

revealed that the α -subunit's carboxy-terminal tail is essential for receptor binding⁵. For instance, single mutations of six amino acids in this tail resulted in a 90% loss of binding activity. But it was not obvious how these amino acids contributed to binding. The structure now reveals that the α -subunit plays a neat trick: it rotates its tail by 180° so that these amino acids become fully conformationally constrained by making extensive contacts with the receptor at the hormone-receptor interface.

The structure of the FSH-FSHR_{HB} complex also provides the first structural evidence that GPCRs form dimers, which might be necessary for their full activity. In the case of FSHR, the dimer contacts are not made through the hormone. Rather, two receptors interact directly with each other, with each receptor binding one molecule of FSH. Yet the structure of the dimer presents a conundrum as well. The transmembrane regions of the two receptors in a dimer are too far apart to associate, so what drives dimer formation? One possibility is that other molecules link receptors through cytoplasmic interactions.

Of course, the next goal is to determine the structure of the full-length receptor. So far, the full-length structure of only one GPCR, rhodopsin, has been determined¹¹, and this molecule is composed solely of transmembrane domains. The role of carbohydrate in activating FSHR also needs to be defined — although receptor binding does not require carbohydrate, full activity following binding does. And it will be essential to determine the structure of FSHR without its ligand, to find out whether rearrangements occur in the receptor upon hormone binding.

Although it is in the nature of science that each advance raises new questions, the new structure² does further our understanding of the key-lock mechanism by which glycoprotein hormones work. This advance defines the specific amino acids that make contact between hormone and receptor, as well as those that repulse hormone binding and thereby provide specificity (Fig. 1). Moreover, the orientation of FSH with respect to the main extracellular regions of the receptor is now resolved, and the structure allows a guess as to how the FSH-FSHR_{HB} complex is oriented relative to the extracellular loops of the receptor's transmembrane domains — goals of researchers in the field for at least two decades. ■

James A. Dias is at the Wadsworth Center, New York State Department of Health, and in the Department of Biomedical Sciences, State University of New York at Albany, David Axelrod Institute, 120 New Scotland Avenue, Albany, New York 12208, USA. e-mail: james.dias@wadsworth.org

1. Wright, V. C., Schieve, L. A., Reynolds, M. A., Jeng, G. & Kissin, D. *MMWR Surveill. Summ.* **53**, 1–20 (2004).
2. Fan, Q. R. & Hendrickson, W. A. *Nature* **433**, 269–277 (2005).
3. Kobe, B. & Kajava, A. V. *Curr. Opin. Struct. Biol.* **11**, 725–732 (2001).

4. Hopkins, A. L. & Groom, C. R. *Nature Rev. Drug Discov.* **1**, 727–730 (2002).
5. Dias, J. A. *et al.* in *Vitamins and Hormones* (ed. Litwack, G.) 249–322 (Academic, New York, 2002).
6. Smits, G. *et al.* *N. Engl. J. Med.* **349**, 760–766 (2003).
7. Vasseur, C. *et al.* *N. Engl. J. Med.* **349**, 753–759 (2003).

8. Laphorn, A. J. *et al.* *Nature* **369**, 455–461 (1994).
9. Wu, H., Lustbader, J. W., Liu, Y., Canfield, R. E. & Hendrickson, W. A. *Structure* **2**, 545–558 (1994).
10. Fox, K. M., Dias, J. A. & Van Roey, P. *Mol. Endocrinol.* **15**, 378–389 (2001).
11. Palczewski, K. *et al.* *Science* **289**, 739–745 (2000).

Climatology

Will soil amplify climate change?

David Powlson

It had been thought by some that rising atmospheric temperatures would have no effect on the rate at which carbon is released from the soil. A study that revisits the data behind this theory now finds otherwise.

Knorr *et al.*¹ in this issue (page 298) claim that rising temperatures brought about by climate change will cause microorganisms in the world's soils to decompose organic matter more rapidly, releasing extra carbon dioxide (CO₂) and accelerating climate change. This may seem unsurprising — a basic property of most biological processes is that they proceed faster with rising temperature, provided that other factors do not become limiting. However, this basic biological tenet was challenged in 2000 by Giardina and Ryan², who suggested that organic carbon decomposition in soil is not sensitive to temperature. If correct, that would mean that our understanding of the process is in serious error and predictions from current models of soil carbon turnover cannot be trusted. But Knorr *et al.* have re-examined the data used in Giardina and Ryan's work, and come to the opposite conclusion. The new analysis resolves the seeming paradox and suggests that the positive feedback from soil to climate might be even greater than is currently thought.

The world's soils hold about 1,500 × 10⁹ tonnes (1,500 Gt) of organic carbon; the atmosphere contains about half this amount as CO₂ (720 Gt), and there is a further 600 Gt in vegetation³. Thus, relatively small changes in the flow of carbon into or out of soils could be significant on a global scale, and various studies have attempted to quantify these flows using models of soil carbon turnover^{4–6}.

