

Export of organic carbon from peat soils

Warmer conditions may be to blame for the exodus of peatland carbon to the oceans.

We have observed a 65% increase in the dissolved organic carbon (DOC) concentration in freshwater draining from upland catchments in the United Kingdom over the past 12 years. Here we show that rising temperatures may drive this process by stimulating the export of DOC from peatlands. Our results indicate that the flux of aged, riverine DOC of terrestrial origin, now recognized as a significant supplier of DOC to oceans¹, may increase substantially as a result of global warming.

DOC concentrations have increased significantly ($P < 0.05$) at 20 of 22 sites in the UK Acid Waters Monitoring Network², according to the Seasonal Kendall trend analysis (Fig. 1a). These sites span a wide range of acid-deposition levels, soils, topographies, land uses and geographical locations. Annual increases, averaging 5.4%, are proportional to mean DOC concentration ($R^2 = 0.81$, $P < 0.001$). As freshwater DOC concentrations are linked to storage of carbon in catchment soil³, this indicates that increases are driven by regionally consistent processes within this carbon store, and that they are greatest at sites with large stores of soil carbon, such as peatlands (Fig. 2).

Although an inverse relationship has been proposed between mineral acidity and the generation of DOC⁴, we observed similar proportional increases in DOC at remote, unacidified sites, as well as at those

recovering from anthropogenic acidification. Changes in land use or river discharge do not account for the observed increases. However, the Central England Temperature Record⁵ shows that mean temperatures were 0.66 °C higher in the 1990s than in the three preceding decades, and this factor could have influenced all sites.

The enzyme phenol oxidase has been proposed to regulate carbon storage in peatlands⁶. We therefore studied the thermal responses of peatland phenol oxidase in relation to the export of DOC. We subjected peat soil to a thermal gradient of 2–20 °C. Phenol oxidase activity was greater at higher temperatures, although this enzyme is known to be highly constrained in these waterlogged soils. An increase of 10 °C led to a 36% increase in activity ($Q_{10} = 1.36$). This was accompanied by an equivalent increase in DOC release ($Q_{10} = 1.33$) and an even greater increase in release of phenolic compounds ($Q_{10} = 1.72$) from the soil matrix. This selective enrichment with phenolic compounds (Fig. 1b) is noteworthy because of the inhibitory character of these compounds⁷. Under warmer conditions, selective enrichment should impair the metabolism of the remaining DOC⁸, allowing even more DOC to reach the oceans.

Pre-aged terrestrial sources of carbon are important contributors to the oceanic carbon budget¹. Peat-accumulating wetlands have created a significant terrestrial store⁹ of such highly aged organic matter, despite exporting more organic carbon per unit area than any other significant biogeographical land type in the world¹⁰. We have shown that a key terrestrial carbon store could currently be being relocated to the oceans. The rate of movement is likely to increase further if global temperatures increase. Investigation of the fate of that material in the recipient ecosystem will be important.

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Resource availability

Ancient homes for hard-up hermit crabs

Mollusc shells are a vital but sometimes scarce resource for hermit crabs, protecting them from mechanical damage and desiccation, but they require continual replacement as the crab grows. I have discovered that *Coenobita rugosus*, a large, tropical, semi-terrestrial hermit crab, will resort to using fossil shells when no other suitable casing is available.



Figure 2 Peatland bog: northern peatlands remove carbon dioxide from the atmosphere faster than it is released, so they now contain 20–30% of the world's soil carbon stock. But this may be changing in response to warmer conditions.

