the use of laboratory results in estimating flow properties of the lithosphere. □

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Orbital forcing of deep-sea benthic species diversity

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Explanations for the temporal and spatial patterns of species biodiversity focus on stability–time[1–3], disturbance–mosaic (biogenic microhabitat heterogeneity)[4,5] and competition–predation (biotic interactions)[6,7] hypotheses. The stability–time hypothesis holds that high species diversity in the deep sea and in the tropics reflects long-term climatic stability[3]. But the influence of climate change on deep-sea diversity has not been studied and recent evidence suggests that deep-sea environments undergo changes in climatically driven temperature[8] and flux of nutrients[9] and organic-carbon[10] during glacial–interglacial cycles. Here we show that Pliocene (2.85–2.40 Myr) deep-sea North Atlantic benthic ostracod (Crustacea) species diversity is related to solar insolation changes caused by 41,000-yr cycles of Earth's obliquity (tilt). Temporal changes in diversity, as measured by the Shannon–Weiner index, $H(S)$, correlate with independent climate indicators of benthic foraminiferal oxygen-isotope ratios (mainly ice volume[11–13]) and ostracod Mg:Ca ratios (bottom-water temperature[8]). During glacial periods, $H(S) = 0.2–0.6$, whereas during interglacials, $H(S) = 1.2–1.6$, which is three to four times as high. The control of deep-sea benthic diversity by cyclic climate change at timescales of 10^3–10^4 yr does not support the stability–time hypothesis because it shows that the deep sea is a temporally dynamic environment. Diversity oscillations reflect large-scale response of the benthic community to climatically driven changes in either thermohaline circulation, bottom temperature (or temperature-related factors) and food, and a coupling of benthic diversity to surface productivity.

We examined ostracods from 125 10-ml samples from the deep-sea drilling project (DSDP) site 607, located on the western flank of the mid-Atlantic ridge (41° N, 19° W; water depth, 3,427 m), and DSDP site 610 near the Rockall plateau (53° N, 19° W; water depth, 2,417 m). Site 607 is located in the path of and is sensitive to deep water forming at high latitudes of the Nordic and Labrador Seas[15]. The study covers the period 2.85–2.40 Myr, a Pliocene interval when continental ice sheets began to wax and wane at the 41,000-year obliquity period of orbital insolation[15]. Well documented climate cycles observed globally in ice volume, sea surface temperature and ocean chemistry signify a linear response of Earth's climate to solar insolation forcing[11–16], and provide an ideal series of natural experiments to test models that call for climatic influence on diversity.

Ostracods are the only metazoan taxon regularly fossilized in deep-sea sediments that allow quantitative analysis of faunal patterns[17]. Moreover, deep-sea ostracod species have distinct habitat preferences[18], making the ostracod assemblage a subset of the deep-sea benthic community containing representative 'functional' groups[19]. Ostracods occur in variable numbers[20,21], averaging 60 specimens per sample (in the range 20–120). The number of species, S, varied from 2 to 15, but this is an underestimate because *Krithe* species were lumped (juveniles are difficult to differentiate; there were usually 2–5 species of *Krithe* per sample). We used the Shannon–Wiener function $H(S) = \Sigma_1 Sp_i \ln(p_i)$ where $H(S)$ is diversity, and p_i is the proportion of species i, which is commonly used to measure diversity[22] and is not as sensitive to abundance[1].

$H(S)$ is plotted against two measures of climate and oceanographic change obtained from site 607 for eleven obliquity cycles (Fig. 1). Oxygen isotope ratios of benthic foraminifers reflect mainly changes in global ice volume (about two-thirds of the total $\delta^{18}O$ signal) and bottom-water temperature changes (about one-third of the signal). Late Pliocene, 41,000-yr, glacial–interglacial $\delta^{18}O$ fluctuations are lower in amplitude than Late Quaternary 100,000-yr cycles[13,23]. Changes in Mg:Ca ratios in *Krithe* signify mainly bottom-water temperature (BWT) change due to variations in the relative amount of cold Antarctic deep water (AABW) and warmer North Atlantic deep water (NADW) over the site. Glacial–interglacial changes in Mg:Ca averaged about 2.3 mmol mol^{-1} for the 11 cycles, which equates to an average temperature change of 2.3 °C. Glacial bottom-water temperatures were ~1.0–1.5 °C; those of interglacials were ~3–4 °C (ref. 8).

