



Supporting Online Material for
**Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity
Gradient**

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Materials and methods

Paleontological data and analyses: We used an updated version of Sepkoski's Compendium (*S1*) to identify all living genera and subgenera of bivalves that originated in the last 11 million years (i.e., from the start of the Late Miocene to the present day). Our revision of Sepkoski's data, using an extensive literature search and museum collections that permitted taxonomic standardization, allowed us to specify the oldest known species for each taxon (*S1*, *S2*). We then determined the place of the first occurrence of each taxon using museum collections and an extensive literature search; all occurrences within a stratigraphic substage (e.g., late Tortonian) were treated as contemporaneous, yielding a temporal resolution of 1 m.y. or less, except within the Tortonian stage where resolution was ~ 2 m.y. Finally, the locality or localities of first occurrence were assigned to tropical or extratropical categories depending on their position relative to the contemporary edge of the zone of massive coral reefs and other tropical indicators (as in *S3*). Uncertainties about past environments doubtless remain, but as discussed in the text, the more intensive sampling of extratropical regions makes erroneous attribution of first occurrences to extratropical regions more likely than erroneous attribution to the tropics, biasing the data against the OTT model.

In order to estimate the effects of among-clade differences in preservation potential on patterns of first occurrences, we calculated the proportion of genera and subgenera within individual families that have a fossil record using a recently compiled database (*S1*). For each taxon with a tropical first occurrence during the time interval covered in this study we determined its current maximum pole-ward range limit (either in the northern or in the southern hemisphere) using either (i) the biogeographic data described below or (ii), for taxa not covered by that database, distributional data from the primary literature. The age distributions of Northern Hemisphere taxa shown in Fig. S2 and S3 were derived from the updated version of the Compendium described above. For estimating tropical versus extratropical extinctions, we followed the same general procedure as for estimating patterns of origination, using the stratigraphic range endpoints from the revised version of the Compendium.

Modern biogeography: We compiled a database of geographic distributions of 3599 species and 621 genera and subgenera of living marine bivalves using an extensive search of the primary literature, supplemented by data from major museum collections in Europe and North America. We restricted our bathymetric coverage to shelf depths (0 - 200 meters water depth, i.e., from the intertidal to the edge of the continental shelf) since deeper parts of the world oceans are poorly represented in the fossil record (*S1*). These data represent an expanded version of those used by Flessa and Jablonski (*S4*) and include the following superfamilies: Arcoidea, Limopsoidea, Mytiloidea, Pectinoidea, Pterioidea, Pinnoidea, Trigonioidea, Carditoidea, Cardioidea, Solenoidea, Tellinoidea, Arcticoidea, Veneroidea. This represents roughly half of present-day marine bivalve diversity (which totals 1292 genera and subgenera, including exclusively deep-sea taxa, according to *S1*). Only taxa present in the northern hemisphere were used to calculate the LDG shown in Fig. S1, because at present sampling of these taxa is much more complete there; for these calculations we assumed that an individual taxon is present throughout the range demarcated by its range endpoints, an assumption commonly used in macroecological analyses (e.g., *S5- S7*). Of the 503 genera in the Flessa-Jablonski database known as fossils, for figures S3 and S3 we excluded 38 genera belonging to poorly preserved families (< 75% of living genera known as fossils, see Fig. 2), and only plotted data for the Northern Hemisphere, where sampling is most complete; this left 431 genera for analysis.

Previous studies that have examined evolutionary dynamics along latitude

We searched the primary literature for individual studies that have attempted to quantify differences in evolutionary rates between tropical and extratropical taxa. The resulting list of studies shown in Table S1 reveal the diversity of approaches taken to address the issue and the relatively few taxonomic groups for which such analyses are available. The majority of these studies involve marine invertebrates and these in turn are dominated by mollusks. Among terrestrial groups, invertebrates in general and insects in particular are seriously underrepresented, despite their tremendously high tropical species richness, and freshwater organisms are absent from the list. Data from the fossil record are used by the majority of these studies to test for differences in evolutionary rates between tropical and extratropical regions, while the rest use various phylogenetic methods. Although roughly half of the studies provide species-level analysis, the spatial and taxonomic coverage of species-level analyses are much smaller compared to those at higher taxonomic levels.

