thermosphere is 4 to 5 times as cold (*4*). The cooling should cause the upper atmosphere to contract; we may thus expect a substantial decline in thermospheric density, as well as a downward displacement of ionospheric layers (*5*).

The primary quantity directly affected by the changing concentration of greenhouse gases is temperature. The first comprehensive review of temperature trends at heights of about 50 to 100 km (*6*) reveals, after slight updating, the following trends: (i) moderate negative trends of about 2 to 3 K per decade at heights of 50 to 70 km, with the largest magnitude in the tropics; (ii) slightly larger cooling trends at heights of 70 to 80 km in the low and middle latitudes; (iii) essentially zero temperature trends between 80 and 100 km. Modeling studies agree reasonably well with the observed vertical and latitudinal structure of the thermal response (*3*).

Over the past three decades, the global temperature at Earth's surface has increased by 0.2 to 0.4ºC, compared with a 5 to 10ºC decrease in the lower and middle mesosphere. Summer-winter differences of mid-latitude land-surface temperatures are comparable in magnitude to the seasonal and 11-year solar cycle variability of mid-latitude mesospheric temperatures. Thus, the signal-to-noise ratio of the trends is much higher in the mesosphere than at Earth's surface.

No direct information on thermospheric temperature trends is available. However, estimated ion temperatures (*7*) at heights near 350 km reveal a negative trend of about –17 K per decade (*8*). Because ion temperature is strongly coupled to thermospheric temperature, these trends are qualitatively consistent with the expected thermospheric cooling.

Temperature directly affects atmospheric density. At altitudes between about 200 and 800 km, atmospheric drag causes measurable decay of the orbits of satellites and space debris. Routine satellite tracking data have been used to derive long-term changes in thermospheric density. The results (*9*, *10*) indicate that thermospheric density has declined during the past several decades at an overall rate of 2 to 3% per decade; these density trends increase with height (*9*). This behavior is qualitatively consistent with model predictions (*2*). Model simulations also show that, in addition to the effects of greenhouse gas increases, the impact of long-term changes in stratospheric ozone and water vapor on atmospheric density may extend well into the thermosphere (*11*).

Thermal contraction of the upper atmosphere should result in a downward displacement of ionospheric layers (*5*). Laštovička and Bremer (*12*) reviewed long-term trends in the lower ionosphere and found a positive trend in electron density at fixed heights, consistent with downward displacement. The maximum electron density of the E-layer and the F1-layer increased slightly (see the figure), and the height of the electron density maximum of the E-region decreased slightly (*13*), in qualitative agreement with model predictions (*2*). These ionospheric trends accelerated after 1980, providing support for their anthropogenic origin (*14*).

The trends described above form a consistent pattern of global change in the upper atmosphere at heights above 50 km (see arrows in the figure). The upper atmosphere is generally cooling and contracting, and related changes in chemical composition are affecting the ionosphere. The dominant driver of these trends is increasing greenhouse forcing, although there may be contributions from anthropogenic changes of the ozone layer and long-term increase of geomagnetic activity throughout the 20th century. Thus, the anthropogenic emissions of greenhouse gases influence the atmosphere at nearly all altitudes between ground and space, affecting not only life on the surface but also the space-based technological systems on which we increasingly rely.

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PALEOECOLOGY

Life's Complexity Cast in Stone

Wolfgang Kiessling

The fossil record shows that since the end of the Paleozoic era, the structure of marine communities has become more complex.

There is no doubt that the complexity of life has increased through the ages, both in the structure of individual organisms and in the ecological structure of communities (*1*, *2*). But to trace the complexity of living systems, we need objective measurements. Species diversity is often regarded as a rough proxy of complexity in local communities, because the more species coexist in a community, the more ecological interactions between species and complex food webs are to be expected (*3*). However, a comprehensive picture cannot emerge when the diversity information is reduced to single numbers such as species richness or measures of how evenly species are distributed in a community. Communities with the same number of species and identical evenness values may still differ substantially in their ecological complexity.

On page 1289 of this issue, Wagner *et al.* (*4*) explore the shape of relative abundance distributions in ancient marine communities to track the evolution of ecological complexity through the past 540 million years. They separate communities whose abundance distributions simply suggest superior access to resources versus those that succeed in their own smaller niche (see the figure). In simple abundance distributions, the relative abundances of species drop rather steadily, which implies that few factors—such as the preemption of resources by dominant species—structure the community. Complex distributions are essentially those in which the dominant taxa add ecological opportunities, and complex niche partitioning is suggested by similar abundances for many species. The big surprise in their analysis is a major difference between Paleozoic (older than 250 million years) and younger communities. In older assemblages, complex and simple distributions are

