Why mountain passes are higher… for endemic snails

Por qué los pasos de montaña son más altos… para los caracoles endémicos

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Palabras clave: especiación alopátrica, endemismo, aislamiento geográfico, barreras de dispersión, Región Mediterránea.

ABSTRACT

Multiple lines of evidence suggest that allopatric speciation is the main mechanism which originates regional species diversity. Thus endemic species, *i.e.* those species restricted to one region, are expected to descend from lineages with high sensitivity to dispersal barriers. Endemics would probably retain this sensitivity as an ancestral state, and so it can be predicted that endemics will be more sensitive than non-endemics to dispersal barriers, such as mountain ranges. Here this prediction is tested for land snails from Andalusia (S. Spain), a snail fauna with a high level of narrow-ranged allopatric endemicity. The maximum altitude cited for endemics is lower than that of non-endemic species, and the difference is statistically significant after phylogeny and range size are controlled. Thus mountain passes tend to be higher for endemic snails. The results support a view of rampant allopatric speciation driven by isolation between elevational barriers in this group, a mechanism that may be widespread in continental biotas.

RESUMEN

Múltiples líneas de evidencia sugieren que la especiación alopátrica es el principal mecanismo que origina la diversidad regional de especies. Por tanto, es de esperar que las especies endémicas, *i.e.* aquellas especies restringidas a una región, desciendan de linajes con alta sensibilidad a las barreras de dispersión, tales como cordilleras. En este trabajo, esta predicción es testada para el caso de los caracoles terrestres de Andalucía (S. España), una fauna de caracoles con un alto nivel de endemismos alopátricos de rango geográfico restringido. La máxima altitud citada para los endemismos es menor que la de las especies no endémicas, y la diferencia es estadísticamente significativa después de controlar la filogenia y el tamaño de rango geográfico. Por consiguiente, los pasos montanos tienden a ser más altos para los caracoles endémicos. Este resultado apoya la perspectiva de una abundante especiación alopátrica en este grupo dirigida por aislamiento entre barreras de altitud, un mecanismo que podría estar muy difundido en las biotas continentales.

INTRODUCTION

Species diversity depends on speciation, extinction and species immigration (Rosenzweig, 1995). Although sympatric speciation can take place (*e.g.* Feder *et al.*, 1998; Savolainen *et al.*, 2006), allopatric speciation prevails as the main process that originates species diversity worldwide (Coyne & Orr, 2004; Rosenzweig, 1995). This is suggested by the widespread observation of remarked geographic separation of recent sister species (Barraclough & Vogler, 2000, but see Losos & Glor, 2003), among many other evidences from mainland (Grant & Grant, 2008) as well as marine case studies (Palumbi, 1994; Rocha & Bowen, 2008; Leray *et al.*, 2010).

Allopatric speciation involves the evolution of genetic barriers between geographically separated populations. Geographic barriers to dispersal are needed to limit the genetic flow between the populations involved in this speciation process. Among these geographic barriers, mountain ranges are important for land organisms: major biogeographical divisions tend to coincide with plate boundaries (Kreft & Jetz, 2010), and thus, very often, with elevational barriers, which usually develop at convergent plate boundaries (Stanley, 1999). In this situation, stenohypse organisms (*sensu* organisms with low altitudinal tolerance) finding mountain ranges would have lesser possibility for crossing them than euryhypse ones (*sensu* organisms with wide altitudinal tolerance). Stenohypse organisms, therefore, would be relegated to valleys among mountains (or to mountains, if they are adapted to high altitude), thus remaining geographically more isolated than euryhypse organisms, in a process that favours speciation. Consequently, endemics are expected to be more stenohypse than non-endemic species, or, in other words, stenohypse organisms are expected to have narrower geographic ranges than euryhypse organisms (Fig. 1). When applied to low-altitude biota, this simple model predicts that endemic species must be more stenohypse and have narrower ranges than non-endemic species.

