggest that parity mode and area have independent effects. In contrast, if all viviparous taxa are temperate and oviparous taxa tropical, and GeoSSE results match BiSSE results, further testing would be needed to hypothesize the directionality of causation.

I use a *G*-test (goodness-of-fit) to compare observed and expected frequencies of oviparous versus viviparous taxa in temperate versus tropical areas, in a 2×2 contingency table for the 3962 taxa that have both parity and location data (from Pyron & Burbrink, 2014; and the temperate versus tropical classification described above). For the purposes of this test, I ignore the relatively small number of reproductively bimodal and trans-tropically distributed species (leaving 3864 total taxa). While this test is not phylogenetically corrected, this is not strictly necessary, as the test is not concerned with whether or not the distribution of character states is phylogenetically correlated, but simply whether GeoSSE and BiSSE are receiving autocorrelated input data. I calculated the test with the expectation that the 3076 tropical taxa and 788 temperate taxa were split between parity modes (1538 and 394 each).

RESULTS

Diversification, dispersal and life history

In the multiple-regression model containing latitude (proportion of temperate species), stem age and crown age ($R^2 = 0.43$), there is no significant effect of latitudinal position ($\beta = -0.14$, $P = 0.18$). In contrast, squamates exhibit a strongly negative stem-age/diversity relationship ($\beta = -0.37$, $P = 0.0054$; Fig. 1a) and a strongly positive crown-age/diversity relationship ($\beta = 0.79$, $P < 0.00001$; Fig. 1a). A flat stem-age/diversity relationship has been reported previously in squamates (Ricklefs *et al.*, 2007; Rabosky *et al.*, 2012), but the crown-age/diversity relationship has not been tested. Testing for a quadratic relationship between crown age and diversity using polynomial regres-

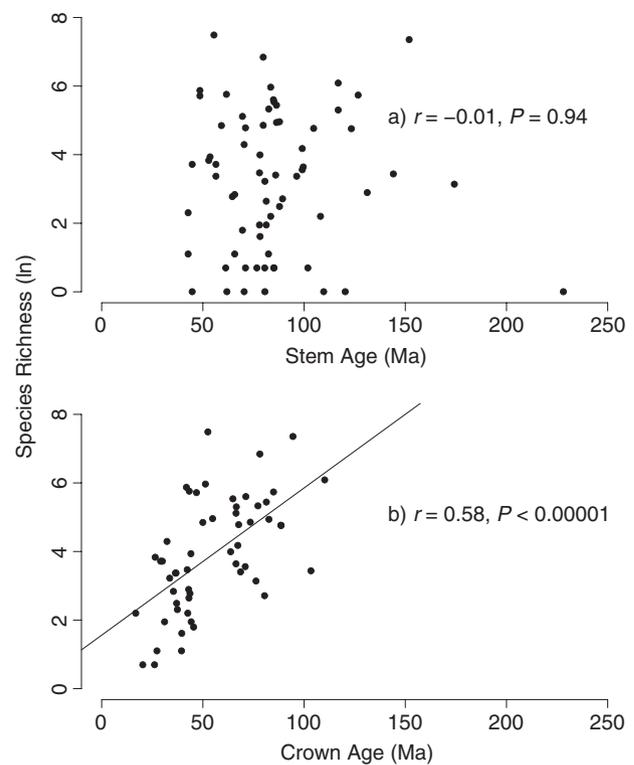


Figure 1 Plot of stem-age/diversity (a) and crown-age/diversity (b) relationships, showing that older crown groups accumulate more species over time but stem groups do not. This suggests that higher extinction is pruning more species from older stem lineages. As older stem lineages are found in predominantly temperate clades, this suggests that higher temperate extinction limits the accumulation of crown-group species richness at higher latitudes, even in older clades.

sion reveals no support for this model over a linear relationship ($P = 0.075$), suggesting that older clades do not show a noticeable slowing of accumulation of diversity, as would be expected under a saturation model (Rabosky, 2009; Cornell, 2013).

The seven-parameter GeoSSE model was strongly supported over alternative submodels ($P = 0.00002$; Table 1). In this model, tropical speciation is lower than temperate speciation, while tropical extinction is estimated to be around zero and temperate extinction is much higher. Trans-region speciation (sAB) is also non-zero, suggesting that expansion between regions and subsequent speciation (e.g. between North and Central America) is an important process. The difference in speciation and extinction induces lower net diversification rates in temperate regions (temperate r range = 0.029–0.045 lineages Myr^{-1}) than in the tropics (tropical $r = 0.065$ –0.070 lineages Myr^{-1} ; Fig. 2a). In contrast, relative extinction fractions are drastically higher in temperate areas (temperate $\epsilon = 0.47$ –0.69, tropical $\epsilon = 0.00$ –0.04; Fig. 2b). Dispersal from the tropics to temperate regions is 4.7 times lower than dispersal from temperate regions to the tropics (Table 1, Fig. 3).

