RESEARCH PAPER

Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini

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ABSTRACT

Aim A latitudinal gradient in species richness, defined as a decrease in biodiversity away from the equator, is one of the oldest known patterns in ecology and evolutionary biology. However, there are also many known cases of increasing poleward diversity, forming inverse latitudinal biodiversity gradients. As only three processes (speciation, extinction and dispersal) can directly affect species richness in areas, similar factors may be responsible for both classical (high tropical diversity) and inverse (high temperate diversity) gradients. Thus, a modified explanation for differential species richness which accounts for both patterns would be preferable to one which only explains high tropical biodiversity.

Location The New World.

Methods We test several proposed ecological, temporal, evolutionary and spatial explanations for latitudinal diversity gradients in the New World snake tribe Lampropeltini, which exhibits its highest biodiversity in temperate regions.

Results We find that an extratropical peak in species richness is not explained by latitudinal variation in diversification rate, the mid-domain effect, or Rapoport's rule. Rather, earlier colonization and longer duration in the temperate zones allowing more time for speciation to increase biodiversity, phylogenetic niche conservatism limiting tropical dispersal and the expansion of the temperate zones in the Tertiary better explain inverse diversity gradients in this group.

Main conclusions Our conclusions are the inverse of the predictions made by the tropical conservatism hypothesis to explain higher biodiversity near the equator. Therefore, we suggest that the processes invoked are not intrinsic to the tropics but are dependent on historical biogeography to determine the distribution of species richness, which we refer to as the 'biogeographical conservatism hypothesis'.

Keywords

Diversification, latitudinal diversity gradients, niche conservatism, Rapoport's rule, snakes, speciation, species richness.

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INTRODUCTION

A latitudinal gradient of species richness, wherein the tropics contain more taxa than temperate areas, is one of the oldest recognized patterns in ecology and evolutionary biology (Wallace, 1878; Brown & Lomolino, 1998; Willig *et al.*, 2003; Hillebrand, 2004; Mittelbach *et al.*, 2007). Numerous hypotheses have been proposed to explain these observations (Pianka, 1966; Rohde, 1992; Willig *et al.*, 2003; Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007), all of which ultimately attempt to address the three factors directly affecting biodiversity: speciation, extinction and dispersal (Ricklefs, 1987). Most of these explanations can be classified into the three broad, though potentially overlapping, categories of ecological, temporal and evolutionary hypotheses (Mittelbach *et al.*, 2007).

Ecological explanations suggest that the tropics evolved and maintain greater species diversity due to environmental effects, such as higher environmental productivity, increased available niche breadth, larger geographical areas or some combination thereof allowing more species to coexist locally (see review in Willig *et al.*, 2003). Temporal explanations assume that earlier origination and longer duration of clades in the tropics allowed for the development of higher biodiversity through the steady accumulation of species over time, such as through time-for-speciation/centre-of-origin effects (TFS/COO; Ricklefs & Schluter, 1993; Brown & Lomolino, 1998; Stephens & Wiens, 2003; Wiens & Donoghue, 2004; Stevens, 2006). Evolutionary hypotheses suggest that higher rates of tropical speciation or temperate extinction are responsible for the diversity gradient (see Rohde, 1992; Cardillo *et al.*, 2005; Ricklefs, 2006; Weir & Schluter, 2007). Additionally, some explanations suggest that the latitudinal species richness gradient is merely a spatial artefact of the overlap of species ranges within a given area, called the mid-domain effect (MDE; Colwell *et al.*, 2004).

Few of these hypotheses offer explanations which are specific to a situation where species diversity increases towards the equator. For instance, ecological patterns such as Rapoport's rule (decreasing latitudinal extent of ranges at lower latitudes; Stevens, 1989) may exist independently of biodiversity gradients. Temporal explanations for higher tropical species richness, which invoke the TFS/COO effects, should also predict higher temperate species richness for groups which originated in temperate zones (Stephens & Wiens, 2003; Smith *et al.*, 2005). Variation in the evolutionary rate could also exist in groups with higher temperate diversity if the rate differences were insufficient to overcome TFS/COO effects, or the differences in rate were complementary (i.e. increased extinction in the temperate areas combined with decreased speciation in the tropics). Finally, spatial patterns such as the MDE would also predict higher species richness for any area at the centre of a bounded domain, not only the tropics.