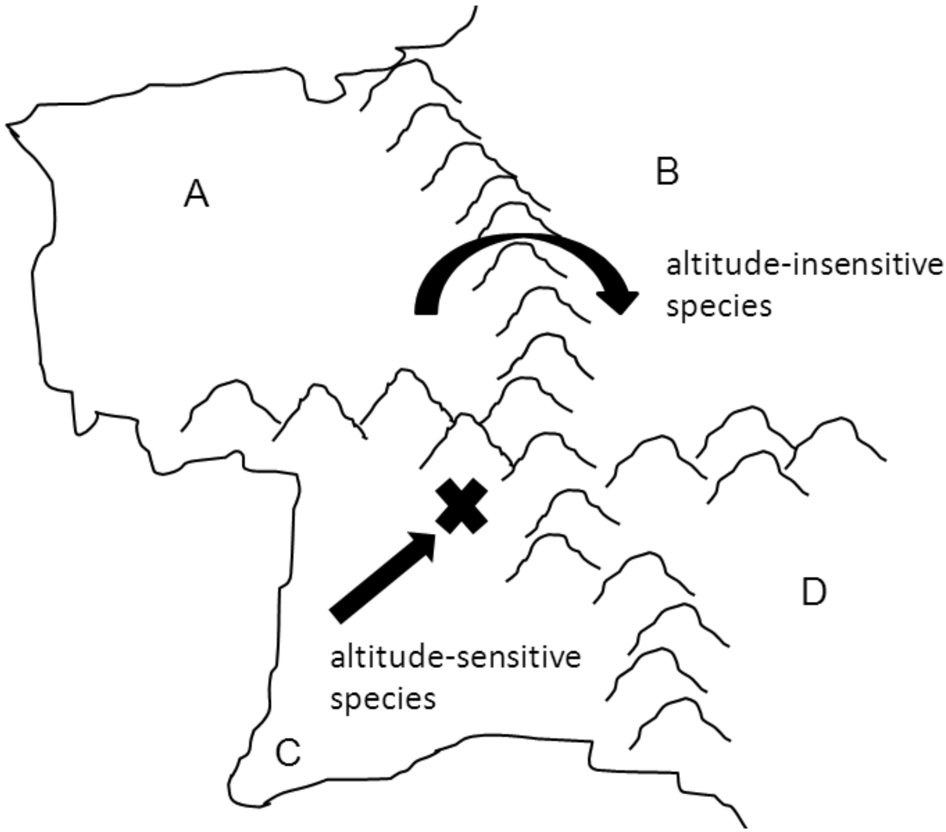

Fig. 1.—Altitude-insensitive species are not so restricted by elevational barriers as altitude-sensitive species, which therefore are more prone to be narrow ranged and to originate endemics by allopatric speciation within the regions limited by mountain ranges (A, B, C, D).
Fig. 1.—Las especies tolerantes a las variaciones en altitud no están tan restringidas por barreras altitudinales como las especies sensibles a la altitud, que de este modo tienen mayor tendencia a presentar rangos de distribución estrechos y a originar endemismos por especiación alopátrica dentro de las regiones limitadas por cadenas montañosas (A,B,C,D).

The biogeographical implications of this model are potentially important. Janzen (1967) proposed that mountain passes are more efficient barriers for tropical biotas than for temperate species because the warm tropical climate would favour stenohypsy as an evolutionary outcome of adaptation to temperature conditions in tropical species. For example, plethodontid salamander species show lower thermal regime in the tropics than in temperate zones (Kozak & Wiens, 2007). Similarly, the range of tolerable temperatures increases with latitude in anuran amphibians (Hua & Wiens, 2010). If this was the general situation in terrestrial biotas, then a new explanation to the latitudinal biodiversity gradient (Willig *et al.*, 2003) would rise: tropical climates promote stenohypsy, which increases the opportunities of isolation by mountain barriers, which makes allopatric speciation commoner than in temperate regions, with the result that tropical biotas have more species.

In this work I test the model illustrated in Fig. 1 by analyzing the relationship between altitudinal range, geographic range size and endemicity in snails from Andalusia (S. Spain). Land snails (Gastropoda, Pulmonata) are especially adequate for this subject due to their poor dispersal abilities, which makes them prone to become isolated by geographic barriers and so to experience allopatric speciation (Cameron, 1992). Narrow-ranged endemicity is rampant in snails to the extent that species range sizes of less than 15 linear km are very common worldwide (Solem, 1984) and ring-species with a diameter of only 5 km have been reported (Clarke & Murray, 1969).

For accomplishing this study, I used the Ruiz *et al.* (2006) dataset, the most complete for Andalusia. As it is the rule in the invertebrate fauna within the Mediterranean Region (Blondel & Aronson, 1999; López-Villalta, 2010), the snail fauna of Andalusia is characterized by a mixture of biogeographical origins (African, Mediterranean, Eurosiberian) and by a high degree of endemicity (26 Iberian endemics out of 95 species).

