the input pulse becomes part of the tail of the exiting pulse.

As a further investigation into the nature of negative group velocities, we performed a second experiment to determine the direction of energy flow within the medium. The layout is shown in Fig. 1B. We observed that the signal strength measured at output ports A and C of the bidirectional 1% taps was barely above the noise floor of our detection system and was consistent with the small amount of back-reflection expected from the large number of splices present in this configuration. In contrast, strong signals were measured from ports B and D, thus demonstrating that the energy flow was only in the forward direction, even though the group velocity was negative. We also observed that the peak of the pulse arrived at port D before it did at port B, thus confirming the backward movement of the peak of the pulse within the optical fiber.

Our experiment shows that within a medium with a negative group velocity, the peak of a propagating pulse does in fact move in the backward direction, even though energy flow is always in the forward direction. These results can be understood in terms of the time dependence of the saturation of the gain of the material, whereby the leading edge of the incident pulse experiences more gain than does the trailing edge. Thus, the peak of the pulse within the medium occurs initially at the distant end of the fiber and progressively moves toward the front end of the fiber. Furthermore, all of these results are consistent with the principle of causality in that these effects are initiated by the far leading edge of the pulse.

References and Notes
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Supporting Online Material
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Movies S1 to S4
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Statistical Independence of Escalatory Ecological Trends in Phanerozoic Marine Invertebrates
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Ecological interactions, such as predation and bioturbation, are thought to be fundamental determinants of macroevolutionary trends. A data set containing global occurrences of Phanerozoic fossils of benthic marine invertebrates shows escalatory trends in the relative frequency of ecological groups, such as carnivores and noncarnivorous infaunal or mobile organisms. Associations between these trends are either statistically insignificant or interpretable as preservational effects. Thus, there is no evidence that escalation drives macroecological trends at global and million-year time scales. We also find that taxonomic richness and occurrence data are cross-correlated, which justifies the traditional use of one as a proxy of the other.

Major trends in the composition of Earth’s biota (1) are widely thought to be evolutionarily important (2, 3), but statistical (4) and taphonomic (5–7) biases might create the appearance that such trends result from ecological interactions. The publicly available Paleobiology Database (8) makes it possible to test (i) the strength of long-term large-scale associations between ecology and macroevolution and (ii) the assumption that global taxonomic richness is a good proxy for ecological abundance, which previously has been demonstrated only for individual groups during certain parts of the Phanerozoic (9, 10).

The two most commonly cited hypotheses explaining trends in the fossil record invoke negative interactions among ecological groups. The escalation hypothesis predicts that long-term ecological shifts are caused by the evolutionary response of prey to predation pressure (2), which has intensified for some groups (11, 12) if not others (13). Two potential faunal responses are progressions to infaunality (moving into the substrate for protection from predators) and mobility (evading predators on or above the substrate, both actively and facultatively). Alternatively, the bulldozer hypothesis (3), a subsidiary of the escalation hypothesis, predicts that epifaunal immobile taxa will decline when there is increased biological disturbance of the sediment by infaunal, actively mobile taxa (bioturbators). Trends involving particular taxa (14) or over short time scales (15) may conform with these predictions, but these hypotheses need to be tested by examining trends in relative diversity and counts of occurrences (fossil collections that include each taxon) among marine metazoans as a whole.

We classified marine invertebrate taxa unassociated with reefs into three ecological categories (diet, life habit, and locomotion) and one preservational category (mineralogical composition (16)). Trilobites were excluded from analyses because their ecological trends are quite inconsistent with escalation, with their dramatic early Paleozoic decline obscuring consistent long-term trends for other groups. Thus, excluding trilobites makes our results more conservative. To avoid problems associated with variation in sampling intensity that plague estimates of global diversity (17), we used proportions within each ecological category instead of raw counts (18).

www.sciencemag.org SCIENCE VOL 312 12 MAY 2006 897
REPORTS

Over the Phanerozoic, there has been a marked shift in the primary composition of marine invertebrate fossils from calcite to aragonite (Fig. 1F). Calcitic taxa are more taphonomically robust than aragonitic taxa (19). We find significant cross-correlations between the ecological proportions and shell mineralogy proportions (table S1). Such associations can exist given two causal scenarios that are not mutually exclusive. First, shifts in the ecological proportions may result from differences in the proportion of aragonitic fossils recovered from one time bin to the next (taphonomy), which in turn may be due to changes in seawater chemistry. Second, escalation may drive shifts in aragonitic taxa, and thus the proportions of aragonitic fossils shift accordingly (macroevolution).