Table 1 Comparison of alternative GeoSSE submodels from diversitree. Parameters given are speciation (*s*), extinction (*x*) and dispersal (*d*) for species in the tropics (*A*), temperate regions (*B*), and both (*AB*).

Model	d.f.	$-\ln L$	ΔAIC	<i>sA</i>	<i>sB</i>	<i>sAB</i>	<i>xA</i>	<i>xB</i>	<i>dA</i>	<i>dB</i>
Full	7	-17,955	0	0.06719	0.08595	0.05034	0	0.0483	0.00135	0.00625
<i>sAB</i> = 0	6	-17,968	24	0.06747	0.09788	–	0.00003	0.06458	0.00136	0.00552
<i>sA</i> = <i>sB</i>	6	-17,964	16	0.06803	–	0.06465	0	0.02689	0.0012	0.00713
<i>xA</i> = <i>xB</i>	6	-17,984	58	0.06702	0.06253	0.08607	–	0.00176	0.00122	0.00695
<i>dA</i> = <i>dB</i>	6	-17,983	55	0.06742	0.10002	0.03925	0	0.06971	–	0.00261
<i>sA</i> = <i>sB</i> , <i>xA</i> = <i>xB</i>	5	-17,986	59	0.06605	–	0.08731	0.00137	–	0.00122	0.00689
<i>sA</i> = <i>sB</i> , <i>dA</i> = <i>dB</i>	5	-18,002	96	0.06685	–	0.06577	0	0.01661	–	0.00203
<i>dA</i> = <i>dB</i> , <i>xA</i> = <i>xB</i>	5	-18,009	105	0.06682	0.06303	0.06944	0.00136	–	0.00181	–
<i>sAB</i> only	4	-18,010	106	0.06604	–	0.06897	0.00107	–	0.0018	–
Equal	3	-18,044	172	0.07479	–	–	0.01486	–	0.00172	–

AIC, Akaike information criterion.

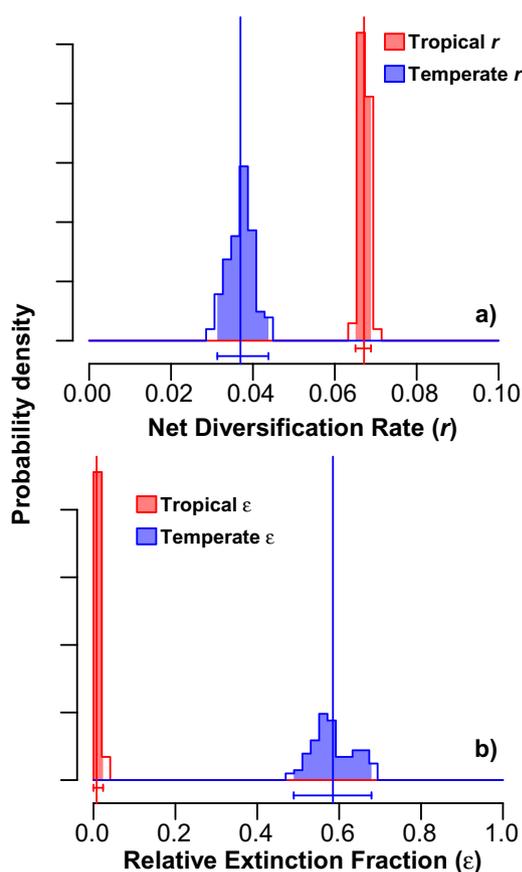


Figure 2 Tropical versus temperate rates of net diversification (a) and relative extinction fraction (b), showing lower rates of species accumulation and higher lineage turnover in temperate regions. Plots are based on 100 Markov chain Monte Carlo samples of the best-fit GeoSSE model (Table 1).

