

Fig. 4. (A) Values of S , L , ΔL (μ_B), and K (meV) per Co atom calculated by the SPR-KKR method for Co particles on Pt(111) as shown in (B). The values of L in parentheses have been computed within the OP scheme with a 50% reduced Racah parameter. (B) Hard-sphere representation of the Co particles considered in the theoretical calculations. The labels indicate the OP values of L for nonequivalent Co sites. S , L , ΔL , and K in (A) are averaged over all Co sites.

changes of L and K . Further, to estimate the MAE due to the induced polarization of the Pt substrate, K can be decomposed in partial contributions arising from Co and Pt sites (28). For a single Co adatom, Pt sites contribute to about 15% of the total MAE. Because of the strong decrease of the Co MAE with increased coordination, the Pt share increases to 30% for the dimer and up to 60% for the pentamer, eventually providing the dominant MAE contribution in Co/Pt multilayers (25).

These results provide a fundamental understanding of the magnetic properties of finite-sized particles and enable the testing of current theoretical models at the atomic scale (9, 29). It is expected that the size of stable ferromagnetic particles at room temperature can be made smaller by artificially reducing the coordination of the magnetic atoms in nanosized particles. If the Co adatom coordination is assumed to equal 2, the present data imply a theoretical lower limit of 400 Co atoms per bit (30).

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- The XMCD measurements were performed at beamlines ID08 and ID12B of the European Synchrotron Radiation Facility in Grenoble. We thank K. Larsson for technical assistance in preparing the experiment. This work was partly supported by the Swiss Science and Technology Council (Top-Nano-21) and the Swiss National Science Foundation.

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The Impact of the Pull of the Recent on the History of Marine Diversity

David Jablonski,^{1*} Kaustuv Roy,² James W. Valentine,³ Rebecca M. Price,¹ Philip S. Anderson¹

Up to 50% of the increase in marine animal biodiversity through the Cenozoic at the genus level has been attributed to a sampling bias termed "the Pull of the Recent," the extension of stratigraphic ranges of fossil taxa by the relatively complete sampling of the Recent biota. However, 906 of 958 living genera and subgenera of bivalve mollusks having a fossil record occur in the Pliocene or Pleistocene. The Pull of the Recent thus accounts for only 5% of the Cenozoic increase in bivalve diversity, a major component of the marine record, suggesting that the diversity increase is likely to be a genuine biological pattern.

The history of global marine biodiversity is controversial because the observed pattern is difficult to separate definitively from sampling biases. During the Cenozoic, however, the taxonomic richness of the marine fauna increases markedly while sampling proxies, such as measures of marine outcrop area, decline and thus diverge from the biodiversity trend. This discordance is taken by some to indicate that the increase is primarily a true biological signal (1). Others invoke additional biases, particularly the "Pull of the Recent," to explain the Cenozoic

biodiversity rise (2–6). The Pull of the Recent (7) arises from the more complete sampling of the Recent biota, which tends to extend the stratigraphic ranges of geologically young genera or higher taxa to the present day across intervals where fossils of those taxa are lacking, thereby increasing calculated richness in these intervening intervals. Extinct taxa cannot benefit from such complete sampling, resulting in fewer range extensions and, therefore, artificially low diversity in time intervals lacking extant taxa for any taxonomic database founded on first and last occurrences. Here we test the effects of the Pull of the Recent for a major constituent of post-Paleozoic biodiversity, the marine bivalves.

The most direct way to evaluate this effect is to omit the Recent fauna and analyze biodiversity data exclusively from the youngest fossil occurrence of each taxon (3, 8). Sepkoski's (8)

¹Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, IL 60637, USA. ²Section of Ecology, Behavior and Evolution, University of California, San Diego, La Jolla, CA 92093, USA. ³Department of Integrative Biology, University of California, Berkeley, CA 94720, USA.

*To whom correspondence should be addressed. E-mail: d-jablonski@uchicago.edu

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very preliminary analysis yielded a diversity curve strikingly similar to his previous results, with a rise to late Cenozoic levels significantly higher than those in the Mesozoic or Paleozoic. However, a recent re-analysis of the same data (5) was skeptical of these conclusions, in part because Sepkoski's in-progress database suggested that the Pull of the Recent extended the stratigraphic ranges of 50% of late Cenozoic marine genera per time interval.

The molluscan class Bivalvia is a good vehicle for evaluating this potential bias: it has an excellent fossil record that is well studied, its present-day generic richness is well known, and its observed Phanerozoic diversity trend mimics the overall pattern of a marked Cenozoic increase in generic richness.