Figure 1 shows a clear relationship between climate change and species diversity. Low diversity generally corresponds to isotopically heavy $\delta^{18}O$ values (large ice volume) and glacial climates; high diversity corresponds to light $\delta^{18}O$ (smaller ice volume) and interglacial climates. This relationship is expressed graphically in Fig. 2a ($r = -0.722$). All 11 of the isotopically defined glacial–interglacial cycles are expressed in the $H(S)$ measure, and only where there are missing isotope values (near 2.54, 2.62 and 2.65 Myr) are there slight offsets between the two curves. Even more striking is that the amplitude of the $H(S)$ measure is greatest during the strongest cycles; $H(S)$ drops the most during the strongest glacial events (for example, those at 2.70, 2.50, 2.46 and 2.42 Myr). These last three glacial events, also characterized by a pronounced flux of ice-rafted detritus to this site, are referred to as isotopic stages 100, 98 and 96, and can be identified in many oceanic proxy records[13]. To investigate further the leads and lags of diversity with environmental indicators, cross-spectral analysis[14] and a new timescale[24] show that $H(S)$ maxima lag behind the maxima in Mg:Ca ratios (warmest bottom-water temperatures) by 1.6 ± 1.5 kyr and lead ahead of the minima in $\delta^{18}O$ (maximum interglacial conditions) by 2.8 ± 1.7 kyr. The correlation between $H(S)$ and Mg:Ca is shown in Fig. 2b ($r = 0.53$). Benthic species diversity is highest just before the minimum ice volume and least just before the maximum ice volume. Figure 2c shows no correlation between abundance of ostracods and oxygen isotope values, suggesting that climatically induced environmental changes do not appear to control abundance. Given the importance of broad spatial and temporal scales in all studies of biodiversity, we investigated whether the patterns observed at site 607 occur in correlative Pliocene deep-sea sediments from other North Atlantic cores or during younger climatic cycles in the same region. Data from the same 2.85–2.50-Myr interval at DSDP site 610 near the Rockall

plateau also show oscillations in $H(S)$ values of 0.2–0.6 during glacials and 1.3–1.6 during interglacials (Fig. 3a); thus, similar diversity changes occurred in the eastern North Atlantic without any obvious relation between $H(S)$ and abundance (Fig. 3b). In Chain core 82–24 near site 607, ostracode diversity over the past 150,000 years (including two glacial cycles) shows high diversity in interglacial periods and glacial periods that are depauperate.

It is important to exclude other factors that may cause apparent secular diversity changes. Carbonate dissolution can selectively affect shells of surface-dwelling planktic foraminifers after they settle to the bottom, especially during Late Quaternary glacial periods when the lysocline in the Atlantic shoaled several hundred metres from its current 4,000 m depth. However, dissolution is not considered to be the cause of the ostracod diversity patterns for several reasons. Deep-sea ostracods are adapted to deep-sea environments, and ecological and zoogeographical factors, not post-mortem alteration, explain their modern and fossil deep-sea distribution[17,18,20,21,25]. Ostracods secrete a carapace formed by an interlocking calcitic–chitinous lattice, with a thin outer organic epicuticle that helps protect the shell from dissolution; the carapace is thicker and less porous than shells of planktic foraminifers, which are adapted to ocean surface layers. Moreover, Pliocene glacials were only half the amplitude of Late Quaternary glacials, so it is doubtful whether lysocline shoaling would impact ostracods at 3,400 m and 2,400 m at sites 607 and 610. Nor would we expect to see similar diversity patterns in cores from both western and eastern North Atlantic basins, if bottom-water changes were selectively influencing species preservation, especially as site 610 is too shallow and isolated from the influence of potentially corrosive AABW. Other evidence argues against dissolution: occurrence in all samples of *Krithe*