If any of these explanations account for both high tropical diversity as well as inverse latitudinal gradients caused by higher temperate species richness, this would suggest that these hypotheses are not restricted solely to explaining higher diversity in the tropics. We test these methods to explain inverse species gradients in the widely distributed New World snake tribe Lampropeltini, the rat, king and milk snakes and relatives. The lampropeltinines comprise at least 31 species, ranging from Canada to northern South America (SA; Williams, 1978; Conant & Collins, 1998). A previous study indicated that the lampropeltinines dispersed into the New World in the late Oligocene or early Miocene and shared a common ancestor approximately 25 Ma (Burbrink & Lawson, 2007). The group exhibits far higher species richness in temperate areas of North America (NA; *c.* 27 species) than in the neotropics (NT; *c.* 4 species). This is unusual for ectotherms such as reptiles and amphibians, which tend to have their greatest diversity in the tropics (Ricklefs *et al.*, 2007; Wiens, 2007), although similar patterns have been observed in temperate clades of turtles and frogs (Stephens & Wiens, 2003; Smith *et al.*, 2005). Determining why these snakes exhibit higher temperate species

richness will help provide a general explanation for distributions of biodiversity on a global scale.

Using a robust phylogenetic estimate for the tribe containing all extant species (Pyron & Burbrink, 2009), we assess several temporal, evolutionary, ecological and spatial explanations for the observed inverse latitudinal species richness gradient. First, we infer the ancestral area of the group to test for the presence of TFS/COO effects (Ricklefs & Schluter, 1993; Stephens & Wiens, 2003). Second, we determine if phylogenetic niche conservatism of relevant ecological traits (e.g. Ricklefs & Latham, 1992) may have limited dispersal between temperate and tropical areas (e.g. Wiens & Donoghue, 2004; Smith *et al.*, 2005). Third, we test for latitudinal variation in diversification rates to assess potential evolutionary explanations for the observed gradient (e.g. Rohde, 1992; Weir & Schluter, 2007). Fourth, we determine if Rapoport's rule (Stevens, 1989) exists in this group independently of high temperate species richness, suggesting that its presence in groups with high tropical diversity is merely correlative. Finally, we test whether the observed latitudinal gradient in species richness is merely a spatial artefact due to the MDE (Colwell *et al.*, 2004), centred on temperate latitudes.

A temperate origin of the group would suggest that historical biogeography and phylogenetic niche conservatism is the primary determinant of species richness, indicating that long-term presence in temperate areas and limited tropical dispersal allowed more time for speciation to increase biodiversity (e.g. Stevens, 2006; Wiens *et al.*, 2006, 2009). Alternatively, a tropical origin of the extant lampropeltinines would suggest that latitudinal variation in diversification rates (e.g. Cardillo *et al.*, 2005; Ricklefs, 2006; Weir & Schluter, 2007) and/or large-scale dispersal into temperate regions was responsible for the observed biodiversity gradients. Rapoport's rule could be rejected as a hypothesis for higher tropical species richness if it is found to be significant in the lampropeltinine snakes, indicating that the pattern can arise independently of species richness patterns (e.g. Rohde, 1996; Gaston *et al.*, 1998). Presence of the MDE would suggest that the pattern of higher temperate species richness fits an artefactual null model (Colwell *et al.*, 2004) and is not indicative of an underlying biological process. Additionally, combinations of these effects are possible. Our data indicate that historical biogeographical processes, rather than spatial effects or ecological or evolutionary rate variation, are responsible for the distribution of species richness in the lampropeltinines.

METHODS AND MATERIALS

Phylogenetic hypothesis

Our phylogenetic estimate of the lampropeltinines is based on a dataset comprising 8294 bp of nuclear and mtDNA from nine genes (Pyron & Burbrink, 2009). This phylogeny contains representatives of all 31 currently recognized lampropeltinine species, and consists of six mtDNA fragments (12S, cyt-*b*, COI, ND1, ND2, ND4) and four nuclear fragments from three loci (c-mos, SPTBN1, Vimentin Intron 4, Vimentin Intron 5). We use the maximum likelihood (ML) estimate of the topology and branch

lengths, which is well supported by nonparametric bootstrap proportion and Bayesian posterior probabilities, as well as the Bayesian divergence time estimates for the internal nodes (Pyron & Burbrink, 2009). We used this phylogenetic estimate and set of divergence times for the following analyses.

Ancestral area reconstruction

The ancestral area of the lampropeltinines was estimated using the ML dispersal–extinction–cladogenesis model implemented in the program LAGRANGE 2.0.1 (Ree et al., 2005; Ree & Smith, 2008). The terminal ingroup species were coded as occurring in one or a combination of four primary New World biogeographical areas based on occurrence records (see below): the neotropics (NT; south of the Tropic of Cancer at 23.4°, excepting the Mexican Plateau in central Mexico south to the Trans-Mexican Volcanic Belt; see Schultz, 2005), eastern NA (E; east of the Mississippi River), central NA (C; between the Mississippi River and the Western Continental Divide, south to the Tropic of Cancer) and western NA (W; from the continental divide to the Pacific Ocean, south to the Tropic of Cancer). Species occurring on the Mexican Plateau, which are likely to cross the continental divide, were coded as both C and W.