For all extant bivalves in Sepkoski's Compendium (9), which provides stratigraphic ranges for marine animal genera and subgenera with a fossil record, we surveyed the literature to determine which have been recorded in the last 5 million years (My) of geologic time (the Pliocene and Pleistocene). This provides a time increment roughly comparable in duration to most of the other standard intervals used in analyses of Phanerozoic biodiversity (10). Complete taxonomic revisions or full phylogenetic analyses are not feasible, but species previously assigned to broadly defined genera were reallocated to the more narrowly defined taxa corresponding to modern usage and taxonomic concepts, according to revisions by experts in particular groups or regional faunas. Following Sepkoski (9) and most other workers, we treated

genera and subgenera as equivalent ranks (hereafter termed "taxa") (11).

Of the 958 taxa of extant marine bivalves having a fossil record, we found that 906 occur in the Pliocene or Pleistocene. The Pull of the Recent thus affects only 52 taxa, or 5.4% of the extant bivalves that have a fossil record; omitting range extensions to the Recent has a trivial effect on the observed rise of bivalve taxonomic richness through the 550 My of the Phanerozoic (Fig. 1A) or even over the past 100 My, where the Pull of the Recent should be most severe (Fig. 1B). Log-transformed data yield a linear trend remarkably similar to uncorrected analyses (12) (fig. S1).

Our results differ significantly from those of Sepkoski (8) and from the electronic version of his database as used by later authors (5, 13), where the Pull of the Recent for marine bivalves is about 47% (fig. S2) (5). These changes derive from reconciling the taxonomies used over many decades by paleontologists, which were largely recorded by Sepkoski as he found them, with current usage by neontologists. When we correct species assignments, the number of living taxa in Sepkoski's database missing from the Pliocene or Pleistocene drops to 73 (9%). By reassigning fossil species that had been languishing in broadly defined taxa, and to a lesser extent by using primary sources that Sepkoski did not consult, we also added paleontological occurrences of 144 living taxa; 120 of these newly added taxa (83%) had been described before the 1969 publication of the *Treatise* (14), which formed the starting point for Sepkoski's database (9) (Fig. 2). With these additions, and the removal of 24 taxa as synonyms and 3 as freshwater, the number of taxa missing from the Pliocene and Pleistocene, and therefore contributing to the Pull of the Recent, drops to 52 (5%).

The 52 fossil taxa missing from the Pliocene and Pleistocene appear to be a random sample of the living bivalves in many respects. However, although the small number of missing taxa hampers statistical evaluation, some general patterns (table S2) are consistent with previous work on fossilization probabilities in marine mollusks (15–17), namely that bivalve taxa missing from the fossil record tend to be small (fig. S3) and fragile (although mineralogy is less important than organic content) (18), from deep-water, or

endemic to regions where a restricted range of sedimentary environments is available for sampling, such as Australia (table S3) (19). These factors are not independent variables, however. For example, most deep-sea taxa are small-bodied and tend to have fragile shells with high organic content (20).

Our Pliocene-Pleistocene inventory is unlikely to have introduced major new biases into the diversity curves plotted in Fig. 1 by focusing attention on a single time interval. We did not survey new regions, collect or describe new faunas, or introduce new taxa for this analysis. We simply placed pre-existing species in an internally consistent taxonomy, which is standard procedure for creating any taxonomic database (21, 22).

One way to test whether the high proportion of Recent taxa recovered in the Pliocene-Pleistocene interval is an artifact of intensive study, or of a uniquely high preservation potential in young strata, is to perform the analogous procedure in older time intervals. For example, the bivalves of the Maastrichtian stratigraphic stage of the Cretaceous Period have also been placed in a standardized taxonomy (21), with 1744 nominal species in 347 genera and subgenera. We find that only $13 \pm 6\%$ (95% binomial confidence interval of the 135 taxa known to range through the Maastrichtian are not actually recorded from that interval (23). An inventory of Maastrichtian echinoids yields similar results, with only $11 \pm 10\%$ of the range-through taxa ($n = 46$) unrecorded from that interval (24).

The comparable recovery rates of genera in the Maastrichtian and the Pliocene-Pleistocene intervals (which are of roughly equal durations, 6.3 My versus 5.3 My, respectively) suggests that the observed diversity increase from Late Cretaceous to Late Cenozoic (8) is robust, at least for this group and for others with similar preservation potential. Such relatively high-preservation groups, including bryozoans, corals, echinoids, gastropods, and foraminifera, are the very ones that contribute most heavily to the diversity rise. Model-based estimates of the probability of taxon preservation per stratigraphic interval, calculated as $\sim 50\%$ for bivalves and $\sim 60\%$ for echinoids (25), are evidently too conservative or subject to wide variation among intervals and thus require empirical calibration. Many of the basic patterns

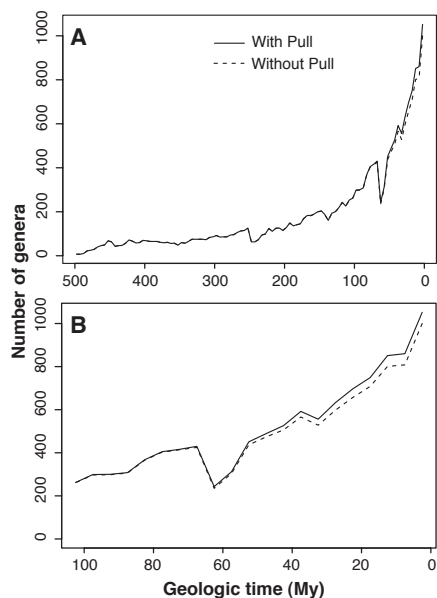


Fig. 1. Genus-level richness of marine bivalves with and without the Pull of the Recent (solid and dashed lines, respectively). The youngest time bin includes 958 extant taxa plus 92 extinct taxa. (A) Through the Phanerozoic. (B) Over the past 100 My. These data are available from the Paleobiology Database Web site (www.paleodb.org).