MATERIALS AND METHODS

A data set was compiled from the field guide by Ruiz *et al.* (2006), which describes the distribution of snails in Andalusia on the basis of 6 852 citations from 2 311 localities. I take from this guide taxon names (species and, eventually, subspecies), maximum altitude cited for the taxa, and range size measured from the reported distribution (number of squared quadrats of c. 2 200 km^2, 47x47 km, with the quadrat counted when it includes at least some portion of the range size of the species). I considered endemic species those restricted to the Iberian Peninsula.

The relationship between maximum altitude and range size was examined for all snail species and adjusted to the best fit model selected among linear, quadratic, logarithmic, potential, exponential, and additive combinations of all of them. As some of these models are not compatible with the zero maximum altitude of some snails, one unit (meter) was added to the maximum altitude cited for each species. The residuals of this maximum altitude with respect to the best fit model were extracted and taken as range-size corrected measures of maximum altitude. These residuals served to compare endemics and non-endemics using phylogenetically independent comparisons as described in Lavergne *et al.* (2004) for plant endemics and López-Villalta (2010) for endemic butterflies. The procedure consists on comparing species pairs formed by one endemic species (or subspecies) and one non-endemic species (or subspecies) of the same genus (or species). Any trend in endemics is detected by plotting the data of the pairs (coordinate x = value of the non-endemic; coordinate y = value of the endemic), adjusting a linear regression (ordinary least squares), and comparing the regression line with the unit line (x=y). If there are significant differences between the slopes of these lines, this indicates a difference between endemics and non-endemics. The significance level was set at 0.05 as usual.

RESULTS

Maximum altitude data show that endemics as a group tend to be more stenohypse than non-endemics (Fig. 2). Although range size and phylogeny are not corrected in Fig. 2, these data suggest the model described in the introduction is valid for these snails.

Maximum altitude is correlated to range size, as shown in Fig. 3A. The best fit model estimated for the relationship between maximum altitude (*M.A.*) and range size (*R*) is:

$$\text{M.A.} = 500.8\ \text{R}^{0.33} - 20.2\ \text{R} + 488.9$$

This model explains a low amount of variance (r^2=0.27). The residuals of maximum altitude as obtained from this model are virtually uncorrelated to range size (Fig. 3B) and thus they are useful as range-size corrected measures of maximum altitude.

Only 7 snail genera contain non-endemic and endemic taxa and so only 7 pairs of endemic *vs.* non-endemic relative were included in the analysis (Table I). Even this small sample is enough to reveal a significant pattern: endemics tend to have lower maximum altitude than their close non-endemic relatives (Fig. 4). The 95% confidence interval for the slope of the regression line ranges from -0.76 to 0.91, thus excluding 1.00, and this implies a significant difference with respect to the unit line at alpha = 0.05.

DISCUSSION

The results support the model of the origin of terrestrial biotas which was described in the introduction, *i.e.* allopatric speciation triggered by isolation in areas limited by elevational barriers (Fig. 1). As altitude-sensitive snails are