A number of species occur within short distances south of the Tropic of Cancer, but are not considered to be Neotropical, occurring either on the Mexican Plateau or in the Sierra Madre Occidental/Oriental mountains. A second analysis was performed in which all such taxa were coded as also occurring in the NT, to ensure that bias in biogeographical coding did not affect the ancestral state reconstructions. A fifth state, the Old World, was coded for the outgroup taxa, and the ancestral state of the tree was constrained to be Old World. The topology used was the dated chronogram (Fig. 1), with branch lengths equal to absolute time (Ree & Smith, 2008). Dispersal probabilities between areas were unconstrained to avoid excessive parameterization; the geographical formation of the New World remained relatively constant over the time period of interest and dispersal between the areas was not given any directional weighting. The model was also not constrained by time for the same reason. Rates of dispersal and local extinction were assumed to be constant (Ree & Smith, 2008).

Phylogenetic niche conservatism

To test for the presence of phylogenetic niche conservatism and infer the possible effects on dispersal, we gathered 4564 presence records comprising all 31 ingroup species and the Old World sister taxon *Coronella austriaca* (see Appendix S1 in Supporting Information; Fig. 2). Occurrences were obtained from museum records, primarily from the HerpNet database. Points with GPS data were used 'as is', all other records were georeferenced to the common locality provided. We extracted climatic data for these points from the WORLDCLIM dataset projected at 30″ spatial resolution, which comprises 19 variables describing averages and seasonal variation in temperature and precipitation, (Hijmans et al., 2005). We then performed a principal components analysis

(PCA) to isolate the factors accounting for primary variance in ecological niche (e.g. Wiens et al., 2006).

To test for significant phylogenetic niche conservatism and infer the ancestral niche of the lampropeltinines, we reconstructed the scores for the significant principal components (PC) axes on the phylogeny using phylogenetic generalized least squares (PGLS; Martins & Hansen, 1997) in the program COMPARE v4.6b (Martins, 2004), using the branch lengths estimated from the ML analysis (Pyron & Burbrink, 2009). We truncated the phylogeny to only include *C. austriaca* as an outgroup, which has been reliably inferred to be the immediate outgroup to the lampropeltinines (Utiger et al., 2002; Burbrink & Lawson, 2007). We then plotted the ancestral reconstructions against the PC scores of the extant species to test for broad-scale conservatism of ecological preferences through time.

To test for phylogenetic conservatism of specific ecological traits limiting dispersal between the temperate and tropical areas, we identified the variables which had the highest positive and negative loadings on the PC axis of greatest separation, and interpreted them to be the primary range-limiting variables of the temperate and tropical species (*sensu* Smith et al., 2005; Wiens et al., 2006). We log-transformed the means of each variable for each species and tested for significant niche conservatism in these variables using the λ statistic (Pagel, 1999) in the program BAYESTRAITS (Pagel & Meade, 2006). A value of $\lambda = 0$ indicates no phylogenetic structure, while $\lambda = 1$ indicates perfect correlation with the phylogeny (but see Revell et al., 2008, for caveats). The presence of niche conservatism was calculated using the standard likelihood ratio (LR) test comparing a model in which λ is set from 0 to 1, where λ is allowed to take its ML value (Pagel & Meade, 2006). All analyses were performed in the program BAYESTRAITS (Pagel & Meade, 2006).

Latitudinal variation in diversification rates

To test for latitudinal differences in diversification rate, *sensu* Weir & Schluter (2007), we performed linear regression analyses for the 10 sister species pairs inferred in the primary phylogenetic analysis. We regressed the age of the divergence of each species pair against the mean latitudinal midpoint of that pair. If higher speciation rates are responsible for increased biodiversity, then species pairs should be youngest where species richness is highest (a positive relationship). The signature of higher extinction rates would be a negative relationship, with younger species pairs where diversity is lowest (Weir & Schluter, 2007). A non-significant relationship between latitudinal midpoint and age of the species pair would suggest that little or no major geographical variation exists in net diversification rate.