Of the 3864 species in the tree with parity and area data, 2505 are tropical and oviparous and 571 are tropical and viviparous. In temperate areas 533 species are oviparous while 255 are viviparous. This differs significantly from an even ratio of modes between areas ($G = 1414$, $P < 0.00001$). Thus, parity modes are

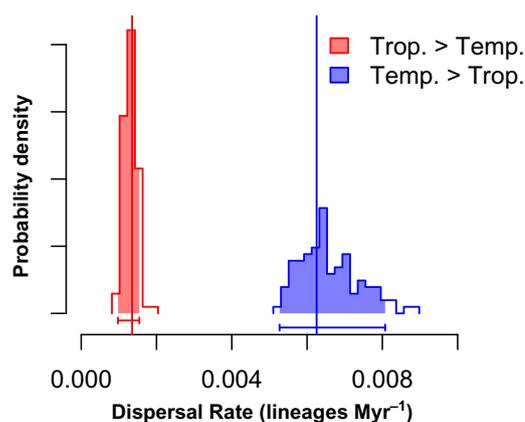


Figure 3 Rates of dispersal between temperate and tropical regions, showing bias towards range expansion into the tropics from temperate regions, and the low rate of dispersal into temperate areas by tropical species. Plots are based on 100 Markov chain Monte Carlo samples of the best-fit GeoSSE model (Table 1).

non-randomly associated with geographic areas. However, the pattern is far from a simple tropical/oviparous, temperate/viviparous dichotomy, as there are more tropical than temperate viviparous species, and more oviparous than viviparous temperate species. Thus, the diversification dynamics of parity mode and latitudinal position appear to be at least partially decoupled, despite having similar directions and magnitudes. In particular, speciation and extinction rates are higher in both viviparous and temperate taxa than in oviparous or tropical species, but net diversification rates are similar in oviparous and viviparous taxa (Pyron & Burbrink, 2014) and are markedly different here between temperate and tropical taxa (Table 1).

DISCUSSION

Squamate diversity

Diversity dynamics in squamates are complex, and appear to be related to characteristics such as geographic area (i.e. temperate

versus tropical) and parity mode (i.e. oviparous versus viviparous). While the evolution of viviparity is correlated with temperate climates (Pyron & Burbrink, 2014), these dynamics appear to be at least partially independent, as there are more tropical than temperate viviparous species and more oviparous than viviparous species in temperate areas. Also, the two alternative life-history strategies have similar net diversification rates (Pyron & Burbrink, 2014). Thus, ecological selection on life-history strategy may explain some, but not all, of latitudinal diversity patterns in squamate reptiles. How then are these structured?

Squamates exhibit a strong LDG, with 1337 temperate species, and 7955 tropical species, with only 124 species spanning both regions. Despite the predominance of tropical lineages, there are numerous relatively diverse radiations endemic to temperate areas, such as the liolaemids of Patagonia, the lacertids of the Palaearctic, the crotaline, lampropeltine and natricine snakes and *Plestiodon* lizards of the Nearctic, and skinks and geckos of New Zealand. The fossil record for squamates is too sparse to attempt a full analysis of latitudinal variation in diversification rates using extinct species (e.g. Jablonski *et al.*, 2006), but the very high known diversity of squamate fossils in temperate regions is certainly not inconsistent with higher temperate extinction rates (see Holman, 2000; Vitt & Caldwell, 2009).

An origin of squamate lineages in the tropics could explain to some degree the greater species richness there due to greater time for speciation, but the magnitude of the LDG appears to be driven primarily by diversification and dispersal rates. Both temperate and tropical areas have apparently been inhabited by squamates for a great deal of time. Older crown groups accumulate more species as expected, while older stem groups have fewer species. Thus, extinction has apparently pruned older temperate taxa (Pyron & Burbrink, 2012). Speciation and extinction in temperate lineages are both very high (low net diversification and high turnover), and temperate clades are thus less diverse. In contrast, speciation is relatively high in tropical squamate clades, and extinction appears to be very low. Similarly, there is reduced dispersal out of the tropics (i.e. poleward range-expansion), but a greater tendency for temperate lineages to invade the tropics.

The tropics thus represent both a 'cradle' and a 'museum' of squamate diversity (Jablonski *et al.*, 2006), as older tropical crown groups accumulate more species at a higher rate (Fig. 1b). In contrast, speciation rates are even higher in temperate regions, but a massive attendant increase in extinction yields lower net diversification and higher turnover. Similar to amphibians and mammals (Pyron & Wiens, 2013; Rolland *et al.*, 2014), this leaves temperate regions disproportionately depauperate, even with older stem lineages (Fig. 1a). This effect is bolstered by the low rate of dispersal out of the tropics, presumably due to niche conservatism limiting colonization of more inhospitable climatic zones (Wiens & Donoghue, 2004). This combination of processes seems to be increasingly recovered in many groups, and I suggest that it may provide a cogent generalized explanation for LDGs in many taxa.