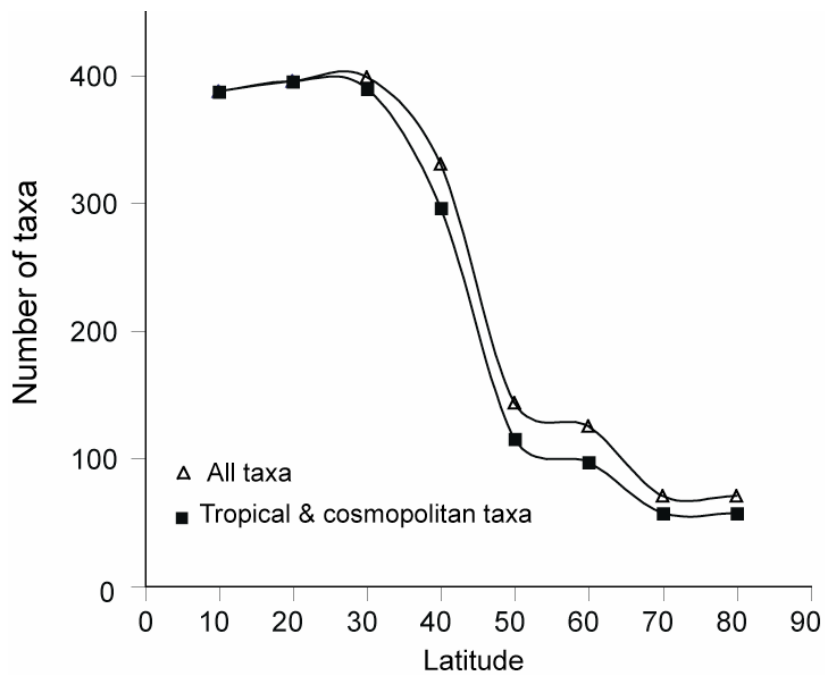


Fig. S1. The latitudinal diversity gradient of living bivalve genera and subgenera in the Flessa-Jablonski database (*S4*; see Methods for taxonomic coverage) that occur in the Northern Hemisphere. The overall trend (open triangles) changes very little when based only on taxa that range into the tropics (solid squares), consistent with the hypothesis that taxa primarily originate in the tropics and expand into extratropical regions (see text for details).