Rapoport's rule

We tested for the presence of the Rapoport effect, decreasing latitudinal extent of ranges with decreasing latitude (Stevens, 1989), using both the raw and the phylogenetically corrected latitudinal midpoints and extents of each species. We characterized the latitudinal midpoint and extent of all 31 extant species using
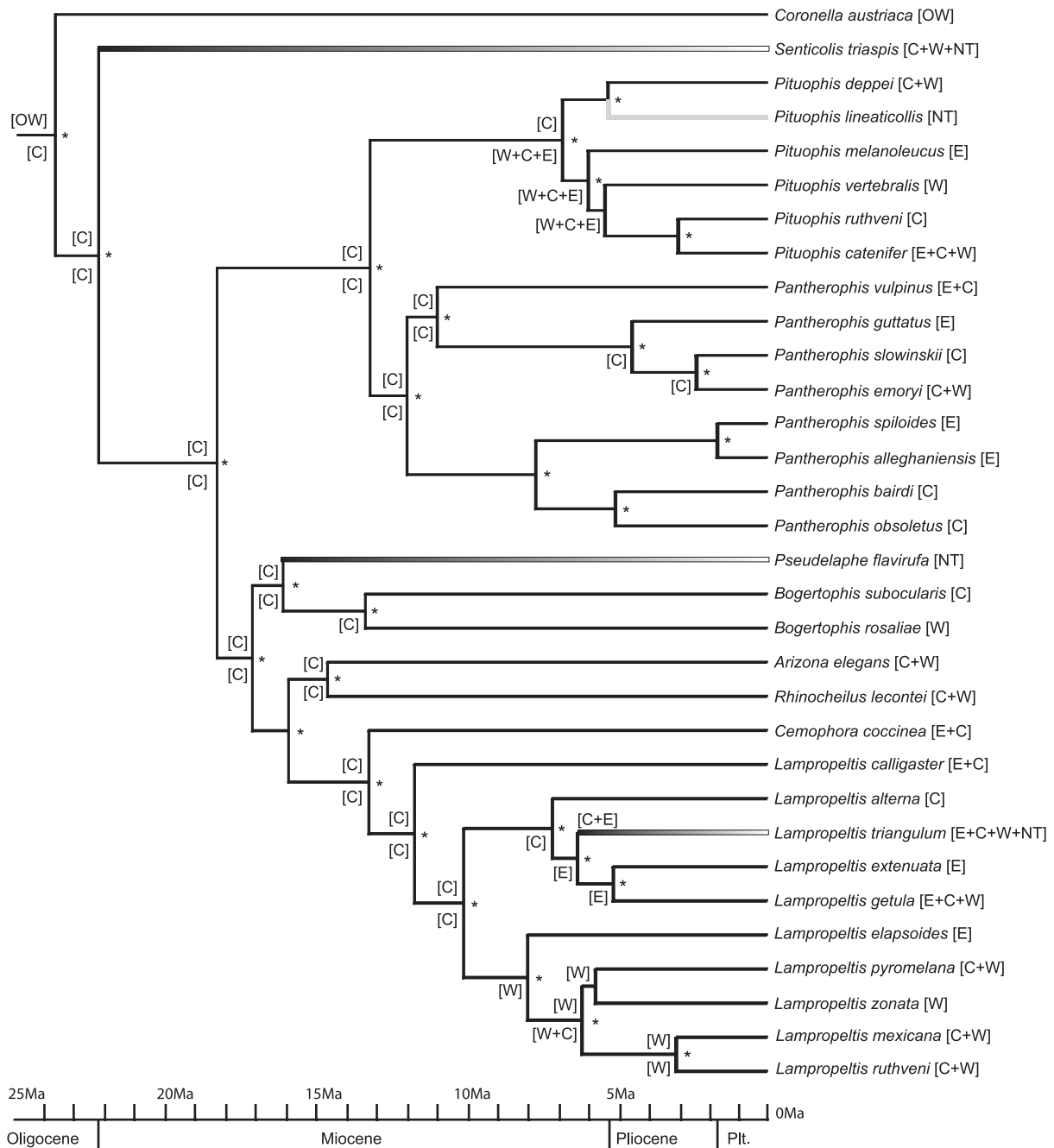
Figure 1 Bayesian inference chronogram from Pyron & Burbrink (2009). Asterisks denote nodes supported by greater than 95% posterior probability. Branch lengths are equal to time (scale on the *x*-axis is millions of years ago, Ma). Labels on branches indicate the biogeographical reconstructions from Lagrange. Labels at the tips are the areas for each species, derived from the occurrence records (see Appendix S1). Codes are as follows: OW, Old World; E, eastern; C, central; W, western; NT, Neotropics. Branches without labels are reconstructed to have the same area as the descendant terminal species. Branches reconstructed to occur in temperate areas are black, while tropical branches are grey. Gradients represent unobservable tropical dispersals by terminal species.