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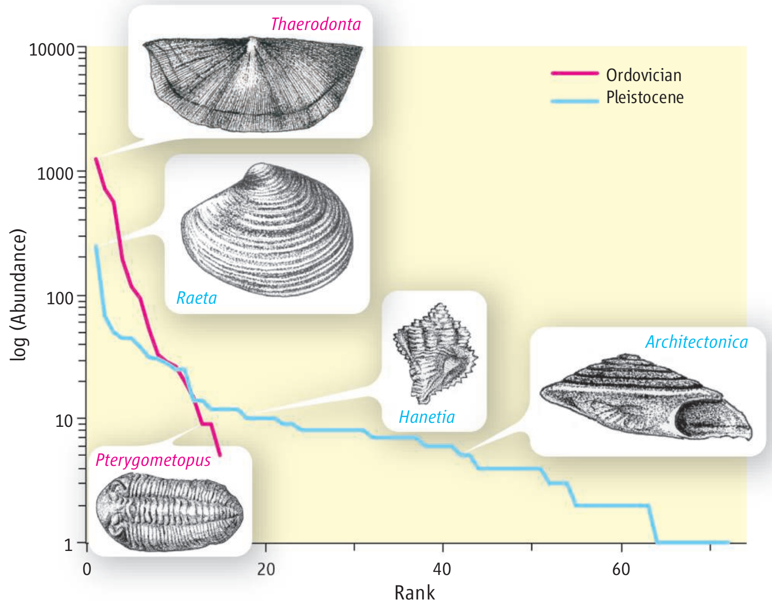
about equally common, but complexly structured assemblages are substantially more common in more recent times.



Gaining complexity. Fossil marine communities of the Paleozoic (542 to 251 million years before the present) differ from younger communities in the partitioning of relative abundances. Although about half of the Paleozoic communities are characterized by simple abundance distributions (red curve, a paleocommunity from the Late Ordovician of Minnesota), Mesozoic and Cenozoic communities predominantly exhibit complex distributions (blue curve, a paleocommunity from the Pleistocene of Ecuador).

With so many paleobiologists looking at local, regional, and global diversity patterns through time, how could this striking pattern have escaped our attention for so long? Previous studies (i) recorded a temporal increase in community diversity but found this to be largely confined to the past 25 million years (*5*–*7*), (ii) argued for a gradual increase (*8*), or (iii) found no distinct trend in particular ecosystems (*9*). I see three explanations for why Wagner *et al.* came out with different results: First, previous analyses usually were designed to find a trend rather than to examine its detailed trajectory. Second, the new study could take advantage of a comprehensive set of fossil communities by mining the Paleobiology Database (*10*), which is arguably the largest database of ancient life. Third, and most important, the previous studies relied on simple diversity metrics such as species richness and evenness, whereas the new analysis uses the shape of abundance distributions of ancient communities and thus goes beyond single numbers. Wagner *et al.* managed to reliably separate abundance distributions, which are usually not as distinctive as depicted in the figure and are notoriously difficult to differentiate by visual inspection or standard statistical tests (*11*).

There is still a chance that the new results are biased. All paleontological studies are plagued by incomplete preservation, and the preservation of anatomical details is usually worse in older rocks. Shells with an unstable aragonitic mineralogy also tend to be much rarer in the Paleozoic than later on (*12*). However, even if preservational bias had affected abundance distributions systematically over time, this should lead to a gradual increase in perceived complexity, rather than the distinct break recorded by Wagner *et al.*

What caused the abrupt change in complexity? The turning point seems to be the most severe mass extinction documented in the fossil record, the double end-Permian mass extinction some 250 million years ago (*13*, *14*). This pair of extinction events, separating the Paleozoic from the Mesozoic, has apparently altered the ecological structure of communities until the present day. But how could end-Permian crisis change the ecological structure of communities so durably?

The most plausible scenario involves preferential extinction of those Paleozoic clades that predominantly lived in ecologically simple communities. Indeed, the Paleozoic seas were dominated by organisms such as brachiopods (lamp shells) and sea lilies, which lived anchored to a surface and exclusively relied on suspended organic material for feeding. These taxa were strongly affected by the end-Permian extinctions and never recovered fully. Other Paleozoic clades, such as trilobites, which were mobile and fed on organic detritus, vanished completely. Clams, snails, and sea urchins rapidly gained dominance in the Mesozoic and proliferate on today's seafloors. The diverse feeding modes of this "modern fauna" and the capability of many species to dig deeply into substrates suggest a broad range of niche exploitation. Complexly structured communities were obviously present in the Paleozoic as well, but they were not more common than the simple communities and only gained dominance after the decline of the Paleozoic fauna.

One is tempted to compare this pattern to what happened on land nearly 200 million years later, when the mammals diversified only after the incumbent dinosaurs became extinct. The ruling taxa in Paleozoic marine ecosystems may have prevented the spread of taxa that were able to construct complex communities, just because they mastered the established communities by niche preemption. Further studies on the ecology of dominant taxa in respective community types are clearly required to test this hypothesis. Additional valuable insights could also be achieved by applying the methods of Wagner *et al.* to ancient terrestrial ecosystems or plankton assemblages. Are there similar patterns, or is the evolution of complexity different in each major habitat?

A second scenario could involve the evolution of predators. Predatory organisms are known to regulate food web complexity and prevent the monopolization of communities by individual species (*15*). Proportional diversities of predators relative to all marine animals suggest a distinct rise at the beginning of the Mesozoic (*16*), which agrees with the idea that increased predation pressure altered the structure of marine communities. Unfortunately, the particularly poor fossil record of predators prevents conclusive statements, but modeling approaches might bring some progress.

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Editor's Summary