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

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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.

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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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 α values for multiple tests (four tests; Rice, 1989).

Results

At the beginning of the Mesozoic (T_0), none of the 26 benthic marine invertebrate orders existed (Fig. 1, T_0; Jablonski, 1993). At present (T_1), these orders exhibit a latitudinal decline in diversity towards the poles (Fig. 1, T_1; $y = 21.2x^{-4}/(62.1^{-4} + x^{-4})$, $r^2 = 0.975$, $F = 119.4$, 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°), Pygasteroida (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
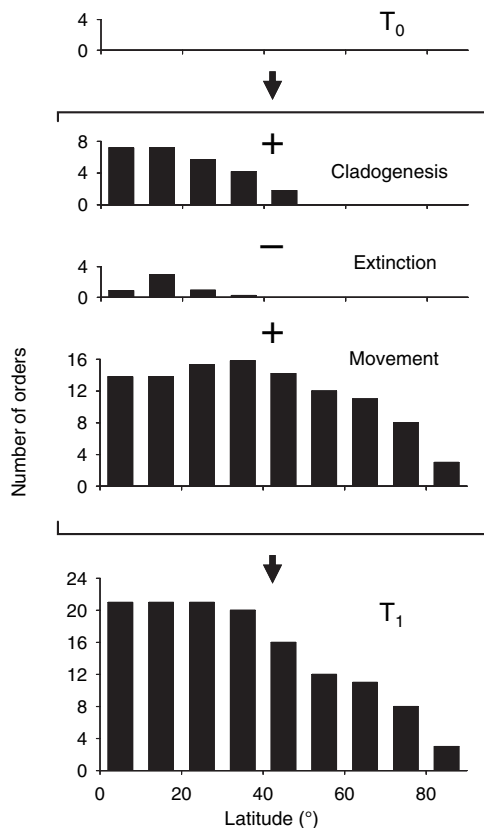
Fig. 1 Net change in richness of 26 benthic marine invertebrate orders that have well-preserved fossil records. Twenty-six orders originated since the beginning of the Mesozoic (T_0) (cladogenesis), with higher estimated rates of cladogenesis in the tropics (Jablonski, 1993). Five of these orders have since gone extinct (extinction). After cladogenesis and extinction, higher range expansion at lower latitudes has dominated net change in ordinal diversity (movement) to create the present-day latitudinal gradient in ordinal richness (T_1).

(Fig. 1, extinction; $y = 1.9x^{-12.4}/(25.0^{-12.4} + x^{-12.4})$, $r^2 = 0.617$, $F = 7.4$, one-tailed $P = 0.98$). Extinction rates were significantly higher at lower latitudes (two-tailed $P = 0.02$), and thus extinction could not have directly caused the latitudinal gradient in ordinal diversity. Furthermore, none of the extinct orders showed distributional shifts poleward prior to extinction (Moore, 1966; Moore & Teichert, 1978), ruling out an indirect contribution of extinction to the latitudinal gradient.

Net movement of orders since cladogenesis and extinction was positive at all latitudes (Fig. 1, movement), but more orders immigrated into lower latitudinal bands more often compared with higher latitudes (Fig. 1, movement; $y = 15.8x^{-5.9}/(72.0^{-5.9} + x^{-5.9})$, $r^2 = 0.938$, $F = 61.3$, one-tailed $P < 0.0001$), resulting in all 21 extant orders occurring at lower latitudes (Fig. 1, T_1). This saturation of extant orders at lower latitudes illustrates that range expansion, rather than range shifting, resulted in the current distributional patterns

over latitude. The slight decline in net movement near the equator (Fig. 1, movement) is an artefact of higher rates of tropical cladogenesis. If we control for rates of cladogenesis and extinction, we find consistently high net movement into tropical belts (0–30°), with a subsequent decline towards the poles (data not shown). Range expansion of orders following cladogenesis had a greater effect on the creation of the present-day latitudinal gradient in ordinal diversity than did cladogenesis itself (cf. Fig. 1).

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; Ghalambor *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; McGlone, 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; Barraclough & 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.