the georeferenced locality records (see Appendix S1). The occurrence records were used to calculate the minimum and maximum latitude of each species. The latitudinal range is the difference between the minimum and maximum latitude, while the latitudinal midpoint is the mean of the two. We performed linear regression analyses with the raw data. We also used PGLS (Martins & Hansen, 1997) and Felsenstein's phylogenetically independent contrasts (F/PIC; Felsenstein, 1985) to control for phylogenetic non-independence of the location of the species in the program compare v4.6b (Martins, 2004).
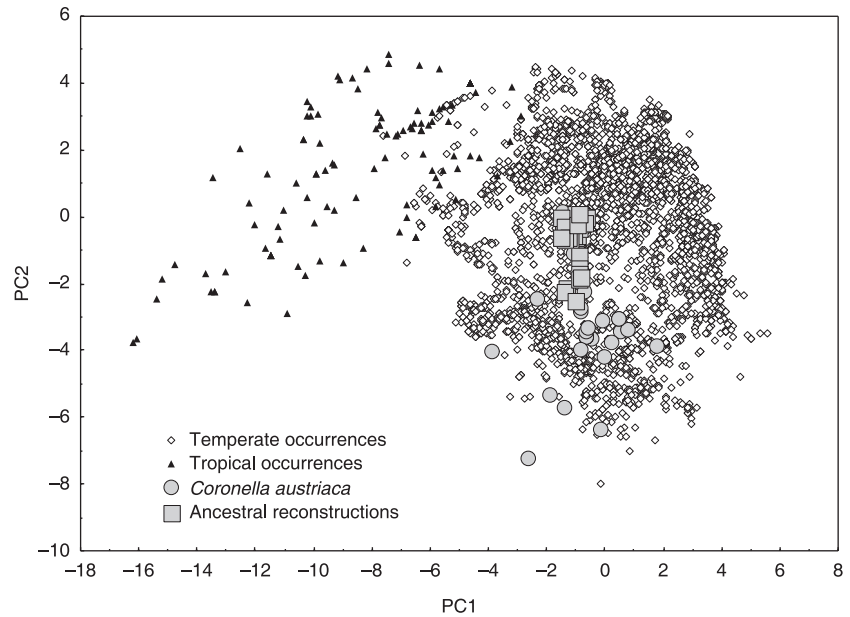
Figure 2 Plot of the principal components (PC) scores on the first two PC axes derived from the 19 BIOCLIM variables for the 4564 occurrence records of the lampropeltinines and *Coronella austriaca*, as well as the phylogenetic generalized least squares (PGLS) ancestral reconstructions.

Species distribution patterns

We tested for a fit to the null MDE model (Colwell *et al.*, 2004) using the program MID-DOMAIN NULL (McCain, 2004). To account for the possibility of domain specification bias we ran three different analyses, one with the domain equal to the latitudinal extent of the Lampropeltini (–3 to 51° N), one in which the domain was the Northern Hemisphere (0 to 90° N) and one in which the domain range was the entire globe (–90 to 90° N). Since the domain must have one bound of zero, we transformed the midpoints of each species by addition so that for any analysis, the lowest latitudinal value was zero (i.e. the domain –90 to 90 became 0 to 180). We sampled both the empirical ranges and the empirical midpoints without replacement, and ran 50,000 replicates of each analysis. We tested for a significant departure from the expected values of species richness from the null model (the midpoint between the upper and lower 95% confidence intervals) at each latitudinal bin using a chi-square test with degrees of freedom equal to 1 minus the number of degrees of latitude in the domain.

RESULTS

Phylogenetic analysis

The primary results of the DNA sequencing, phylogenetic analysis and divergence time estimations are given in Pyron & Burbrink (2009), and the GenBank accession numbers are available in the Supplementary Online Material of that paper. We reconstructed ancestral areas (see below) on the dated chronogram from Pyron & Burbrink (2009; see Fig. 1).

Ancestral area reconstruction

The ancestral area of the extant lampropeltinines is inferred to be in temperate central North America (Fig. 1), between the Western

Continental Divide and the Mississippi River. The earliest putative lampropeltinine fossils are known from this area (Wyoming) dating to the early Miocene (Holman, 2000). The results from LAGRANGE suggest that the extant lampropeltinines have persisted in central NA for > 20 Myr. Excepting the unobservable dispersal events of the terminal species *Senticolis triaspis* and *Pseudelaphe flavirufa*, the first dispersal into the NT at an internal bifurcation occurred approximately 6.6 Ma in the late Miocene (*Pituophis lineaticollis + deppei*; Fig. 1). Dispersal into eastern and western NA was also recent (< 10 Ma). Thus, the TFS/COO effects appear to explain the high temperate species richness of the lampropeltinines due to the longer time span during which biodiversity could accumulate in temperate NA.

Phylogenetic niche conservatism

The first six PC axes account for 97.24% of the total variance (Fig. 2; only PC 1 and 2 are shown). The PCA scores reveal that the temperate and tropical species are separated into two primary centroids, with the greatest amount of differentiation occurring along PC 1 (Fig. 2). The two variables with the highest loadings on PC1 are BIO7 (annual temperature range; 0.84) and BIO13 (precipitation of the wettest period; –0.87). This indicates that the primary ecological separation between the temperate and tropical species occurs along a gradient of rainy-season precipitation and temperature seasonality. Temperate species occupy drier, more seasonal habitats, whereas tropical species inhabit wetter areas with a smaller annual temperature variation (Fig. 2).