A major consideration not accounted for by this study or many others is the drastic variation in climatic zones and the

associated ranges of species through space and time (Wiens & Donoghue, 2004; Jetz & Fine, 2012). Both continental landmasses and local climatic conditions have shifted geographically and exhibited drastically varying geographic extents over time. In some ways this might actually be a powerful explanation for the patterns observed here, if the greater past extent of the tropics is a primary driver of: (1) more clades arising over time in these larger areas, and (2) lower extinction rates over time facilitated by these larger areas (Wiens & Donoghue, 2004). This could also account for high squamate diversity in some desert areas of present-day 'temperate' regions such as the Middle East and south-western North America. The time-integrated area of ecoregions (Jetz & Fine, 2012) may provide a powerful explanation for the greater diversification rates in tropical squamates. Accordingly, the greater oscillation of available habitat in temperate regions over time may drive higher extinction and turnover rates (Hewitt, 1996; Dynesius & Jansson, 2000).

These analyses also make a number of assumptions that may be violated. First, the continuous spatial component of the LDG is broken down into a simple dichotomy of temperate versus tropical species, and the rates are not allowed to vary over time. A continuous, multiregion analysis should be a priority for future studies, estimating rate differences in different time periods, as well as integrating species-specific ecological or climatic data. The geographic context (temperate versus tropical) is very coarse, particularly given how these climatic zones have shifted over time. Second, the interaction between parity modes and areas was not measured explicitly, such as with a multitrait SSE-type analysis (FitzJohn, 2010). Such analyses are not currently implemented in a tractable way, but may be possible in the future.

Nevertheless, the analyses presented here seem to show a robust signal of two simple but provocative patterns. First, lineages at predominantly temperate latitudes have a strong phylogenetic signal of low speciation and high extinction, with the reverse in tropical areas. Second, this is at least partially independent of a similar relationship between speciation, extinction and climatically correlated reproductive modes. It will be important to test these baseline results in future studies using more detailed climatic and geographical data, with more species included in the phylogeny. Furthermore, it will be crucial to examine how the strength and position of LDGs have varied over time, as currently observed patterns may be specific to recent climatic and geological fluctuations (Jetz & Fine, 2012; Mannion *et al.*, 2014).

Tropical speciation and temperate extinction rates

An increasingly large number of studies using molecular phylogenies to test evolutionary hypotheses for the origin and maintenance of LDGs seem to be converging on a few simple and intuitive results. First, net diversification rates are higher in tropical clades and lower in temperate lineages (Cardillo *et al.*, 2005; Ricklefs, 2006). Second, rates of speciation and extinction are higher in temperate regions, leading to higher lineage turnover in temperate areas in addition to the lower net diversifica-

tion rates (Weir & Schluter, 2007; Pyron & Wiens, 2013). Third, dispersal is asymmetrically biased against movement out of the tropics (Wiens & Donoghue, 2004). In several groups (including squamates) the primacy of diversification rates rather than ecological limits in controlling species richness is reflected in positive crown-age/diversity relationships (Pyron & Wiens, 2013). Accordingly, the importance of extinction over long time-scales is reflected by flat or negative stem-age/diversity relationships as lineages are pruned from stem branches (Pyron & Burbrink, 2012; Rabosky *et al.*, 2012). I suggest that these processes provide a general framework that is likely to explain aspects of LDGs in many groups, and that high temperate extinction in particular is likely to be the dominant force for originating and maintaining LDGs.

Were evolutionary time (the length of time a region has been colonized) the main determining factor for LDGs when integrating over variation in diversification rates (Wiens & Donoghue, 2004), then future temperate diversity would eventually equal, then exceed, present-day tropical diversity. This is not to say that LDGs would vanish, as proportionally more tropical species would also have accumulated in that time. Rather, the 1337 present-day temperate squamates would eventually become 7955 temperate species (then even more), and the 7955 present-day tropical species would become even more, perhaps > 25 000 (for example). This seems unlikely. Thus, LDGs in some younger taxa may be due to different times of origin in temperate versus tropical areas (Wiens *et al.*, 2006, 2009, 2011). In contrast, for any group with many ancient temperate clades (e.g. birds, mammals, reptiles, amphibians), a long-term LDG with depauperate temperate faunas must have arisen through differences in net diversification rate. This can be confirmed coarsely by testing for a positive crown-age/diversity relationship, indicating that clades are accumulating species through time (Rabosky, 2009), and a latitudinal bias in crown- and stem-group ages (Pyron & Wiens, 2013).