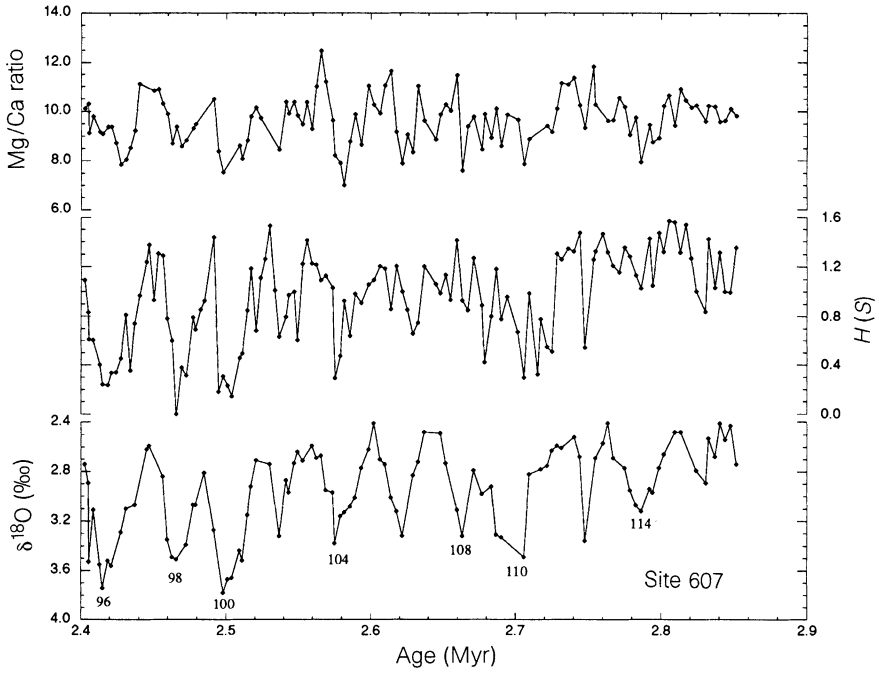

Figure 1 Deep-sea ostracod species diversity at DSDP site 607 measured by the Shannon-Wiener information function $H(S)$. $H(S)$ against benthic foraminiferal $^{18}O/^{16}O$ ratios[12,13] (mainly global ice volume); heavier-isotope values reflect high ice volume during glacial periods; lighter-isotope values signify interglacial warm periods with low ice volume. Mg:Ca ratios (from ref. 9) are indicative of bottom-water temperatures: lower ratios indicate that temperatures were less than about 1 to 2 °C; higher ratios signify warmer temperatures of ~3–4 °C. The age model for site 607 (ref. 12) gives a sampling interval of ~3,500–4,000 yr. Selected oxygen isotope stages are indicated.

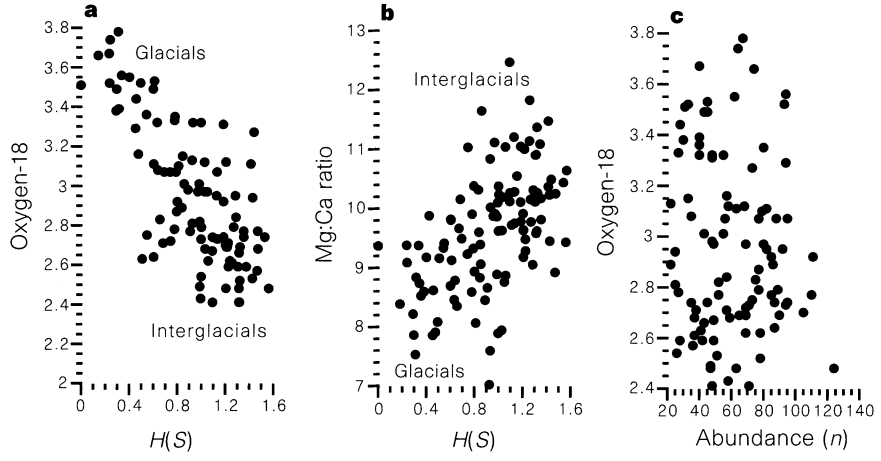

Figure 2 a, Relation between $H(S)$ and benthic foraminiferal isotope values ($r = -0.72$); **b**, relation between $H(S)$ and Mg:Ca ratios ($r = 0.53$); **c**, relation between the abundance n and oxygen isotope values.

juveniles (which have high Mg:Ca ratios and are thus more susceptible to dissolution), absence of thick-shelled, dissolution-resistant genera (*Henryhowella*) in glacial intervals, 'asymmetry' of faunal assemblages during preglacial and deglacial phases of each cycle[26], and lack of correlation between either valve fragmentation or species proportions and foraminifer $\delta^{13}C$, an indicator of AABW.