We tested whether a preservational bias was involved by recomputing the ecological cross-correlations after excluding the occurrences from fossil collections that did not preserve aragonitic forms (14% of the total). The remaining collections should be relatively less taphonomically biased. Because other preservational indicators, such as molds or casts, were inconsistently recorded in the database, they were unusable. Two of the six cross-correlations (carnivore versus infaunal genera and bioturbating versus immobile epifaunal genera) that were not significant remained so, and the three correlations involving occurrences ceased to be significant. Although marginally significant (carnivore versus mobile genera: Spearman’s $\rho = 0.398$, $P = 0.011$), this remaining correlation is not found in the corresponding occurrence data and is no longer significant after a Bonferroni correction (in which the alpha level of the null hypothesis was divided by 6, because there are six ecological comparisons). The results are unlikely to be due to a lack of power because we have adequate sample sizes (at least 40 in each case) to detect biologically interesting correlations.

The correlations between ecological and shell mineralogy proportions are much the same even if collections that fail to preserve aragonite, presumably for taphonomic reasons, are excluded from the analysis (table S1). Thus, the data suggest that apparent trends in the frequency of aragonitic forms are not taphonomic but are driven by the coincidental, statistically independent expansion of groups that happen to be aragonitic in composition (heterodont bivalves and neogastropods), which is a different process from escalation.

These results suggest that escalation, if it is the causal driver, does not occur within periods shorter than the 11-million-year time bins. However, a time lag might be expected if, for example, (i) dominance increased and allowed higher rates of speciation over millions of years, or (ii) dominance was depressed but taxa persisted for a long time before going extinct. To check for time lags, cross-correlations were recalculated for several lag periods in either direction (up to ±3 time bins or about 33 million years), and the resultant associations were as weak, or absent. Additional treatments of the data would be unlikely to find strong correlations. For example, analyzing the Paleozoic and post-Paleozoic data separately or increasing the length of the bins would leave so few data points that the correlations would have little power. Furthermore, restricting the data to specific environments, geographic regions, or latitudinal belts, or

![Fig. 1. Proportions of genera (dashed line) and occurrences (solid line) for taxa classified as carnivorous (A), noncarnivorous infaunal (B), noncarnivorous mobile (actively and facultatively) (C), bioturbating (D), immobile epifaunal (E), and aragonitic (F). For statistical independence of groups, proportions of carnivores are given relative to all taxa, but proportions of noncarnivorous groups (B) and (C) are given relative to all noncarnivorous taxa. Bioturbating and immobile epifaunal genera do not exhibit both modes of life habit or diet; therefore, proportions of bioturbators are given relative to all taxa, whereas proportions of immobile epifauna are given relative to all nonbioturbating taxa. Single letters at the bottom of each panel are abbreviations for geological periods. Ma, million years ago.](https://example.com/fig1.png)
using shorter bins, would create large gaps in the time series.

The raw data (Fig. 1) illustrate trends in the relative frequency of ecological groups during the Phanerozoic that seem to agree with the predictions of the two macroevolutionary hypotheses: (i) a proportional increase in carnivores corresponding with increases in noncarnivorous infaunal and mobile ecological strategies and resembling published curves showing drilling frequencies (11), and (ii) a proportional increase in bioturbators corresponding with a decline in immobile epifauna. However, the differencing analyses show that these correspondences are strictly coincidental, in a statistical sense.

Secular trends consistent with each hypothesis are seen even though some carnivorous groups (such as vertebrates, malacostracans, and asteroids) and bulldozing groups (such as vertebrates, malacostracans, and asteroids) do not fossilize well and thus are presumably underrepresented. Occurrences from collections including one or more aragonitic forms are tallied. Dashed lines represent least-square lines of best fit. ∆Logit, change in the logit-transformed proportion.

large-scale databases do not contain counts of occurrences (21). However, if one ecological group is systematically less abundant on a per-species basis, greater sampling will increase the relative taxonomic richness of that group (9, 10). Counts of occurrences, on the other hand, provide an improved proxy for ecological importance because an ecological group with more occurrences is likely to have been more abundant locally and had a greater geographic range and a broader environmental distribution (22).

