

NEWS AND VIEWS

PERSPECTIVE

Environmental harshness, latitude and incipient speciation

JASON T. WEIR

Biological Sciences, University of Toronto Scarborough, Toronto, Ontario, Canada, M1C 1A4

Are rates of evolution and speciation fastest where diversity is greatest – the tropics? A commonly accepted theory links the latitudinal diversity gradient to a speciation pump model whereby the tropics produce species at a faster rate than extra-tropical regions. In this issue of *Molecular Ecology*, Botero *et al.* (2013) test the speciation pump model using subspecies richness patterns for more than 9000 species of birds and mammals as a proxy for incipient speciation opportunity. Rather than using latitudinal centroids, the authors investigate the role of various environmental correlates of latitude as drivers of subspecies richness. Their key finding points to environmental harshness as a positive predictor of subspecies richness. The authors link high subspecies richness in environmental harsh areas to increased opportunities for geographic range fragmentation and/or faster rates of trait evolution as drivers of incipient speciation. Because environmental harshness generally increases with latitude, these results suggest that opportunity for incipient speciation is lowest where species richness is highest. The authors interpret this finding as incompatible with the view of the tropics as a cradle of diversity. Their results are consistent with a growing body of evidence that reproductive isolation and speciation occur fastest at high latitudes.

Keywords: environmental harshness, latitudinal diversity gradients, speciation, subspecies richness

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Botero *et al.* used a mixed model that makes use of recently published supertrees for mammals and birds to correct for phylogenetic effects, while estimating the relationship between subspecies richness and a variety of potential predictors. The model they tested included several previously highlighted predictors of subspecies richness (Phillimore *et al.* 2007) including geographic range size, island occupation, habitat heterogeneity, occupation in formerly glaciated regions and geographic range dissection by mountains. Each of these predictors has positive correlations with subspecies richness. The authors also added

body mass, which negatively correlates with subspecies richness. What is most novel about their approach is the replacement of latitude in their model with a variety of environmental covariates of latitude relating to temperature, precipitation and net primary productivity. They used principal component analysis to pull out key axes of variation from these covariates and used these as predictors in their model. The first principal component (PC hereafter) represented an axis of environmental harshness with large values indicating low annual values and high seasonality for temperate and precipitation, unpredictable temperate cycles, low net primary productivity and high levels of habitat heterogeneity. The third PC represented unpredictable precipitation cycles. PC 2 and 4 were influenced mostly by body size and geographic range size.

All four PC's were significant predictors of subspecies richness, but the most surprising result was that environmental harshness (PC1) was positively correlated with subspecies richness, suggesting that those regions of the globe with the harshest and least predictable climates function as the engines of evolution. Because environmental harshness generally increases with latitude (Fig. 1 in Botero *et al.*), the authors suggest evolution is occurring most rapidly at high latitudes and not in the tropics, as is generally assumed. For this to be true, subspecies richness should also increase with latitude and the authors did not directly demonstrate this in their study. Indeed, past studies on birds failed to find a latitudinal increase in subspecies richness either across (Phillimore *et al.* 2007) or within species (Martin & Tewksbury 2008). To address this, I used a data set of latitudinal centroids (provided upon request by the authors and included in their data set deposited in Dryad) for species whose latitudinal ranges were less than 40 degrees (to exclude those species with the widest latitudinal spans) and which were not restricted to Oceanic islands (for birds). The local loess fits in Fig. 1 illustrate that subspecies richness does increase with latitude in the Northern Hemisphere for both mammals and for nonmigratory birds (migratory birds did not show a positive relationship with either latitude or environmental harshness). This positive relationship with latitude in the Northern Hemisphere remains even while correcting for geographic range size and body mass in a linear model (mammal centroid $P < 0.0001$; bird centroid $P < 0.0001$). In the Southern Hemisphere, subspecies richness declines strongly away from the equator despite correcting for geographic range size and body size (mammal centroid $P < 0.004$; bird centroid $P < 0.0001$). For the Southern Hemisphere, it is less certain that environmental harshness gradients have a strong bearing on explaining latitudinal differences in subspecies richness. Given this uncertainty, I will focus primarily on the implications of the authors' results as they apply to the Northern Hemisphere.

Correspondence: Jason T. Weir, Fax: +1 416-287-7676;
E-mail: jason.weir@utoronto.ca