Whereas seasonal and geographical changes in the distribution of solar insolation caused by variations in the Earth's tilt drive deep-sea benthic diversity, the translation of orbitally induced changes to the deep-sea ecosystem must involve complex community interactions that occur during each cycle. These may involve the creation of new niches and/or niche partitioning which reflect community restructuring in response to environmental change. For instance, a bottom-water temperature change of 2–3 °C is small relative to those occurring in mid–high latitude, shallow marine environments during climatic cycles, but it is nonetheless large compared to short-term deep-sea temperature changes. Temperature itself may be a direct factor responsible for diversity changes, but as $H(S)$ lags behind BWT by only ~1,500 yr, BWT change might catalyse a series of biotic interactions that take 1,500 yr to equilibrate.

A second environmental change that could have an impact on diversity involves nutrients (for example, phosphorus and nitrogen). Modern NADW is relatively low in nutrients; AABW is high in nutrients. Cadmium/calcium ratios in benthic foraminifera (proxy for phosphorus) and $\delta^{13}C$ oscillations have been used to trace changes in bottom-water circulation and infer nutrient changes[9,13]. At site 607, the $\delta^{13}C$ record shows that Pliocene glacial periods of low diversity correspond to inferred periods of high nutrient concentrations and vice versa[13]. Thus inferred nutrient content of bottom waters is inversely correlated with diversity, and high nutrient content does not lead to higher diversity.

A third, more plausible explanation of diversity involves changing food resources stemming from surface-water productivity changes. Climatically induced surface productivity changes are coupled to benthic organisms[27] and occur during the last deglaciation in benthic foraminiferal assemblages[10]. Dinoflagellate changes in late Pliocene sediments at site 607 record major changes in surface water productivity[27], also indicated by planktic foraminifers and discoasters cycles[28], which would lead to decreased food resources for benthic organisms like ostracodes. Thus, long-term diversity changes in the deep-sea benthos are probably reflecting changing total abundance and/or temporal variability in food resources[5,10], and their effect on the community, a factor that also explains large-scale spatial diversity patterns[29]. Decreased or more variable food supply during glaciations may increase stress in the deep-sea community, increasing competition for limited resources and possibly also decreasing habitat (sediment?) heterogeneity on small spatial scales.

Where then do those taxa that inhabit the deep North Atlantic during interglacials live during glacial periods? Faunal evidence suggests that during the last glacial some deep-sea ostracods (*Henryhowella*, *Bradleya*, some *Krithe*) inhabited mid-depth (1,000–2,000 m) bathyal environments in the Arctic Ocean[30] and off the Bahama islands. Bathyal regions may provide the resource requirements and/or physical chemical conditions necessary to survive and may therefore act as an ocean-margin refuge from which species can later return to deep-sea abyssal environments following deglaciation. An analogous situation exists when shallow marine organisms show poleward zoogeographic range expansion of thermophilic species during interglaciations and equatorward expansion of cryophilic species during glaciations.

The correlation of deep-sea benthic species diversity with orbitally induced cyclic changes challenges the stability–time hypothesis[3], which holds that patterns of high species diversity in the deep sea result from long-term environmental stability that allows new species to evolve over time. Deep-sea environments are dynamic in temperature and food over timescales of 10^3–10^5 yr; our results show that biodiversity is also inherently unstable. Thus, assumptions of constant deep-sea resources do not hold over timescales of 10^3–10^5 yr. Likewise, temporal patterns of diversity do not appear to be random, as are some diversity patterns over small spatial scales (centimetres to metres)[5], but instead are linked to external, abiotic solar insolation changes. Our data also underscore the importance of historical factors in understanding biodiversity over long timescales and on regional and ocean basin scales, and suggest that predicting the impact of anthropogenically forced climate change on diversity will remain difficult until we gain a better understanding of how climate has affected biodiversity in the past. □