Our phyloclimatic reconstructions also indicate that the ancestral lampropeltinines inhabited a temperate niche. The Old World sister taxon to the Lampropeltini, *Coronella austriaca*, inhabits a temperate niche which occurs well within the range of the New World temperate species, and the PC reconstructions at all of the internal nodes are temperate as well (Fig. 2). While
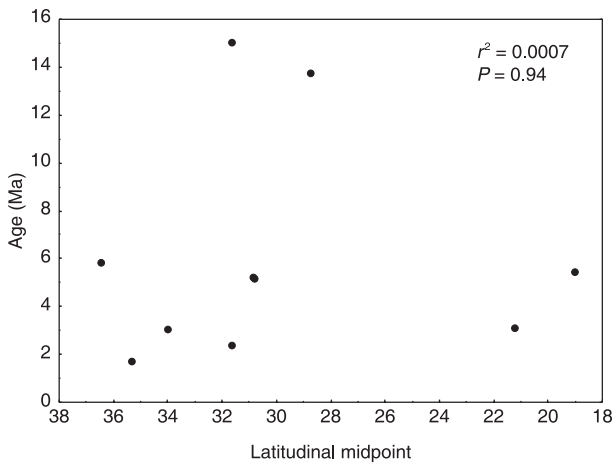
Figure 3 Linear regression analysis of sister species age versus latitude. No significant relationship indicates that net diversification rates do not vary latitudinally.
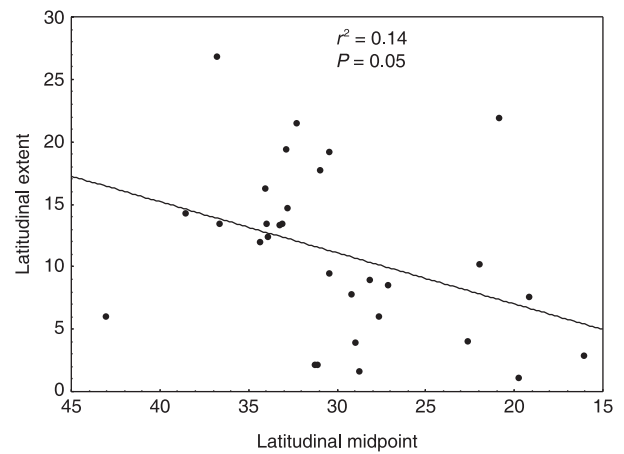

Figure 4 Linear regression analysis of latitudinal extent of geographical range versus latitudinal midpoint (excluding *Lampropeltis triangulum*). Significant relationship indicates an apparent adherence to Rapoport's rule.

BIO7 exhibits significant phylogenetic signal ($\lambda = 1.07$, LR = 172.35, $P < 0.001$), BIO13 does not ($\lambda \sim 0$, $P > 0.05$). We extended this analysis to the next two variables which loaded most heavily on PC1, BIO16 (precipitation of the wettest quarter) and BIO4 (temperature seasonality). The same pattern was observed, where BIO16 does not exhibit significant phylogenetic signal ($\lambda \sim 0$, $P > 0.05$), while BIO4 does ($\lambda = 1.08$, LR = 242.49, $P < 0.001$). This indicates that temperature seasonality is the primary phylogenetically conserved limiting environmental factor, while lampropeltinine species are more tolerant of variation in precipitation. Since there have only been four tropical invasions, all of which were single dispersals of terminal species and not diversified clades of taxa (Fig. 1), this strongly suggests that an evolutionarily conserved preference for a temperate ancestral niche has limited dispersal into the tropics.

Latitudinal variation in diversification rate

No significant relationship was found between the age of sister species divergence and mean latitudinal midpoint ($r^2 = 0.0007$, $P = 0.94$; Fig. 3). This indicates that there is no geographically influenced bias in the timing of currently observable speciation events, suggesting that species turnover rates are similar at varying latitudes and net diversification rates do not vary latitudinally (Weir & Schluter, 2007).

Rapoport's rule

Linear regression analysis does not reveal a significant relationship between the raw values of the latitudinal extent of each species and its latitudinal midpoint ($b = 0.081$, $r^2 = 0.007$, $P = 0.67$). The relationship is also not significant when the phylogenetic non-independence of the species is taken into account using both PGLS ($b = 0.12$, $r^2 = 0.006$, $P = 0.69$) and F/PIC ($b = 0.22$,

