Revisiting Jablonski (1993): cladogenesis and range expansion explain latitudinal variation in taxonomic richness

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Introduction

Biodiversity increases dramatically from the poles to the equator (Gaston, 2000; Willig et al., 2003; Hillebrand, 2004). This latitudinal gradient in taxonomic richness is caused by one or more abiotic factors that vary over latitude (Francis & Currie, 2003; Hawkins et al., 2003; Currie et al., 2004; Jetz et al., 2004; Ricklefs, 2004). From a mechanistic perspective, abiotic factors produce the gradient in diversity by creating latitudinal variation in rates of cladogenesis, extinction, immigration and/or emigration, the latter two processes resulting from range expansion, contraction and shifting.

A higher rate of tropical cladogenesis has been suggested by both direct and indirect evidence (Jablonski, 1993; Flessa & Jablonski, 1996; Cardillo, 1999; Martin & McKay, 2004; Cardillo et al., 2005; Goldberg et al., 2005; Allen & Gillooly, 2006; Jablonski et al., 2006); however, extinction rates have been described as both higher and lower in the tropics (Stanley, 1984; Jablonski, 1985; Jablonski et al., 1985, 2006; Coope, 1995, 2004; Flessa & Jablonski, 1996; Bennett, 1997; Goldberg et al., 2005; see also Gaston & Blackburn, 1996; Chown & Gaston, 2000; Chek et al., 2003; Pimm & Brown, 2004). Few studies have examined latitudinal variation in rates of immigration and emigration outside the cyclic expansion, retraction and shifting of taxa during recurrent Milankovitch (glacial) cycles (Silvertown, 1985; Haskell, 2001; Harrington, 2004; see Jablonski et al., 2006 for a notable exception).

Determining the extent to which each of the four processes (cladogenesis, extinction, immigration, emigration) are involved in creating the latitudinal gradient in taxonomic richness would provide a major advance in our understanding of the causes of latitudinal variation in diversity, as it would distinguish the mechanisms by which abiotic factors cause the gradient. Previous work by Jablonski (1993) on 26 benthic marine invertebrate orders is widely cited as evidence for higher rates of tropical cladogenesis. Here we revisit this data set to examine the role of all four processes in the creation of the present-day latitudinal gradient in these 26 marine invertebrate orders. Given that the latitudinal increase in

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Abstract

The increase in diversity towards the equator arises from latitudinal variation in rates of cladogenesis, extinction, immigration and/or emigration of taxa. We tested the relative contribution of all four processes to the latitudinal gradient in 26 marine invertebrate orders with extensive fossil records, examined previously by David Jablonski. Coupling Jablonski’s estimates of latitudinal variation in cladogenesis with new data on patterns of extinction and current distributions, we show that the present-day gradient in diversity is caused by higher rates of cladogenesis and subsequent range expansion (immigration) at lower latitudes. In contrast, extinction and emigration were not important in the creation of the latitudinal gradient in ordinal richness. This work represents one of the first simultaneous tests of the role of all four processes in the creation of the latitudinal gradient in taxonomic richness, and suggests that low tropical extinction rates are not essential to the creation of latitudinal diversity gradients.

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taxonomic diversity towards the equator is evident across species, genera, families and orders (Willig et al., 2003), the causes of latitudinal variation in ordinal richness are probably generalizable to other taxonomic levels (see also Sepkoski, 1999 for evidence showing coincident patterns of orders and species in the fossil record).

Methods

Present-day distributions

We documented the present-day latitudinal distribution of each of the 26 marine invertebrate orders using published literature (Appendix 1). For each order, we recorded presence or absence within 10° latitudinal belts (nine belts, hemispheres combined). For consistency, we followed the same taxonomy as Jablonski (1993), detailed in Jablonski & Bottjer (1990).

Cladogenesis and extinction

Data on latitudinal variation in cladogenesis come directly from Jablonski (1993) where methodology is detailed. Briefly, Jablonski (1993) recorded the location of first occurrence of each of the 26 well-preserved marine invertebrate orders that appeared since the beginning of the Mesozoic, with respect to nine, 10° paleolatitudinal belts, hemispheres combined. He then estimated latitudinal variation in cladogenesis by examining the latitudinal distribution of first occurrence for these 26 orders after controlling for a temperate-zone bias in sampling effort. Controlling for variation in sampling effort addressed both issues of collection effort and variation in the size of 10° latitudinal belts that could bias the location of first occurrence of orders (Jablonski, 1993).