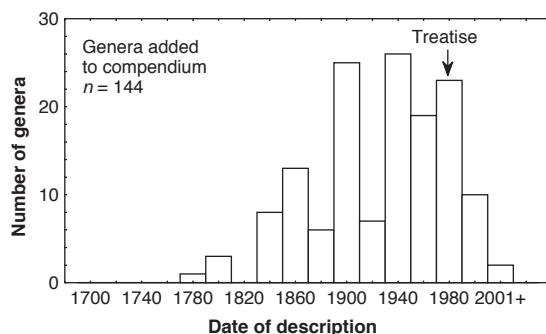


Fig. 2. Date of description of added genera. The arrow indicates the publication date of the bivalve *Treatise* (14); virtually all of these earlier genera were in the *Treatise* and other sources as Recent-only, and were treated as such by Sepkoski (9).

in the fossil record appear to be robust to outmoded or incomplete taxonomy (22), including, as we have shown, the first-order history of biodiversity (8, 26–29). However, our results underscore the importance of taxonomic consistency in more detailed studies, from the evaluation to sampling biases to spatially explicit analyses of extinction and origination.

We have not eliminated all of the factors that could potentially impose or exaggerate diversity increases through the Cenozoic. For example, younger sediments are less likely to be lithified than older rocks, and this would facilitate the retrieval or identification of small, delicate or rare taxa in younger time intervals. However, we have no reason to believe that this shift in the nature of the stratigraphic record would impose the relatively smooth increase observed in Cenozoic richness, particularly in the presence of a decline in the extent of fossiliferous deposits over the Cenozoic and indeed over the past 100 My (1, 5). This conclusion is corroborated by recovery rates of range-through taxa in latest Cretaceous strata, which are comparable to our latest Cenozoic value despite much more extensive lithification, tectonism, erosion, and diagenesis in the earlier interval. The marked Cenozoic diversification of marine bivalves helped shape modern benthic marine communities and remains an intriguing biological phenomenon. Postextinction recovery dynamics (12), provincialization (26, 30), interhabitat differentiation (31), and changing nutrient regimes (32) are all thought to have contributed to this diversification. The relative effects of these and other processes must be quantified for a fuller understanding of the origin and maintenance of modern marine biodiversity.

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Supporting Online Material

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Local Selection and Latitudinal Variation in a Marine Predator-Prey Interaction

Eric Sanford,^{1,2*} Melissa S. Roth,¹ Glenn C. Johns,¹ John P. Wares,³ George N. Somero¹

Although pairs of species often interact over broad geographic ranges, few studies have explored how interactions vary across these large spatial scales. Surveys along 1500 kilometers of the Pacific coast of North America documented marked variation in the frequency of predation by the snail *Nucella canaliculata* on the intertidal mussel *Mytilus californianus*. Laboratory rearing experiments suggest that regional differences in drilling behavior have a genetic basis, and mitochondrial sequence variation confirms that gene flow is low among these snail populations. Marine communities separated by hundreds of kilometers may have intrinsically different dynamics, with interactions shaped by restricted gene flow and spatially varying selection.

Pairs of species often co-occur over broad latitudinal ranges marked by strong environmental gradients that may alter the nature or intensity of species interactions by changing the ecological (1–3) and evolutionary (4, 5) context in which they occur. Theory suggests that species are more likely to exhibit local adaptation to spatial variation in selection when gene flow is low (6, 7). Thus, in terrestrial and freshwater systems, where dispersal is often limited, there are many examples of species interactions modified by site-specific selection (4, 5). In contrast, the prevalence of planktonic larvae in marine species has caused local selection to be neglected as a potential source of variation in marine interactions (8,

9). However, growing evidence of genetic differentiation among many invertebrate and fish populations (10–14) highlights the importance of understanding the ecological consequences of restricted gene flow in marine systems.

The mid-intertidal mussel *Mytilus californianus* is a dominant competitor and habitat-forming species on rocky shores along the Pacific coast of North America (15, 16). Our results suggest that predation by the whelk *Nucella canaliculata* on this important species is often strong in California, but weak in Oregon, and that these differences in drilling behavior have a genetic basis. Potential for population differentiation is high in *Nucella* because this