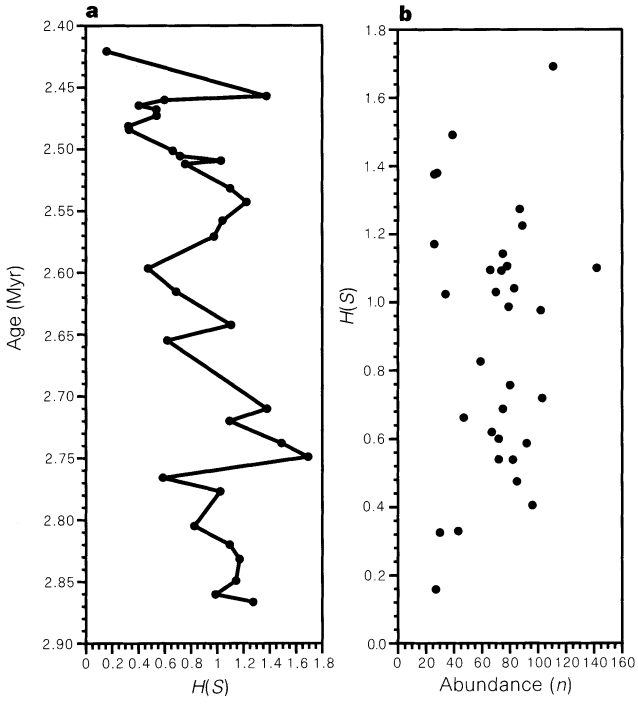

Figure 3 a, Deep-sea ostracod species diversity at DSDP site 610. **b**, Relation between ostracod abundance and diversity at site 610.

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Evolutionary origin of insect wings from ancestral gills

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Two hypotheses have been proposed for the origin of insect wings. One holds that wings evolved by modification of limb branches that were already present in multibranched ancestral appendages and probably functioned as gills[1–5]. The second proposes that wings arose as novel outgrowths of the body wall, not directly related to any pre-existing limbs[6]. If wings derive from dorsal structures of multibranched appendages, we expect that some of their distinctive features will have been built on genetic functions that were already present in the structural progenitors of insect wings, and in homologous structures of other arthropod limbs. We have isolated crustacean homologues of two genes that have wing-specific functions in insects, *pdm* (*nubbin*) and *apterous*. Their expression patterns support the hypothesis that insect wings evolved from gill-like appendages that were already present in the aquatic ancestors of both crustaceans and insects.

Developmental studies have shown that wings and legs originate in a common primordium in early insect embryos[7] and that they share a common regulatory mechanism for patterning along the antero–posterior (AP) axis[8], based on the contiguous domain of *engrailed* (*en*) expression at the posterior of each segment. Crustaceans appear to be the closest living relatives of insects that retain a primitively multibranched structure in their limbs[9,10], and these limbs show comparable expression of *engrailed*, in a contiguous domain that runs along the posterior of each limb branch (N. Patel and M.A., manuscript in preparation; Fig. 1). Thus, the embryonic origin and relative organization of insect legs and wings appear comparable to those of ventral and dorsal branches of crustacean limbs. Although AP patterning appears to be similar in legs and wings, several genes, including *vestigial*, *scalloped*, *wingless*, *pdm* and *apterous*, have been identified with distinctive roles in establishing the wing primordiun and in patterning the wing along the dorso–ventral (DV) axis[11–17] (Fig. 1).

To determine whether genes with wing-specific functions in insects might play a specific role in patterning dorsal elements of multibranched crustacean appendages, we isolated homologues of the *Drosophila* genes *pdm* and *apterous* (*ap*) from the branchiopod crustacean *Artemia franciscana* (named *Af-pdm* and *Af-ap*, respectively). Amino-acid sequence comparison reveals a high degree of conservation within regions of known sequence motifs and indicates that these are orthologues of the *Drosophila pdm* and *apterous* genes (Fig. 2). In *Drosophila* there are two closely related *pdm* genes, *pdm1* and *pdm2*, with largely overlapping expression patterns and functions[18–20]. We have recovered a single *pdm* gene in *Artemia* (7/7 sequenced clones) with sequence that is approximately equidistant from *pdm1* and *pdm2* (Fig. 2b). In view of the close functional relationship of the two *Drosophila pdm* genes[19,20], we suspect that *Af-pdm* may be functionally equivalent to both.