Extinction is defined here as the global extinction of the order. We estimated the contribution of extinction to the present-day latitudinal gradient in ordinal richness by examining the location of first occurrence of orders that subsequently went extinct, and plotting the latitudinal distribution of those orders after correcting for sampling bias using the same methodology as Jablonski (1993). If orders originated in the tropics, shifted their distributions out of the tropics and into high latitudes, and then went extinct, extinction could contribute to the latitudinal gradient in ordinal richness indirectly. We tested predictions of this hypothesis as well, using distributional summaries of extinct orders from Moore (1966) and Moore & Teichert (1978), specifically looking for evidence of distributional shifts of each order from tropical to high latitudes prior to extinction.

Net immigration/emigration

Immigration is defined here as the movement (i.e. range shift or expansion) of an extant order into a latitudinal belt; emigration is defined as the movement (i.e. range shift or retraction) of an extant order out of a latitudinal belt, where that order did not become globally extinct. Current levels of ordinal richness in each latitudinal belt \( R_b \) can be partitioned into the contributions of cladogenesis \( c_b \), extinction \( x_b \), immigration \( i_b \) and emigration \( e_b \) as:

\[
R_b = (c_b - x_b) + (i_b - e_b). \tag{1}
\]

The net contribution of immigration and emigration to the present-day gradient can be defined as net movement \( M_b \) into or out of latitudinal belts. We calculate this value as:

\[
M_b = (i_b - e_b) = R_b - (c_b - x_b). \tag{2}
\]

where positive, \( M_b \) indicates a net gain of orders (i.e. net immigration), where negative, a net loss of orders (i.e. net emigration).

We hypothesized that the present-day pattern of ordinal richness should decline towards the poles if these taxa show a typical latitudinal gradient in richness. If cladogenesis contributed to the present-day gradient, then it should be negatively related to latitude. If extinction contributed to the gradient, then it should be positively related to latitude. If net movement of orders contributed to the gradient, then it should be negatively related to latitude, with greater immigration into lower latitude regions. We tested all these predictions using nonlinear regression, with latitude as the independent variable. We used Hill three-parameter equations to model the data, as these equations best described the distribution of most of the data (e.g. present-day distribution, cladogenesis). We use one-tailed tests of significance as all predictions were a priori and directional. All significant results remain significant after adjusting \( z \) values for multiple tests (four tests; Rice, 1989).

Results

At the beginning of the Mesozoic (T₀), none of the 26 benthic marine invertebrate orders existed (Fig. 1, T₀). Jablonski, 1993). At present (T₁), these orders exhibit a latitudinal decline in diversity towards the poles (Fig. 1, T₁): y = 21.2x⁻⁴/(62.1⁻⁴ + x⁻⁴), \( r^2 = 0.975, F = 119.4, \) one-tailed \( P < 0.0001 \). As shown previously (Jablonski, 1993), cladogenesis was higher at lower latitudes (Fig. 1, cladogenesis; y = 7x⁻⁵.8/(36.4⁻⁵.8 + x⁻⁵.8), \( r^2 = 0.984, F = 242.8, \) one-tailed \( P < 0.0001 \). Only 5 of the 26 orders became extinct since cladogenesis. Their locations of first occurrence (uncorrected for variation in sampling effort) were: Encrinida (21–30°), Hemicidaroida (21–30°), Pygastereoida (11–20°), Oligopygoida (concurrently found at 0–10° and 21–30°) and Disasteroida (31–40°) (Jablonski, 1993). The distribution of locations of first occurrence remained similar after we corrected for variation in sampling effort, with extinction reducing the effects of cladogenesis, and reducing diversity, at lower latitudes.
Results illustrate that the present-day latitudinal gradient in ordinal richness was caused by declines in cladogenesis and range expansion with increasing latitude. Extinction and net emigration played no significant role in the creation of the latitudinal gradient in ordinal richness.