$r^2 = 0.01$, $P = 0.55$). However, these relationships appear to be heavily influenced by two outliers, *Lampropeltis triangulum* and *Senticolis triaspis*, the only two species whose ranges span both temperate NA and the NT. The relationship between the raw values becomes significant with the removal of *L. triangulum* ($b = 0.37$, $r^2 = 0.14$, $P = 0.05$; Fig. 4) and of both species ($b = 0.50$, $r^2 = 0.25$, $P = 0.01$). Though no justification for the exclusion of *S. triaspis* is evident, the validity of *L. triangulum* as a single taxon or even a monophyletic species complex is in dispute (Bryson *et al.*, 2007). The species is extremely polymorphic (*c.* 25 subspecies; Williams, 1978), and preliminary phylogeographical analyses suggests that it consists of multiple lineages which appear to conform to the pattern otherwise observed (S. Ruane *et al.*, unpublished data). To test the effect on the phylogenetic comparative analyses of removing *L. triangulum* as a potential outlier, we substituted the mean of the latitudinal extents and midpoints of *Lampropeltis getula* and *Lampropeltis extenuata*, the closest relatives of *L. triangulum* (Fig. 1). This yields a significant relationship for both PGLS ($b = 0.41$, $r^2 = 0.13$, $P = 0.05$) and F/PIC ($b = 0.71$, $r^2 = 0.20$, $P = 0.01$). Thus, we tentatively conclude the presence of the Rapoport effect, which, despite ostensibly allowing higher species density at lower latitudes, seems to have no direct relationship to the distribution of species richness.

Species distributions

Results from the null MDE model for all three domains exhibited similar patterns; only the data from the empirical domain (–3 to 51° N) are shown (Fig. 5). The observed number of species across the domain was significantly different from that predicted by the null MDE model using the empirical ranges of the species sampled without replacement ($\chi^2 = 216.1$, $P < 0.01$, d.f. = 53). Species richness was higher than predicted at latitudes above 23° N, and lower than predicted below 23° N (Fig. 5). Rejection
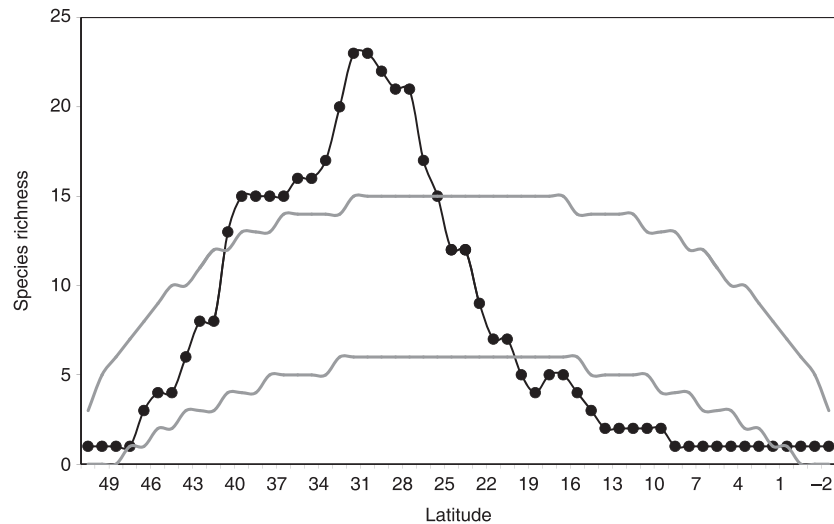
Figure 5 Plot showing the results from the null mid-domain effect (MDE) model (McCain, 2004) on the empirical domain (−3 to 51°, black line and points), indicating that the observed pattern of species richness does not fit the expectation of the MDE model (grey). The lampropeltinines exhibit an extratropical peak in diversity and lower than expected species richness in the tropics.

of the null MDE model indicates that the observed species richness pattern is not explained by a random distribution of species through geographical space, centred on a temperate latitude.

DISCUSSION

Though the vast majority of species richness gradients exhibit decreasing diversity with increasing latitude (Hillebrand, 2004), this is not always the case. In addition to the Lampropeltini, organisms such as pond turtles (Stephens & Wiens, 2003), Holarctic tree frogs (Smith *et al.*, 2005), penguins (Cody, 1966) and ichneumonid parasites (Owen & Owen, 1974) also exhibit extratropical peaks in diversity. It has been suggested that the observed commonality of latitudinal gradients in species richness is likely to have a common cause (Pianka, 1966; Rohde, 1992). As we have noted, many explanations for biodiversity gradients do not exclusively mandate high tropical species richness. Furthermore, not all of the proposed explanations are necessarily causative (Rohde, 1992; Pianka, 1966). As such, a generalized explanation for latitudinal biodiversity gradients does not necessarily hinge on gradients specific to higher tropical diversity. A common mechanism that describes species richness gradients, regardless of whether the centre of diversity is tropical or temperate, would provide a far more robust explanation for observed patterns of global species richness than those restricted to explaining high tropical diversity.

Historical biogeography, as exemplified by TFS/COO effects, best explains the pattern of high temperate species richness in the Lampropeltini. The latitudinal distribution of taxa indicates significantly higher species richness at temperate latitudes than would be expected under the null MDE model, indicating that the diversity in the temperate areas is due to non-random processes. No differences were detected in the latitudinal diversification rate, suggesting that variation in extinction or speciation rates between temperate and tropical areas has not contributed to the observed patterns. The group originated in temperate NA

in the Miocene, leaving > 20 Myr for speciation to increase biodiversity in the temperate areas, and only dispersed to the tropics relatively recently. Therefore, there has not been enough time for diversity to accumulate from these young tropical lineages (< 6 Myr). This is similar to the more common reverse patterns observed in many groups that exhibit high tropical species richness, where early origin occurred in the tropics with only recent dispersal to temperate regions explains higher tropical diversity (Stevens, 2006; Wiens *et al.*, 2006, 2009).