One of the *Drosophila pdm* genes, *pdm1* (*nubbin*), is expressed throughout the prospective wing and has been implicated in the early specification of the wing primordium[13,14]. It is also expressed more weakly in a set of rings in the primordia of legs, where its function is unknown[13]. To compare the expression of *pdm* in *Artemia* with that seen in *Drosophila*, we have raised antibodies against Af-PDM. Af-PDM is expressed in a dynamic pattern in the developing thoracic limbs (Fig. 3c–e). At early stages, the gene is expressed over most of the developing limb bud. However, as soon as the appendage shows the first signs of regionalization, this expression becomes restricted to a dorsal lobe that will give rise to the distal epipodite. During subsequent stages, expression is maintained specifically in the distal epipodite.

In insects, *apterous* is expressed specifically on the dorsal surface of developing wings[21,22] and appears to be the primary determinant for DV patterning of wings[11,16,17]. It is also expressed in a ring in the fourth tarsal segment of *Drosophila* legs, although this expression appears to have no function[21]. Using antibodies raised against Af-AP, we find that this protein is expressed in a pattern similar to that of Af-PDM, with expression in the early limb primordium becoming restricted to the distal epipodite at the time when this structure first becomes morphologically distinct (Fig. 3f–h). Expression is not restricted to the dorsal aspect of this branch; this is not surprising as this lobe shows no sign of dorso–ventral differentiation in its morphology. In addition, at late stages Af-AP expression appears in the limb muscles.

It is of interest that Af-PDM and Af-AP become specifically expressed in the cells of the distal epipodite before these acquire their characteristic differentiated morphology (large nuclei, large intercellular spaces). These expression patterns contrast markedly with that of *Distal-less* (*Dll*), which is expressed in all outgrowing appendages (including insect legs and wings, and all crustacean limb branches[23,24]; Fig. 3b).

One of our antibody preparations, raised against Af-PDM, fortuitously recognizes a conserved epitope in PDM proteins of

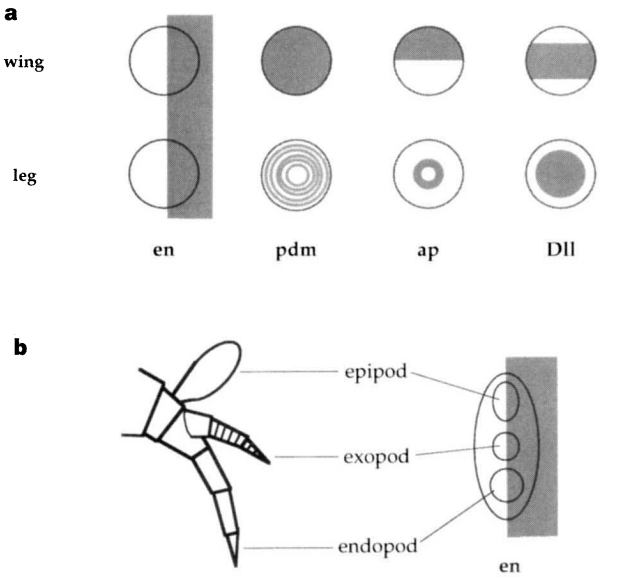

Figure 1 a, Representation of insect legs and wings, indicating the expression of *engrailed* (*en*), *nubbin/pdm*, *apterous* (*ap*), and *Distal-less* (*Dll*) (based on refs 13, 26). The expression of *ap* in the leg appears to have no function[21]. Orientation: dorsal is up, anterior is to the left, and the proximo-distal axis runs perpendicular to the page, with distal regions represented at the centre and proximal regions (attachment to the body wall) at the periphery of each disc. **b**, The multibranched structure of a diagrammatic crustacean limb, indicating its anteroposterior organization relative to the expression of *engrailed* (N. Patel and M.A., manuscript in preparation). The drawing showing *engrailed* expression is oriented as in **a**.