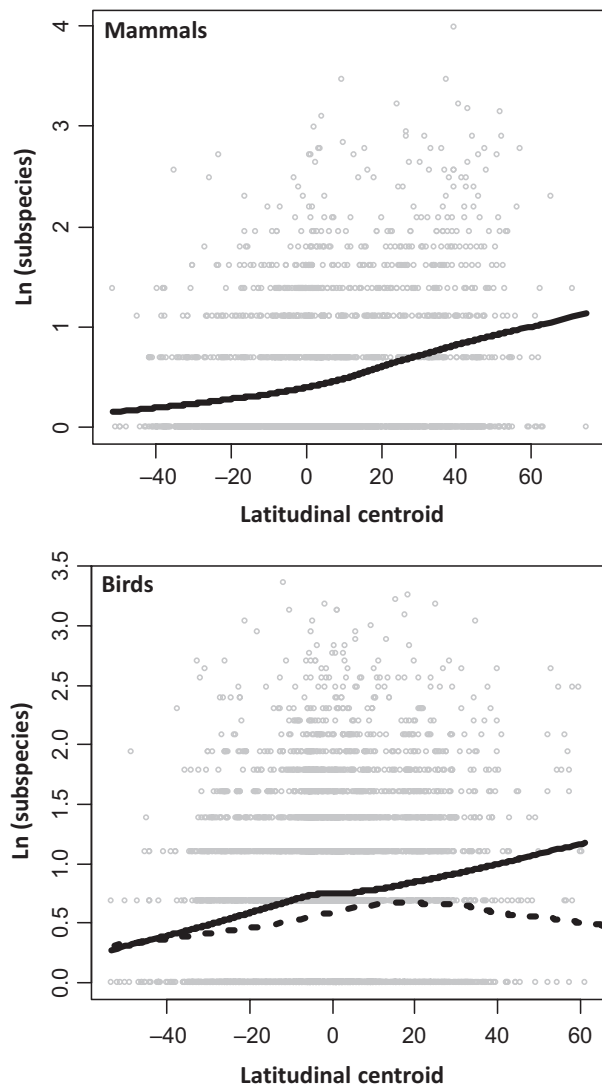


Fig. 1 Local polynomial regression fits of log subspecies richness and latitudinal centroids for terrestrial species of mammals and birds. For birds, nonmigratory species are shown by grey dots, best fit lines are shown for both nonmigratory (solid line) and migratory (dashed line) species. Fits made using the loess function in R with smoothing parameter = 0.75 and degree = 1.

The positive association between environmental harshness, latitude and subspecies richness in the Northern Hemisphere paints a clear picture of high latitude regions as the hotbed of evolution. The authors interpret their findings as indicative of higher incipient speciation rates at high latitudes where environmental harshness is greatest. Speciation rates in recently derived birds and mammals show a similar pattern, with accelerated rates towards the poles (Weir & Schluter 2007). Allopatric speciation – presumed to be the major mode of speciation in birds and mammals – involves two key steps. First, speciation is initiated when populations become geographically isolated. Second, the speciation process is completed when populations evolve

reproductive isolation. Botero *et al.* suggest that environmental harshness might influence either the initiation or completion of speciation. For example, high latitude regions of the globe with high environmental harshness have also generally experienced extensive palaeoclimate fluctuations. These fluctuations may result in opportunities for the initiation of allopatry as species geographic ranges become fragmented. As for the completion of speciation, recent avian studies show that both plumage coloration (Martin *et al.* 2010) and the syllable and pitch aspects of song (Weir & Wheatcroft 2011; Weir *et al.* 2012) diverge faster at high latitudes. These traits are important in species discrimination, and their faster divergence at high latitudes suggests that pre-mating reproductive isolation may be accumulating there at a faster rate. Plumage coloration is also an important trait used by taxonomists to define subspecies boundaries. Together, these studies of colour, song, subspecies richness and speciation rates point to high latitude regions (at least in the Northern Hemisphere) as the cradle of evolutionary divergence and speciation.

If species evolve and diversify so rapidly at high latitudes, then why are high latitude regions species poor? To answer this, Botero *et al.* point to a much higher rate of extinction at high latitudes as previously estimated for terrestrial birds and mammals (Weir & Schluter 2007) and for marine environments (Jablonski *et al.* 2006). High extinction rates can temper the high speciation rates found at high latitudes, resulting in a lower net accumulation of species compared with tropical latitudes. This effect of extinction could be the key underlying driver of the latitudinal diversity gradient. To test this further, robust estimates of extinction from across latitudinal gradients are needed for a greater variety of taxa. Unfortunately, extinction rates are difficult to measure from molecular phylogenies (e.g. Rabosky 2010), and the fossil record is often too incomplete to obtain latitudinal estimates for terrestrial groups.

The present study does an exemplary job of tying patterns in subspecies richness with environmental gradients, but is not without limitations. First, the authors' interpretations of their results hinge on a latitudinal increase in subspecies richness. The latitudinal results presented here (Fig. 1) demonstrate such an increase in the Northern Hemisphere, but not in the Southern Hemisphere (where the opposite pattern is displayed). This suggests that the interplay between latitude, environmental harshness and subspecies richness in the Southern Hemisphere may benefit from further investigation. Second, the authors treat subspecies richness as a proxy for incipient speciation rate opportunity, when a more appropriate method might have been to directly calculate rates of subspecies origination (see Phillimore 2010). Indeed, speciation rates within bird clades correlates positively with subspecies origination rates, but not with subspecies richness (Phillimore 2010). Subspecies origination rates are likely to show an even steeper latitudinal gradient than subspecies richness, because high latitude species are generally younger than in the tropics (Weir & Schluter 2007). Third, the study heavily

criticized the widespread practice of using latitudinal midpoints or centroids in comparative studies. Despite this, the authors employ a similar simplification by reducing environmental variation within the geographic range of each species, to a mean value. Whether using a latitudinal centroid or a mean value of environmental harshness, widespread species are poorly represented by these measures. Despite this limitation, the authors still find meaningful patterns in their data, as have studies which used latitudinal midpoints or centroids.

To summarize, the study links high subspecies richness to environmentally harsh regions of the globe, which tend to occur at higher latitudes. This result allows the authors to reject the long-standing view that accelerated rates of evolution and speciation in the tropics drive the latitudinal diversity gradient (at least over the past several million years). Whether these current patterns of subspecies richness are indicative of the evolutionary dynamics that have played out over the Cenozoic radiation of mammals and birds, or are the product of recent Plio-Pleistocene climatic fluctuations, remains to be determined.

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J.T.W. wrote the piece and performed the model fits.

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