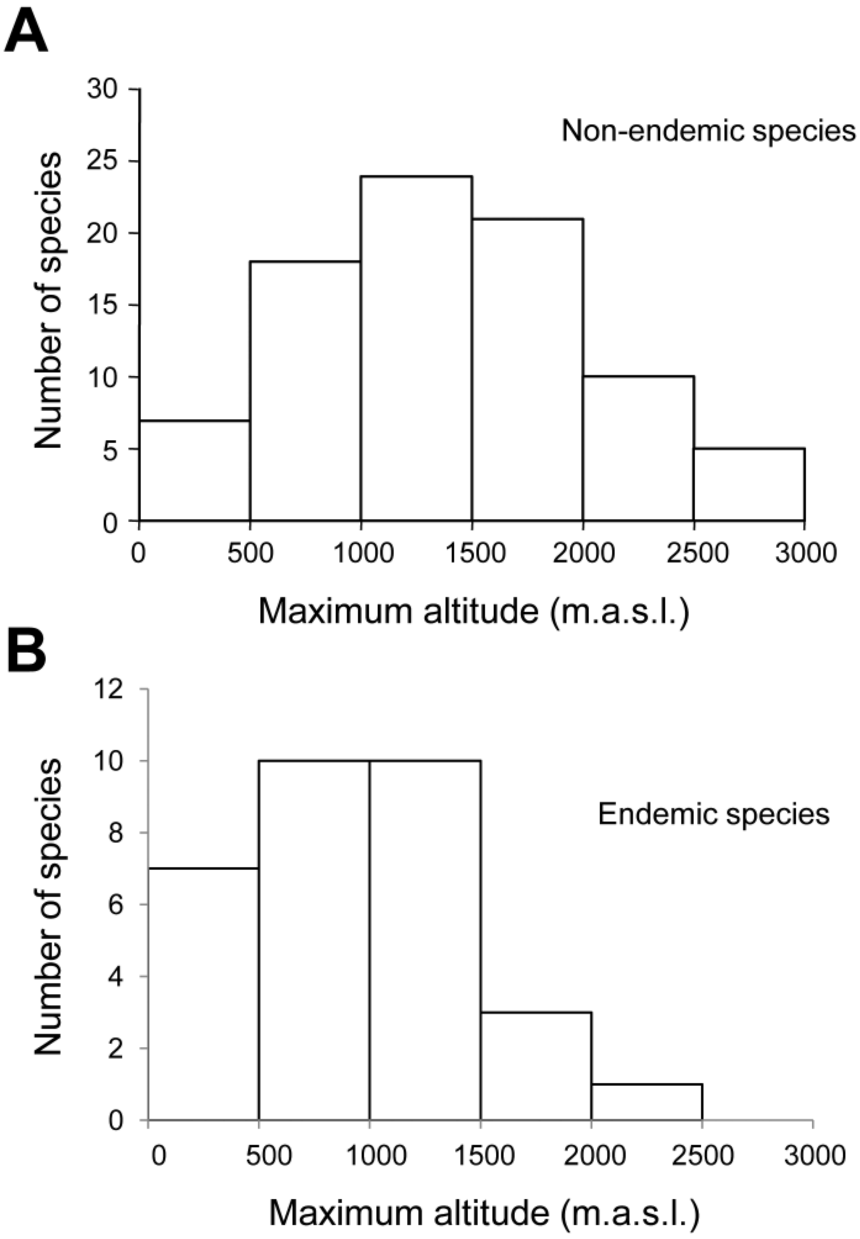

Fig. 2.—Frequency histogram of maximum altitude in non-endemics (A) and endemics (B). m.a.s.l. = meters above sea level.
Fig. 2.—Histograma de frecuencias de máxima altitud en especies no-endémicas (A) y endémicas (B). m.a.s.l. = metros sobre el nivel del mar.