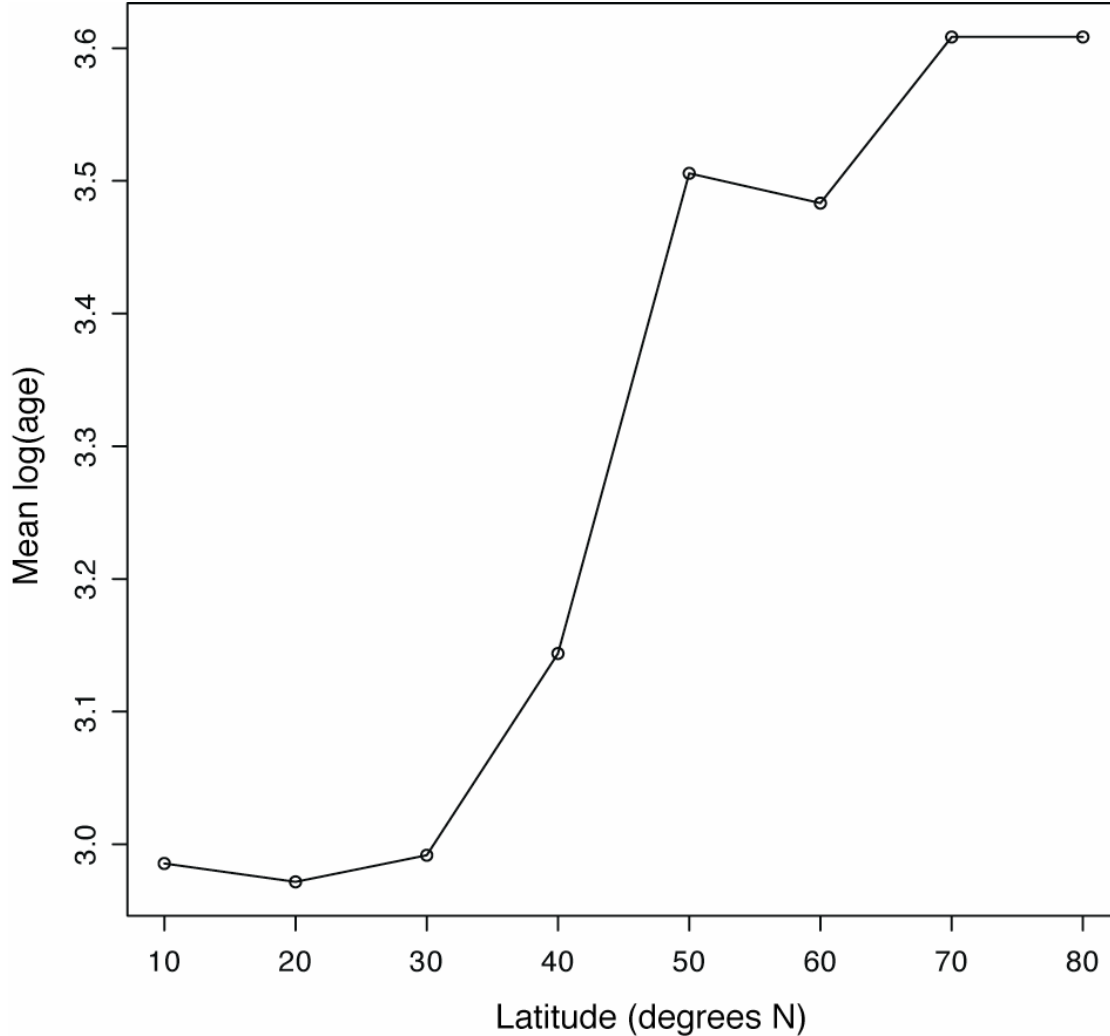


Fig. S2. The average geologic age (log-transformed) of living bivalve genera and subgenera in the Flessa-Jablonski database (S2, S4; see Methods for taxonomic coverage) occurring in 10-degree latitudinal bins in the Northern Hemisphere. Average age of assemblages increases from the equator to the Arctic Ocean; a similar trend is seen if median geologic ages are used instead. This difference is unlikely to be due to the less complete sampling of the tropical fossil record, as the vast majority of living tropical genera also occur in the extratropics (see main text); qualitative results are unchanged if 38 additional genera in this database belonging to poorly preserved families (i.e. <75% of living genera known as fossils, see Fig. 2) are also included.