The question then becomes: why was tropical dispersal so infrequent? The tropics exhibited a far greater latitudinal extent in the past, but began to recede no later than 30 Ma (Behrensmeyer *et al.*, 1992; Morley, 2000). The lampropeltinines dispersed into temperate NA across Beringia (Burbrink & Lawson, 2007) during or after the expansion of the temperate areas to their current extent, and presumably existed in close proximity to the tropics for most of their history. Yet, dispersal into the tropics occurred only four times, and only in terminal taxa and not diverse tropical clades. The most likely explanation for a lack of tropical dispersals is phylogenetic niche conservatism (Wiens & Graham, 2005), predicting a strong preference for a temperate ancestral niche. Several authors have cautioned against direct inference of evolutionary patterns or niche conservatism based solely on the presence of phylogenetic signal (Revell *et al.*, 2008). However, the Old World sister groups of the Lampropeltini all inhabit temperate areas in the Palaearctic, a condition which is inferred to have existed for at least 30 Myr (Burbrink & Lawson, 2007).

The reconstruction of ancestral niches indicates that the Lampropeltini have existed in temperate environmental conditions since their origin (Figs 1 & 2). Thus, an evolutionary preference for temperate environments appears to have led to climatic constraints on dispersal into the NT, based primarily on temperature seasonality gradients. This also explains the large number of present-day lampropeltinine species which abut but do not enter the NT in Mexico (Figs 1, 4 & 5). Some authors have also suggested the importance of interspecific competition in

limiting species ranges (e.g. MacArthur, 1972; Case & Taper, 2000). Given both the strong indications of phylogenetic niche conservatism (Fig. 2) and the extensive penetration and co-existence of tropical lampropeltinine species into Central and South America (Figs 1, 4, 5), this is may only be a secondary factor.

Remarkably, the primary explanations we find for the observed patterns of high temperate species richness in the lampropeltinines are the latitudinal inverse of the predictions made by the tropical conservatism hypothesis (TCH; Wiens & Donoghue, 2004) for groups exhibiting high tropical species richness. The TCH makes three predictions. First, groups with high tropical diversity will have originated in the tropics and dispersed to temperate regions only recently, wherein the TFS/COO effects account for increased tropical diversity. Second, temperate dispersals will be limited due to phylogenetic conservation of the tropical ancestral niche. Third, more clades will have arisen in the tropics due to their large former extent. Here, we find that inverse of the TCH predicts that groups with high temperate species richness originated in temperate areas and dispersed to the tropics only recently, that a preference for the ancestral temperate niche likely limited tropical dispersal, and that dispersal into and diversification in the New World was related to the expansion of the temperate areas to their current extent. Thus, it would appear that the underlying processes which the TCH proposes as the primary factors responsible for high tropical species richness are not intrinsic to the tropics. Rather than dub this the 'temperate conservatism hypothesis', we propose that these processes be generally referred to as the 'biogeographical conservatism hypothesis'.

Identical underlying patterns have now been shown to be responsible for several latitudinal biodiversity gradients regardless of their area of origin: the time-for-speciation effect acting in the geographical area of origin (e.g. Ricklefs & Schluter, 1993), a phylogenetically conserved preference for an ancestral niche (e.g. Smith *et al.*, 2005; Wiens *et al.*, 2006) and the geographical availability of suitable habitat (e.g. Fine & Ree, 2006). These processes can explain both high temperate and tropical diversity without reference to the MDE, as well as in the presence of potential red herrings such as Rapoport's rule. We suggest that these factors may underlie similar gradients of both temperate and tropical latitudinal origin in numerous other taxa, and should form a starting point for future investigations of latitudinal species richness gradients. We note that there is still no firm explanation as to why instances of high tropical species richness vastly outnumber those of high temperate diversity. The TCH suggests that more groups probably originated in the tropics during the occupancy of their larger former extent (Wiens & Donoghue, 2004). Alternatively, some research has indicated that at deeper phylogenetic time-scales there may indeed be higher rates of tropical diversification, leading to more clades of tropical origin (Wiens, 2007). Explanations for global biodiversity should take into account the possibility that both the BCH as well as differences in evolutionary rates explain different aspects of species richness at different phylogenetic time-scales (Mittelbach *et al.*, 2007; Wiens, 2007).

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SUPPORTING INFORMATION

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

Appendix S1 Point localities for all 31 lampropeltinine species and *Coronella austriaca*, from which the biogeographical areas, latitudinal midpoints, latitudinal extents and climate data were derived.

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