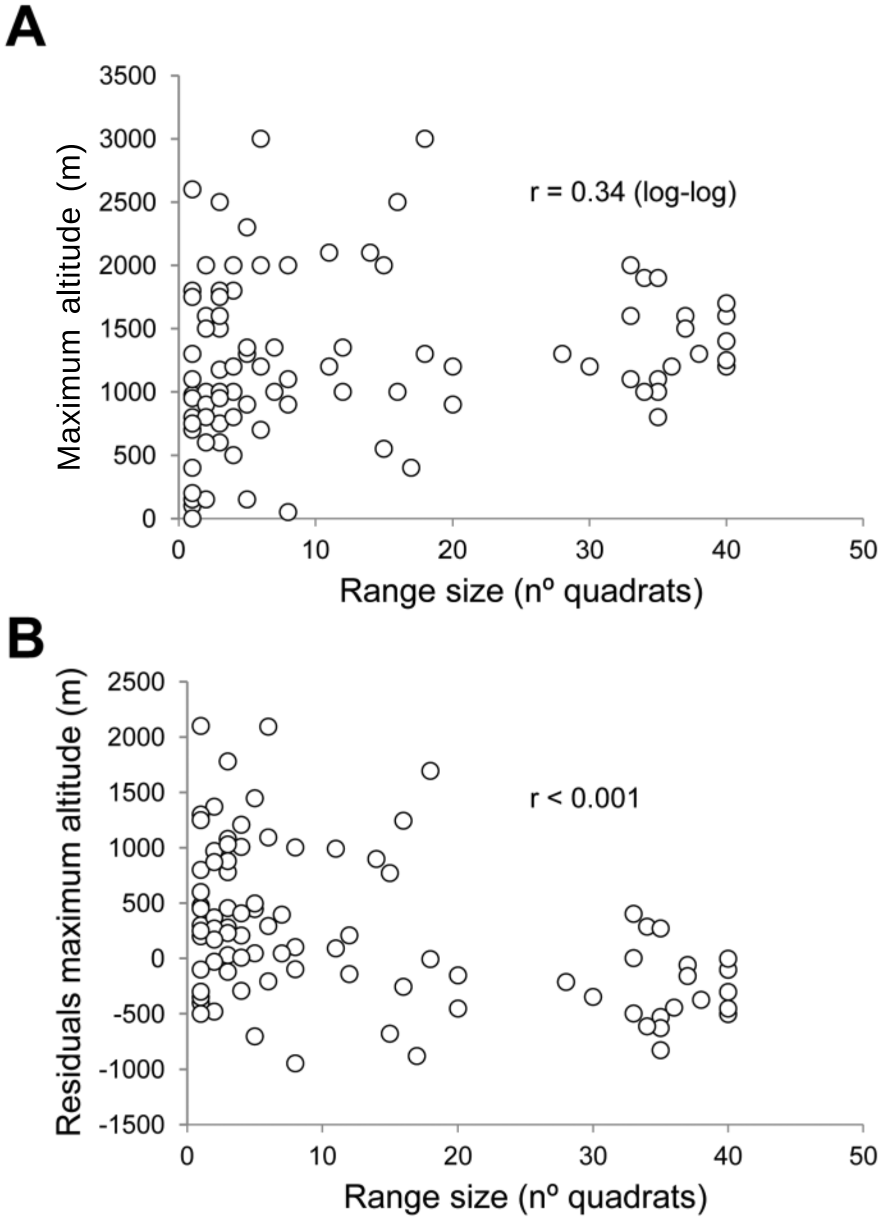

Fig. 3.—A) Maximum altitude *vs.* range size for the 95 snail species of Andalusia. B) Residuals of maximum altitude *vs.* range size for these snails (see the results for more details).
Fig. 3.—A) Máxima altitud *vs*. amplitud de rango para las 95 especies de caracoles de Andalucía. B) Residuales de máxima altitud *vs*. amplitud de rango para estos caracoles (ver resultados para más detalles).

Table I.—Snail taxa compared in Fig. 4. N.E. = non-endemic species; E. = endemic species.
Tabla I.—Taxones de caracoles comparados en la Fig. 4. N.E. = especies no endémicas; E = especies endémicas.

Species pair	Maximum altitude (m)	Residuals max. altitude (m)
Chondrina calpica (Westerlund 1872) N.E.	1300	58.6
Chondrina maginensis (Arrébola & Gómez 1998) E.	800	–168.6
Oestophora barbula (Rossmäsler 1838) N.E.	1000	–421.8
Oestophora ebria (Corbellá 2004) E.	1100	131.4
Oxychilus (Oxychilus) draparnaudi (Beck 1837) N.E.	1100	–341.3
Oxychilus (Ortizius) rateranus (Servain 1880) E.	900	–311.3
Sphincterochila (Albea) candidissima (Drarpnaud 1801) N.E.	1350	48.1
Sphincterochila (Cariosula) cariosula (Westerlund 1886) E.	150	–927.9
Theba pisana pisana (Müller 1774) N.E.	1000	–411.3
Theba pisana arietina (Rossmäsler 1846) E.	200	–768.6
Trichia hispida (Linnaeus 1758) N.E.	2000	922.1
Trichia martigena (Férussac 1832) E.	1200	–74.5
Xerosecta (Xeromagna) cespitum (Draparnaud 1801) N.E.	1600	179.8
Xerosecta (Xeromagna) adolfi (Pfeiffer 1854) E.	0	–968.6

more prone to become isolated by this mechanism, it is not surprising that endemics usually have lower maximum altitudes compared to non-endemic species. This is in line with the works remarked in the introduction (Kozak & Wiens, 2007; Hua & Wiens, 2010).

Speciation driven by sensitivity to elevational barriers fits with our current knowledge on the biogeography of these snails. Mayoral *et al.* (2007) recognizes three big biogeographical divisions for Andalusian snails: Sierra Morena (low siliceous mountains), the Guadalquivir river depression (alluvial sediments) and Sierras Béticas (medium to high limestone mountains). The limits of these divisions are elevational barriers, and the last division has both the highest topographic complexity and the highest endemicity, in relict as well as in new species (Mayoral *et al.*, 2007). This is exactly what we would have expected from the mechanism here proposed, because a region with high topographic complexity implies increased opportunities for allopatric speciation in stenohypse organisms.