Discussion

Fossil and present-day patterns of the 26 well-preserved, benthic marine invertebrate orders examined here suggest that greater tropical richness is the result of higher rates of cladogenesis and subsequent range expansion at low latitudes (Fig. 1). The roles of both cladogenesis and range expansion are consistent with the idea of two distinct patterns comprising the latitudinal gradient in diversity: higher rates of cladogenesis and a greater number of sympatric species in the tropics (cf. Terborgh, 1992, p. 7; Fjeldså, 1994; Martin & McKay, 2004). The latter pattern is strongly correlated with estimates of available energy (Wright, 1983; Currie, 1991; Francis & Currie, 2003; Hawkins et al., 2003; Currie et al., 2004), which may allow more taxa to expand their ranges into sympatry in tropical areas. Causes of latitudinal variation in rates of cladogenesis remain obscure, but possibilities include: (1) reduced energy at higher latitudes that causes higher rates of population extinction and subsequent recolonization, degrading population structure and impeding cladogenesis (Simpson, 1964; Maruyama & Kimura, 1980; but see Whitlock, 1992 and references within), (2) greater seasonality in temperature at higher latitudes that favours broader physiological tolerance and high dispersal, reducing population divergence and cladogenesis (Janzen, 1967; Ghalmambor et al., 2006), (3) increased shifting of distributions at higher latitudes during Milankovitch (glacial) cycles that causes population mixing, bottlenecks and sampling bias during recolonization, reducing rates of population divergence and cladogenesis (Dennis et al., 1995; McGloine, 1996; Dynesius & Jansson, 2000; Hewitt, 2000; Jansson & Dynesius, 2002; Jansson, 2003; Coope, 2004), and (4) greater energy at lower latitudes that causes faster rates of evolution and cladogenesis by reducing generation time, increasing metabolic rates and/or increasing exposure to ultraviolet radiation (Rohde, 1992, 1999; Barralough & Savolainen, 2001; Bromham & Cardillo, 2003; Davies et al., 2004; Allen et al., 2006; Wright et al., 2006;
see also Fischer, 1960; Wright et al., 2003; Brown & Pauly, 2005; Pawar, 2005).

Our results provide support for recent work by Jablonski et al. (2006) who found evidence for an ‘out of the tropics’ model for the creation of the latitudinal gradient in genera of marine bivalves, where lineages preferentially originated in the tropics and persisted there as they expanded poleward. The main difference between the bivalve genera and marine invertebrate orders examined here is that estimated extinction rates were higher in extratropical vs. tropical bivalve genera, suggesting that low tropical extinction rates contributed to the present-day latitudinal gradient in bivalve diversity (Jablonski et al., 2006). In the present study, the latitudinal gradient in ordinal diversity originated in spite of higher tropical extinction rates, illustrating that low tropical extinction rates were not required for the evolution of the latitudinal diversity gradient.

Although fossil evidence suggests that most of the 26 marine invertebrate orders examined here arose in tropical waters (Jablonski, 1993), the coarse nature of controlling for sampling bias across latitudes may overstate the slope of decline in cladogenesis towards the poles (Fig. 1, cladogenesis). Intensified fossil sampling in tropical regions would improve the accuracy of our estimates of the location of origin of these orders. In addition, we should note that cladogenesis and levels of endemism, particularly at lower taxonomic levels, vary between polar regions, being notably higher in the Southern Ocean (see Crame, 1997, 2000; Clarke & Johnston, 2003). Such variation between high-latitude regions may provide important insight into the abiotic causes of latitudinal variation in rates of cladogenesis. Finally, although we correct for latitudinal variation in sampling intensity, such a correction does not control for potential bias in taphonomy across latitudes that could result from reduced preservation in warm tropical waters (Kidwell & Baumiller, 1989), or enhanced preservation of larger tropical taxa (Vermeij, 1978; Martin, 1999, p. 132).

This analysis provides one of the first examinations of all four possible mechanisms underlying the latitudinal gradient in taxonomic diversity. Consistency in the latitudinal gradients in diversity across taxa (invertebrates, vertebrates and plants) and environments (marine, freshwater and terrestrial) (Willig et al., 2003; Hillebrand, 2004) suggests that these patterns result from the same causes. If latitudinal variation in the richness of these 26 marine invertebrate orders is representative of other taxonomic levels and groups, then cladogenesis and range expansion may be the critical mechanisms that link abiotic causes with the resulting pattern of latitudinal variation in diversity.

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References


Davies, T.J., Savolainen, V., Chase, M.W., Moat, J. & Barracough, T.G. 2004. Environmental energy and evolutionary


Appendix 1 Present distribution of marine invertebrate orders examined in this study. Superscripts denote references for presence/absence data following table.

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<th>30–40°</th>
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