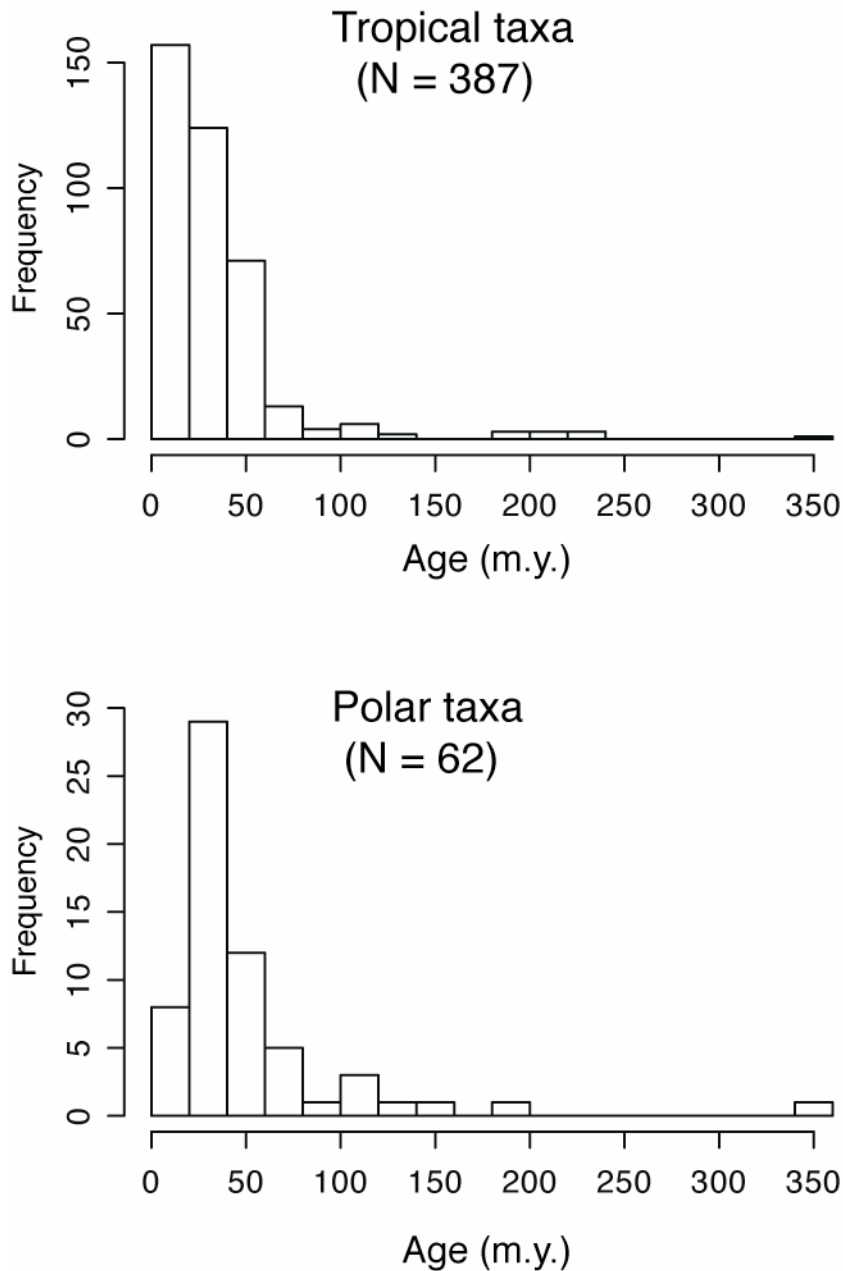


Fig. S3. Comparisons of the age-frequency distributions of living bivalve genera and subgenera at the latitudinal extremes of the LDG in the Northern Hemisphere. Taxonomic coverage restricted to those in the Flessa-Jablonski database. Age distributions of the tropical (0° - 23° N) and polar ($>60^{\circ}$ N) assemblages differ significantly ($p = 0.0002$, Kolmogorov-Smirnov test; as many genera are shared by the two faunas the p-value is conservative); the greater average ages of the polar taxa are consistent with the prediction of the OTT model (see main text for details). Qualitative results are unchanged if 38 additional genera in this database belonging to poorly preserved families (i.e. $<75\%$ of living genera known as fossils, see Fig. 2) are also included.

Table S1. Result of a literature search for studies that have empirically tested for differences in evolutionary rates between tropical and extra-tropical assemblages. We only included studies that undertook quantitative comparisons.