Further work with other organisms would be necessary to have an idea about the generality of this mechanism. It might be very common in altitude-sensitive organisms, especially in ectotherms. The mechanism might hold to endemic amphibians and reptiles of the Mediterranean Region, which tend to be stenohypse compared to non-endemic relatives of the same genus

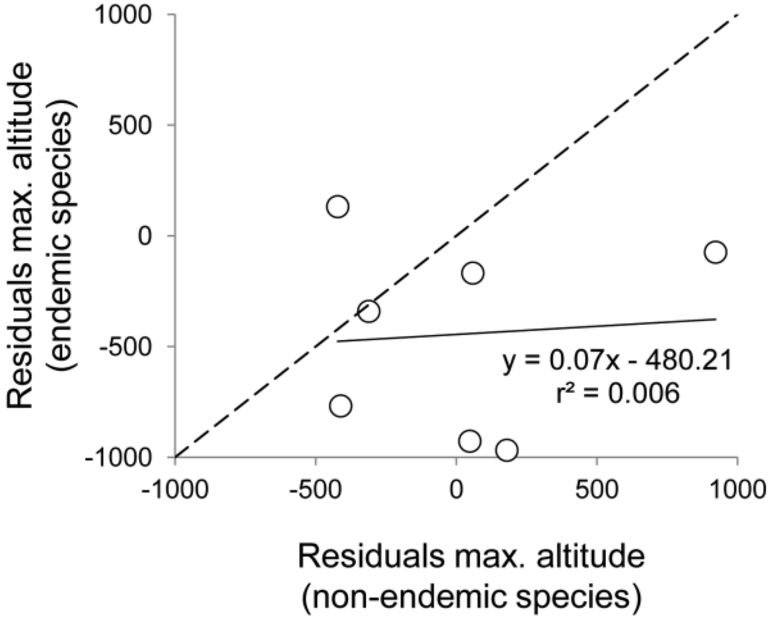

Fig. 4.—Maximum altitude (range-size corrected) of endemics *vs.* non-endemic relatives. Endemics tend to be below the unit line (dashed line), which indicates they tend to be more stenohypse than their non-endemic relatives. The solid line shows the OLS linear regression.
Fig. 4.—Máxima altitud (corregida por la amplitud de rango) de especies endémicas vs. no-endémicas emparentadas. Los endemismos tienden a estar por debajo de la línea de la unidad (línea discontínua), lo cual indica que tienden a ser mas estenohipsos que sus parientes no-endémicos. La línea continua muestra la regresión lineal de mínimos cuadrados ordinarios (OLS).

(unpublished personal data, in preparation). The situation is the same in some mammals, such as shrews (unpublished personal data, in preparation), the group which shows the highest endemicity among the Mediterranean mastofauna. The sensitivity of small mammals to elevational barriers might explain the correlation between genetic diversity and tectonically active regions (Rosenzweig, 1995), as these areas tend to have a young topography and so a high topographic complexity, which could provide more opportunities of geographic isolation and genetic divergence compared to less active regions.

Although it is still not clear whether speciation associated to stenohypsy and elevational barriers is a "rule of thumb" in the tropical and temperate regions of the terrestrial realm, in such a case some interesting consequences would raise. Climate change by global warming would help endemics to pass along mountain ranges, thus extending their geographic range. This would probably increase their chances of survival to local environmental aggressions in their geographic range, since metapopulation dynamics across the mountain ranges would allow the colonization of patches where the species has become extinct. A further speculation can be proposed: in the history of life on Earth, cold global climates would increase the barrier effect of mountain ranges, and *vice versa*. Thus, during cold geological periods, narrow-ranged endemics would be more abundant than in warm geological periods. So may be the latitudinal gradient of species diversity is stronger during cold periods. The effect of climate on species ranges would interact with the origin of species by geographic isolation *via* the uplift and subsequent erosion of mountain ranges. In this way, climate and plate tectonics might influence regional endemicity, which would be another example of how large-scale processes of the Earth system drive the evolution of species diversity (Benton, 2009).

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