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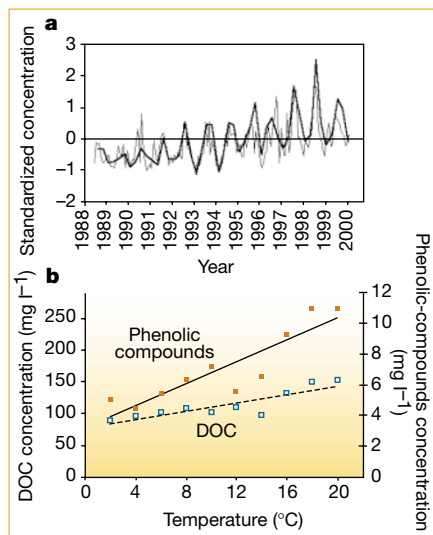


Figure 1 Changing concentrations of dissolved organic carbon (DOC). **a**, Time series of median standardized DOC concentrations determined from quarterly data for 11 lakes (thick line) and monthly data for 11 streams (thin line) in the UK Acid Waters Monitoring Network (standardized concentrations for each site have a mean of zero and a standard deviation of one). **b**, Laboratory observations of increased concentrations of DOC and phenolic compounds in peat soil in response to rising temperature.

These unlikely mobile homes fall out of coastal limestone as it is eroded by the sea in southwestern Madagascar, placing the occupants alongside *Homo sapiens* as resourceful exploiters of prehistoric animal remains.

Hermit crabs procure their protective casing, typically a gastropod mollusc shell, from other hermit crabs^{1,2}, rather than directly from living molluscs³. Reducing predation is thought to be the most important factor in determining shell selection by tropical hermit crabs⁴, but adults of intertidal species living above the high-water

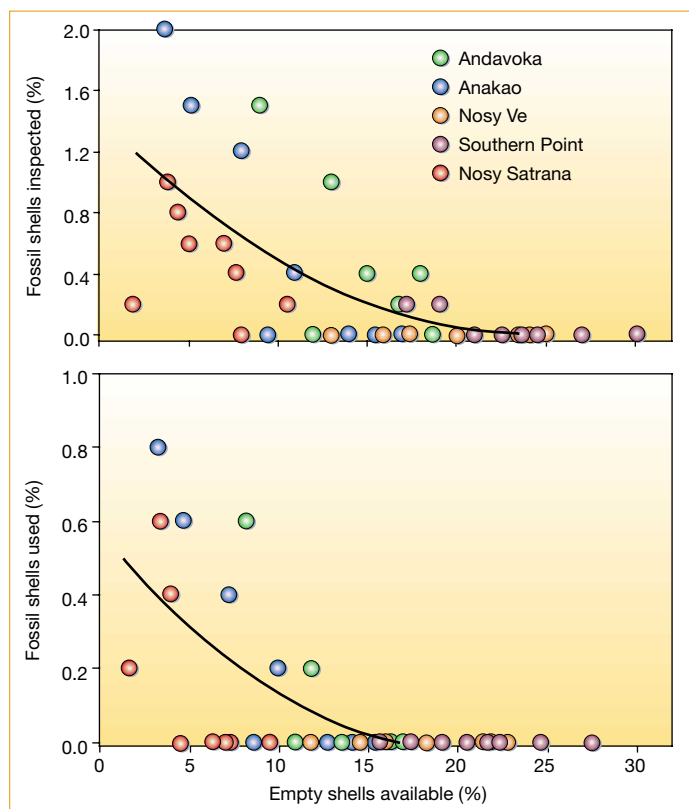
mark also pick them for their anti-desiccation properties⁵. Hermit crabs often suffer from a shortage of shells, however, and so are forced to make do with less suitable shells or even with artificial materials⁶. *Coenobita rugosus* is one species that uses fossil shells as a substitute (Fig. 1) — a much scarcer resource that drops out of limestone rocks as they are eroded.