Acknowledgments

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

Phylum	Class	Order	0–10°	10–20°	20–30°	30–40°	40–50°	50–60°	60–70°	70–80°	80–90°
Porifera	Hexactinellida	Lychniscosida	Present[19]	Present[19]	Present[19]	Absent[19]	Absent[19]	Absent[19]	Absent[19]	Absent[19]	Absent[19]
Coelenterata	Hydrozoa	Milleporina	Present[25]	Present[25]	Present[25]	Present[25]	Absent[25]	Absent[25]	Absent[25]	Absent[25]	Absent[25]
Coelenterata	Hydrozoa	Stylasterina	Present[2]	Present[2]	Present[2]	Present[2]	Present[2]	Present[2]	Present[2]	Absent[2]	Absent[2]
Coelenterata	Anthozoa	Helioporacea	Present[25]	Present[25]	Present[25]	Present[25]	Absent[25]	Absent[25]	Absent[25]	Absent[25]	Absent[25]
Coelenterata	Anthozoa	Scleractina	Present[25]	Present[25]	Present[25]	Present[25]	Present[25]	Absent[25]	Absent[25]	Absent[25]	Absent[25]
Mollusca	Gastropoda	Neogastropoda	Present[26]	Present[26]	Present[26]	Present[26]	Present[26]	Present[26]	Present[24]	Present[1]	Present[1]
Bryozoa	Gymnolaemata	Cheilostomata	Present[17]	Present[17]	Present[17]	Present[17]	Present[17]	Present[17]	Present[17]	Present[17]	Present[11]
Echinodermata	Crinoidea	Isocrinida	Present[13]	Present[13]	Present[9]	Present[9]	Present[9]	Absent[20]	Absent[20]	Absent[20]	Absent[20]
Echinodermata	Crinoidea	Millericrinida	Present[12]	Present[20]	Present[12]	Present[9]	Present[4]	Present[20]	Present[20]	Present[20]	Absent[20]
Echinodermata	Crinoidea	Cyrtocrinida	Present[20]	Present[13]	Present[13]	Present[9]	Absent[20]	Absent[20]	Absent[20]	Absent[20]	Absent[20]
Echinodermata	Crinoidea	Bourgueticrinida	Present[12]	Present[9]	Present[12]	Present[12]	Present[8]	Present[8]	Present[8]	Present[9]	Absent[20]
Echinodermata	Crinoidea	Encrinida	Extinct[22]	–	–	–	–	–	–	–	–
Echinodermata	Echinoidea	Pedinoida	Present[12]	Present[18]	Present[18]	Present[18]	Present[18]	Absent[18]	Absent[18]	Absent[18]	Absent[18]
Echinodermata	Echinoidea	Hemicidaroida	Extinct[21]	–	–	–	–	–	–	–	–
Echinodermata	Echinoidea	Salenoida	Present[6]	Present[6]	Present[6]	Present[6]	Present[6]	Absent[6]	Present[6]	Absent[6]	Absent[6]
Echinodermata	Echinoidea	Phymosomatoida	Present[18]	Present[18]	Present[18]	Present[18]	Present[7,18]	Present[7,18]	Present[18]	Absent[18]	Absent[18]
Echinodermata	Echinoidea	Temnopleuroida	Present[12]	Present[12]	Present[12]	Present[12]	Present[18]	Present[18]	Present[18]	Absent[18]	Absent[18]
Echinodermata	Echinoidea	Echinoida	Present[12]	Present[12]	Present[12]	Present[12]	Present[12]	Present[12]	Present[18]	Present[18]	Absent[18]
Echinodermata	Echinoidea	Pygasteroida	Extinct[21,23]	–	–	–	–	–	–	–	–
Echinodermata	Echinoidea	Holectypoida	Present[18]	Present[18]	Present[18]	Present[3,18]	Present[18]	Absent[18]	Absent[18]	Absent[18]	Absent[18]
Echinodermata	Echinoidea	Cassiduloida	Present[16]	Present[16]	Present[16]	Present[16,10]	Present[16,10]	Present[10]	Absent[16]	Absent[16]	Absent[16]
Echinodermata	Echinoidea	Oligopygoida	Extinct[23]	–	–	–	–	–	–	–	–
Echinodermata	Echinoidea	Clypeasteroida	Present[15]	Present[15]	Present[15]	Present[15]	Present[15]	Present[15]	Present[15]	Present[15]	Absent[15]
Echinodermata	Echinoidea	Disasteroida	Extinct[23]	–	–	–	–	–	–	–	–
Echinodermata	Echinoidea	Holasteroida	Present[12]	Present[12]	Present[12]	Present[12]	Present[12]	Present[12]	Present[5]	Present[14]	Present[14]
Echinodermata	Echinoidea	Spatangoida	Present[12]	Present[12]	Present[12]	Present[12]	Present[12]	Present[12]	Present[18]	Present[18]	Absent[18]

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