If taxonomic richness is a direct function of ecological dominance, then the proportions of genera and occurrences should have similar averages, and their changes should be cross-correlated (Fig. 1). We find significant cross-correlations between differentiated proportions (16) of genera and occurrences for the five focal ecological groups ($P$ values $< 0.001$, df = 39, Pearson’s $r = 0.56$ to 0.77, Spearman’s $p = 0.52$ to 0.70); three of these correlations are shown in Fig. 3. Moreover, two-sample $t$ tests reveal no significant differences between average proportions. Despite the variation in total sample size per bin, the close match of the curves indicates that the frequencies of genera would not change substantially if sampling intensity were standardized. This result implies that hierarchical levels are not evolutionarily independent (23). Instead, taxonomic richness is a reliable surrogate for ecological importance, as is traditionally assumed (22).

Our results suggest either that Phanerozoic-scale patterns in the ecological proportions examined here are not driven by direct ecological interactions, or that these processes are obscured by other factors. Instead, the major ecological groups may wax and wane independently.

References and Notes
16. Materials and methods are available as supporting material on Science Online.
Fall in Earth’s Magnetic Field Is Erratic

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Earth’s magnetic field has decayed by about 5% per century since measurements began in 1840. Directional measurements predate those of intensity by more than 250 years, and we combined the model of directions with paleomagnetic intensity measurements to estimate the fall in strength for this earlier period (1590 to 1840 A.D.). We found that magnetic field strength was nearly constant throughout this time, in contrast to the later period. Extrapolating to the core surface states that, given perfect directional information and no more than two dip-poles (places where the magnetic field is vertical, of which the

Jackson et al.’s historical model of the geomagnetic field (1) covers the period 1590 A.D. to the present (Fig. 1). Measurements of direction (declination and inclination) are available throughout this period, although inclination is scarce in the 17th century. No absolute intensity data are available until 1837, when C. F. Gauss devised the first method to measure it; intensity measurements became widespread by 1840. The EarthRef Digital Archive (ERDA) has an internally consistent paleointensity database compiled by Korte et al. (2). It contains 315 measurements on rock samples and archaeological remains from the interval 1590 to 1840 A.D., and we can, in principle, use these to determine field strength during the early period when there were no direct measurements.

The paleointensity data have error estimates on both intensity and age. Dating errors vary from 1 year, when historical records date the specimen precisely, to centuries, when only radiocarbon dates are available. Geographical coverage is poor (Fig. 2), with concentration in Europe and very little representation in the Southern Hemisphere, but temporal coverage is good (Fig. 3).

Intensities have typical errors of 4000 nT, or about 10%. This error is comparable with any change expected during the entire period, so paleointensity measurements provide no usable information on intensity variation at a single site. However, given good directional information from the historical model, each intensity measurement can be converted to an estimate of the dipole moment, or \( g_0^1 \), because a theorem (3)

Earth has only two), a single intensity measurement determines the field uniquely. The poor geographical coverage of intensity is therefore largely irrelevant, provided the global coverage of direction is good. Here we assume that \( g_0^1(t) \) fell linearly from 1590 to 1840 and fix its value at 1840 to be that of the historical field model. This leaves just one parameter, the slope of the line, to be determined from 315 measurements. This large number of data are able to produce a meaningful estimate of a single unknown, the slope, despite the large errors on an individual datum.

We use the iterative maximum likelihood method of Williamson (4), closely related to that described by Press et al. (5), to fit a straight line through data having errors in both magnitude and time. \( g_0^1(t = 1840) \) is constrained by

![Fig. 1. Fall of the geomagnetic coefficient \( g_0^1 \) (in nT) since measurements began in 1590. \( g_0^1 \) is proportional to the Earth’s dipole moment. Intensity measurements became available in 1840; the two slopes before 1840 are (a) the extrapolation back in time based on the average fall since 1840 and (b) paleointensity measurements using the method described in the present study. Shaded area gives the ±1 SD slopes.](image)

![Fig. 2. Geographical distribution of the paleointensity data from 1590 to 1840 A.D. Data are mostly from the Northern Hemisphere, but the Southern Hemisphere is well covered by directional measurements.](image)