Taxon	Taxonomic level	Method	Conclusion	Comments	Source
Angiosperms	Genus, species	Species-genus ratios and other evidence	Extinctions lower in the tropics	One of the few studies to argue that the LDG is primarily shaped by low extinctions in the tropics; however the data used to support this argument do not provide direct estimates of extinction rates	(S8)
Angiosperms (Dicotyledonous taxa)	Family	Character states	Low tropical extinction	Archaic characters persist in tropical rain forests	(S9)
Angiosperms (selected groups)	Family	Morphological phylogenies	Tropical taxa older (basal); implies major groups tend to originate in tropics	Does not quantify how diversification rates vary with latitude or the effects of distributional changes	(S10)
Birds (New World endemic clades)	Genus	Regressions of diversification rates and latitude and other environmental variables	Higher net diversification rates in low latitude clades	Effects of extinction unknown; assumes taxa originated at the mid point of their present geographic distribution	(S11)

Birds (New World)	Tribes	Ages of tribes based on DNA hybridization data	Tropical tribes older	Effects of extinction unknown; does not take into account distributional changes	(S12)
Birds (New World)	Species	Basal vs derived position of families based on DNA hybridization (non-passerines) and nuclear genes (passerines)	Higher extratropical extinction rates, no support for speciation role	Extinction rates inferred by steepness of gradient of basal vs derived families: basal clades are species-poor in north temperate zone relative to derived clades	(S13)
Birds (passerine)	Species	Sister-group comparison	Higher net diversification rate towards equator	Effects of extinction unknown; assumes taxa originated at the mid point of their present latitudinal range	(S14)
Birds (passerine)	Higher taxa (Tribe, Family)	Tropical-temperate comparisons of diversification rates within clades	Net diversification rates higher in tropical regions; diversification rates decrease with clade age	Consistent with higher rate of diversification in lower latitudes; does not separate effects of speciation, extinction and changes in distributions	(S15)
Corals (Hermatypic)	Genus	Time of first appearance, from fossil record	Average age decreases as diversity increases	Effects of extinction unknown; does not take into account distributional changes	(S16)

Foraminifera (benthic)	Genus	Time of first appearance, from fossil record	Average age declines with latitude	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S17)
Foraminifera (benthic; Cenozoic)	Species	Comparison of within habitat diversities in temperate and tropical latitudes through the Cenozoic	Higher net diversification in tropics, higher origination and extinction rates in tropics	Tropical diversity may result from greater accumulation of long-lived species	(S18)
Foraminifera (planktonic)	Species	Paleontological data on region of first occurrence	Higher origination in the warmer waters	Suggests that speciation rates are higher in warmer waters	(S19)
Foraminifera (planktonic; Cretaceous)	Genus	Time of first appearance, from fossil record	Average age younger for tropical assemblage	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S20)
Foraminifera (planktonic; Neogene)	Species and subspecies	Taxonomic survivorship curves	No difference in taxon durations and extinction rates between tropics and extratropics	Origination rates not quantified; high latitude assemblage has shorter mean duration and higher extinction rates than tropics, but not statistically significant	(S21)

Foraminifera (planktonic; Neogene)	Species	Taxon ages, from fossil record	Extinction higher in the tropics, low at the poles but no difference in mean species durations between tropics and extratropics	Data and results could be consistent with a model of higher tropical originations followed by range expansions.	(S22)
Insects (phytophagous)	Species (five sister group pairs)	Sister-group comparison	No difference in net diversification between tropical and temperate taxa	Small sample size; effects of extinction unknown	(S23)
Swallowtail butterflies	Species	Sister-group comparison	Higher net diversification rate towards equator	Effects of extinction unknown; assumes taxa originated at the mid point of their present latitudinal range	(S14)
Mammals	Family	Time of first appearance, from fossil record	Average age younger for tropical assemblage	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S20)
Mammals	Family	Time of first appearance, from fossil record	No difference in average age between tropical and temperate assemblages and taxa	Reanalysis of Stehli et al. (20) data; does not take into account distributional changes	(S24)