As there cannot be an infinite number of species, this accumulation must eventually slow and then stop as niches became saturated and net diversification goes to zero (Walker & Valentine, 1984; Rabosky, 2009). However, the action of ecological limits, regardless of their ecological causes (such as limiting local co-occurrence), must be through modulation of diversification rates (Rabosky & Lovette, 2008), as extinction and speciation become equal and net diversification falls to zero (Wiens, 2011). There does seem to be evidence in some groups (and it seems logically necessary) that rates of accumulation have slowed over time (damped increases) as regional diversity saturated (Cornell, 2013). This must still be related to changes in diversification rate, such as decreasing speciation or increasing extinction.

In all robustly evaluated cases thus far, lower net diversification rates in temperate regions (birds, mammals, amphibians and reptiles) are associated with higher temperate extinction rates (Weir & Schluter, 2007; Pyron & Wiens, 2013; Rolland *et al.*, 2014). Some recent large-scale studies of birds and mammals did not find a latitudinal gradient in net diversification rates, but they did not separate speciation or extinction

rates or estimate per-lineage rates using model-based estimators (Jetz *et al.*, 2012), and were based only on genus-level analyses (Soria-Carrasco & Castresana, 2012). For analyses using phylogenetic branch-length information, temperate extinction and tropical speciation are higher in amphibians, reptiles and mammals. Based on the results here for squamates and from some other studies of birds and mammals (Weir & Schluter, 2007), temperate speciation is also higher. Analyses of the full mammal tree suggest that this result is driven by Carnivora, for which it is strongly supported, but does not characterize all mammals (Rolland *et al.*, 2014). In all groups, the end result is the same: lower net diversification rates and higher relative extinction fractions in temperate areas. I suggest that the most important fundamental process for generating and maintaining LDGs is this increase in temperate extinction, in both absolute and relative terms.

Regardless of whether temperate speciation is higher or lower relative to tropical speciation (affecting the magnitude of the difference in net diversification rate), higher temperate extinction ultimately limits the accumulation of diversity in temperate regions and clades. Net diversification rates are essentially zero at the poles in almost all organisms. This does not appear to be due to the existence of stable populations at the poles, which simply diverge into additional species at an extremely slow rate (low speciation). Rather, most groups simply cannot maintain viable populations in poleward regions, as they quickly experience local extinction. Similarly, the present-day habitat of numerous temperate squamate species in the Holarctic was covered by hundreds of metres of ice during recent glacial cycles, which presumably prevented occurrence during those periods.

The rate of speciation is apparently increased by events such as glaciations, as populations are carved up into refugia (Hewitt, 1996). However, it is the action of higher extinction rates, as evidenced by higher turnover rates, that prevents the long-term accumulation of temperate diversity (Dynesius & Jansson, 2000), despite these speciation processes. As noted above, if this were not the case, one would eventually expect the accumulation of hundreds or thousands of reptiles in the Arctic Circle given enough time, which seems unlikely.

Of crucial importance is the fact that non-zero net diversification rates do not lead to unbounded diversification (i.e. an infinite number of species) when extinction is sufficiently high to prune entire clades (Benton & Emerson, 2007). Thus, temperate diversity will not perpetually increase (the argument I use above against evolutionary time), due to high turnover, despite speciation exceeding extinction (Cornell, 2013). The exact mechanisms by which ecological factors such as climate induce changes in temperate and tropical rates merits more study and may be historically contingent (Burbrink *et al.*, 2012). Explicit tests of the macroecological causes of rate differences through time and space and in different climates will be an important next step for understanding LDGs.

Another question that remains is whether diversity accumulation is slowing or saturating at regional scales (Cornell, 2013). The results from the polynomial regression suggest that this pattern is not apparent at the broadest scales; older crown

groups exhibit diversity in line with what would be expected under a constant-accumulation model. Were diversity saturating at the regional level, we would expect a curvilinear relationship between crown age and diversity, with the oldest crown groups only slightly more diverse than those of intermediate ages (Rabosky, 2009). This is not to say that diversification is proceeding unbounded in squamates; as noted above, saturation must occur eventually. Squamates may not have yet reached that point yet, at least at the global level. This could be tested in future analyses by applying models of diversity dependence to those clades occupying different areas (Etienne *et al.*, 2012).

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SUPPORTING INFORMATION

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Appendix S1 Geographic range data for the 4162 species in the phylogeny, and the proportion of temperate species, stem age, crown age and diversity for 68 families.

BIOSKETCH

Alex Pyron studies the systematics and historical biogeography of reptiles and amphibians; he moves fluidly, with an economy of motion, like a dancer moves when he’s not dancing.

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