I found that the number of fossil shells inspected and used by these crabs is proportional to the lack of availability of local shells (referred to as the degree of resource restriction and measured as the proportion of suitable empty shells at three of five sites; Fig. 2). The fossil shells used were from the short-spined, shore-dwelling marine snails *Nassarius*, *Nerita* and *Turbo*. Fossil shells were not used at any locality where suitable empty shells comprised over 13% of all shells; however, when the proportion of these fell below 9%, one or more of 500 crabs examined were found to use fossil shells. One other local hermit-crab species (of seven species investigated), *Calcinus latens*, was seen to use fossil shells (*Nerita*), but only on one occasion. The relationship between the percentage of fossil shells inspected and the restricted availability of non-fossil shells (Fig. 2, top) was similar to that for actual usage of fossil shells and restricted non-fossil-shell availability (Fig. 2, bottom).

Explanations for this behaviour are complex, as the crab is unlikely to appreciate the nature of a shell until it has inspected it. Fossil shells are generally found in close association with the limestone rock of their origin, rather than in locations at which hermit crabs might find many empty shells, such as at the strand line. The relationship between fossil-shell inspection and shell restriction suggests that crabs in shell-restricted areas search for local shells first.

Shelter for hermit crabs could potentially be provided by discarded shells, shells

Figure 2 Percentage of fossil shells inspected and used by the hermit crab *Coenobita rugosus* as shelter in relation to the availability of empty shells at five different sites in southwestern Madagascar. Each point corresponds to 500 inspections by hermit crabs (top) or to usage by 500 crabs (bottom). Fitted curves are second-order regressions with r^2 values of 0.47 and 0.46, respectively; $P < 0.01$ (ANOVA) in both cases. Eight counts of 500 gastropod shells were made in each of 5 supralittoral study sites (listed in upper right). Crabs inhabiting fossil shells were identified (as species), as was the fossil (as genus). Percentages of empty mollusc shells, fossil shells and used shells that were mechanically damaged or blocked were all recorded and are not represented in the graphs. Further details are available from the author.



already occupied by another hermit crab or by a living mollusc, and by buried or fossil shells. Of the fossil shells I examined, 93–100% had severe structural hindrances that would block any potential occupant. But the rarity of exploitation by hermit crabs of fossil shells cannot simply be due to the scarcity of usable fossil shells, because otherwise the extent of usage would be three times higher (average frequency of non-fossil shells is 99% of usable shells and average usage is 99.7%; average frequency of fossil shells is 1% of usable shells and average usage is 0.3%). Despite this, fossil shells are probably the third-largest shell supplier of all the potential shell sources as, in common with observations made elsewhere, no shell excavation^{6,7} or requisition from living molluscs³ was seen.

In southwestern Madagascar, as in many parts of the world, particularly East Africa⁸, collecting of shells on the shore is important in artisan fisheries⁹. Living molluscs are generally removed from their shells at the high-tide mark, where piles of shells, which are mostly too large to be of use to hermit crabs, are deposited. However, as shorelines become more intensively exploited, the mean shell size of molluscs collected in this way is getting smaller^{8,9}. These piles of discarded shells should therefore eventually help to release hermit crabs from the prevailing shell restriction, and render the use of fossil shells unnecessary.

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correction

Early visual experience and face processing

R. Le Grand, C. J. Mondloch, D. Maurer, H. P. Brent *Nature* **410**, 890 (2001)

There is a mistake in Table 1 and its legend, as the result of a coding error. The final two sentences of the legend should read: “For adults, inversion reduced the accuracy of the configural set significantly more than that of the featural set (significant interaction between orientation and stimulus set ($F_{1,25} = 13.13$, $P < 0.01$), followed by analyses of simple effects ($F_{1,27} = 62.57$, $P < 0.01$)). Patients were less accurate than controls (matched for age, gender, race and handedness) only for the upright configural set (significant interaction between group, orientation and stimulus set ($F_{1,26} = 21.92$, $P < 0.01$)).” Values in the ‘featural, upright’ column should be 80, 89 and 85 for adults, controls and patients, respectively. This error does not affect our conclusions.



Figure 1 Houses for hermit crabs: sometimes very old homes are better than newer ones, particularly in situations where non-fossil shells are in short supply.