Marine bivalves	Family	Species richness versus family ages (from fossil record)	Younger families contribute more species in the tropics	Implies higher net diversification in tropics; effects of extinction unknown; does not take into account distributional changes	(S25)
Marine bivalves	Family	Time of first appearance, from fossil record	Average age younger for "warm-water" groups	Higher extinction in tropics or higher origination or both; does not take into account distributional changes	(S20)
Marine bivalves	Genus	Age of genera, from fossil record	Tropical genera younger	Effects of extinction unknown; does not take into account distributional changes	(S4)
Marine bivalves	Genus	Time of first appearance, from fossil record	Average age decreases as diversity increases	Whether the trend is statistically significant is not known; effects of extinction unknown; does not take into account distributional changes	(S26)
Marine bivalves	Species, Genus	Comparison of Late Jurassic and Recent regional faunas	Tropical richness increased at a higher rate resulting in a steepening of the LDG over time	Consistent with higher rate of diversification in lower latitudes; does not take into account distributional changes	(S27)

Marine invertebrates (Post-Paleozoic)	Orders	Paleontological data on region of first occurrence	Tropics: significantly more first appearances	Major groups originate in the tropics, and persist there while expanding polewards; does not quantify rates of diversification	(S3, S28)
Marine mollusks	Genus Subfamily, Family	Net diversification rate using geological age of group and its current species richness	No difference in net diversification rates between tropics and extratropics	Effects of extinction unknown; does not take into account distributional changes	(S29)
Marine mollusks (Japan & western N. America)	Species	Lyellian percentages from fossil faunas	No difference in extinctions rates of tropical vs. temperate faunas	Implies higher tropical diversity is driven by higher origination	(S30)
Primates (Cercopithecoid)	Species	Regression model to test for associations between latitude and diversification rate; also used nested sister-taxon comparisons	Regression results suggest negative relation between latitude and net diversification rates, but nested sister group comparisons do not support an association between latitude and diversification rates	Overall favors the hypothesis of higher diversification in lower latitudes; reconstructions of ancestral ranges suggest that lower latitudes are "sources regions" for species	(S31)

Table S2, Percentage of tropical first occurrences among living genera and subgenera in the major clades of marine Bivalvia, for families with $\geq 75\%$ genera known as fossils (*S1*). The high proportion of taxonomic origination in the tropics is not restricted to the heteroconch clade; note also that the proportion of tropical originations is strongly correlated ($r^2 = 0.82$, $p = 0.002$, simple linear regression) with the proportion of taxa known fossil for the entire order (including families with $<75\%$ of their genera and subgenera known), corroborating family-level results in Fig. 2. Classification follows (*S25*), but with unguinids and thyasirids moved from Lucinoidea to Heteroconchia following (*S32*); lucinoids and anomalodesmatans may be monophyletic groups nested within the heteroconchs (*S33*). The low number of anomalodesmatan first occurrences is consistent with previous studies (*S1*).

Clade	Total number of genera and subgenera occurring in Late Miocene-Pleistocene fossil record	Number with unknown 1 st species or unresolved to region	Percent resolved first occurrences that are tropical	Percent genera and subgenera known fossil for entire order (<i>S1</i>)
Anomalodesmata	5	1	0	55
Arcoida	14	1	69	85
Heteroconchia	111	9	71	75
Lucinoidea	7	1	83	94
Mytiloidea	11	2	78	80
Protobranchia	8	1	57	76
Pteriomorpha	18	1	94	85

Literature Cited

- S1. J. W. Valentine, D. Jablonski, S. M. Kidwell, K. Roy, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 6599 (2006).
- S2. D. Jablonski, K. Roy, J. W. Valentine, R. M. Price, P. S. Anderson, *Science* **300**, 1133 (2003).
- S3. D. Jablonski, *Nature (London)* **364**, 142 (1993).
- S4. K. W. Flessa, D. Jablonski, in *Evolutionary Paleobiology* D. Jablonski, D. H. Erwin, J. H. Lipps, Eds. (University of Chicago Press, Chicago, 1996) pp. 376-397.
- S5. K. Roy, D. Jablonski, J. W. Valentine, *Proc. Roy. Soc. Lond. B.* **267**, 293 (2000).
- S6. K. Roy, D. Jablonski, J. W. Valentine, *Phil. Trans. Roy. Soc. Lond. B* **351**, 1605 (1996).
- S7. K. Roy, D. Jablonski, J. W. Valentine, G. Rosenberg, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 3699 (1998).
- S8. G. L. Stebbins, *Flowering plants: evolution above the species level* (Belknap Press, Cambridge, Massachusetts, 1974), pp.
- S9. K. R. Sporne, *New Phytol.* **72**, 1175 (1973).
- S10. W. S. Judd, R. W. Sanders, M. J. Donoghue, *Harvard Papers in Botany* **5**, 1 (1994).
- S11. M. Cardillo, C. D. L. Orme, I. P. F. Owens, *Ecology* **86**, 2278 (2005).
- S12. K. J. Gaston, T. M. Blackburn, *Proc. Roy. Soc. Lond. B.* **263**, 63 (1996).
- S13. B. A. Hawkins, J. A. F. Diniz-Filho, C. A. Jaramillo, S. A. Soeller, *Jour. Biogeogr.* **33**, 770 (2006).
- S14. M. Cardillo, *Proc. Roy. Soc. Lond. B.* **266**, 1221 (1999).
- S15. R. E. Ricklefs, *Ecology* (in press).
- S16. F. G. Stehli, J. W. Wells, *Syst. Zool.* **20**, 115 (1971).
- S17. J. T. Durazzi, F. G. Stehli, *Syst. Zool.* **21**, 384 (1972).
- S18. M. A. Buzas, L. S. Collins, S. J. Culver, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 7841 (2002).
- S19. A. P. Allen, J. F. Gillooly, V. M. Savage, J. H. Brown, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 9130 (2006).
- S20. F. G. Stehli, R. G. Douglas, N. D. Newell, *Science* **164**, 947 (1969).
- S21. K.-Y. Wei, J. P. Kennett, *Nature* **305**, 218 (1983).
- S22. S. M. Stanley, K. L. Wetmore, J. P. Kennett, *Paleobiology* **14**, 235 (1988).
- S23. B. D. Farrell, C. Mitter, in *Species diversity in ecological communities* R. E. Ricklefs, D. Schluter, Eds. (University of Chicago Press, Chicago, 1993) pp. 253-266.
- S24. L. Van Valen, *Science* **166**, 1656 (1969).
- S25. J. A. Crame, *Paleobiology* **26**, 188 (2000).
- S26. A. D. Hecht, B. Agan, *Syst. Zool.* **21**, 308 (1972).
- S27. J. A. Crame, *Paleobiology* **28**, 184 (2002).
- S28. D. Jablonski, *Jour. Exp. Zool.* **304B**, 504 (2005).

- S29. A. Clarke, J. A. Crame, in *Marine Biodiversity: Patterns and processes* R. F. G. Ormond, J. D. Gage, M. V. Angel, Eds. (Cambridge University Press, Cambridge, 1997).
- S30. S. M. Stanley, W. O. Addicott, K. Chinzei, *Geology* **8**, 422 (1980).
- S31. M. Böhm, P. J. Mayhew, *Biol. J. Linn. Soc.* **85**, 235 (2005).
- S32. S. T. Williams, J. D. Taylor, E. A. Glover, *Jour. Moll. Stud.* **70**, 187 (2004).
- S33. G. Giribet, W. Wheeler, *Invert. Biol.* **121**, 271 (2002).