Increasing CO₂ in the atmosphere can enhance plant growth⁷ through 'CO₂ fertilization', thus removing some of the excess CO₂. For long-lived plants such as trees, part of this carbon is sequestered for decades or centuries. With all plants, some organic carbon is transferred by roots and litter-fall into soil organic matter, some fractions of which are so strongly stabilized that they turn over on timescales of centuries or even millennia⁸. This carbon sequestration would tend to slow climate change⁹, so management practices such as re-forestation are considered as mitigation measures under the

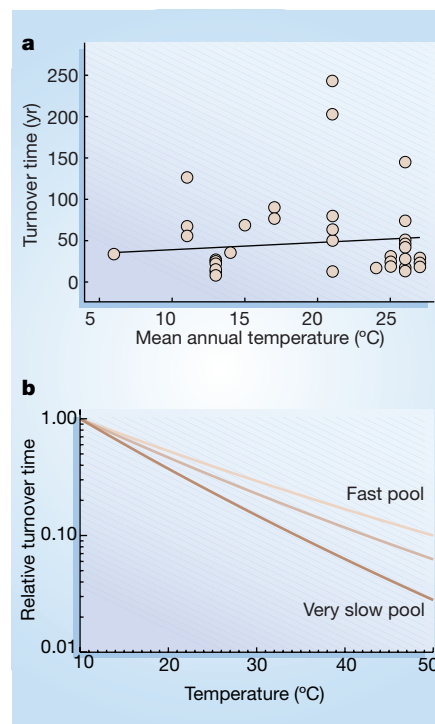


Figure 1 One question but two answers. Is the rate of decomposition of organic carbon in soil influenced by temperature? a, Giardina and Ryan² used a model with a single carbon pool, and calculated soil organic carbon turnover times that were independent of temperature. b, Knorr *et al.*¹ used a model containing three carbon pools (fast, intermediate and very slow). Turnover time for each pool at different temperatures is shown relative to that at 10 °C. The turnover times all decrease as temperature increases; that is, decomposition speeds up as temperature rises.

Kyoto Protocol on climate change. However, current soil models predict that, in the longer term, rising temperatures will speed up the decomposition of organic carbon in soil, releasing CO₂ into the atmosphere in excess of any carbon sequestered in the soil, and adding to climate change.

Giardina and Ryan² challenged this view with an analysis of published data from 82 experiments across five continents. They

used field measurements and laboratory incubations to calculate the turnover time of soil organic carbon. Turnover time is the inverse of the first-order rate constant for the decomposition process. They calculated that turnover times were almost independent of mean annual temperature over the range 5–35 °C (Fig. 1a).

Crucially, their analysis used the simplifying assumption that all soil organic carbon behaves in the same way and can be regarded as a single pool. Most current models, however, divide soil organic carbon into at least three pools that differ in their turnover time, and these models are fairly successful in simulating long-term changes in the organic carbon in soil¹⁰. The dangers of treating soil organic carbon as a single pool were highlighted by Davidson *et al.*¹¹, who showed that the activity of small, very active pools can mask the effects of a large, slow pool, especially in short-term experiments.

Knorr *et al.*¹ have now re-analysed Giardina and Ryan's results using a soil model with more than one carbon pool. To create their model, they used published data in which soil from a tropical rainforest in Brazil was incubated for 24 weeks at temperatures between 15 and 45 °C, and the CO₂ release was measured. They then tested how well the results were predicted by simple models of decomposition using different numbers of carbon pools, each with a temperature-sensitive rate constant. To explain the results, they found it necessary to have two active pools (one with a much faster turnover time than the other), and a very slow pool that was effectively inert during the 24 weeks of the experiment. The very slow pool was large, comprising about 95% of total soil organic carbon.

By applying this model to the incubation experiments considered by Giardina and Ryan², Knorr *et al.* demonstrate a fascinating paradox that is particularly marked if a single-pool model is assumed: because of the dominance of the large, very slow pool, short-term incubations of one to two years can seem to show no sensitivity of decomposition to temperature, even when each pool does in fact have a built-in temperature dependence. This is because, as the temperature rises, fast pools turn over even faster and their effect on the overall result is very short-lived.

By applying their model to other data sets, Knorr *et al.* reveal the perils of drawing conclusions about the impacts of climate change from short-term studies such as soil-warming experiments. Such experiments rarely continue for more than a few years, and so never provide information on the response of the large, slower pools that will dominate feedbacks from soil to atmosphere over timescales of decades or more.

Several experimental studies^{12,13} have seemed to show that decomposition is

insensitive to temperature. The reasons for this are unclear, but as Davidson *et al.*¹¹ point out, the effects of climate change are much more complex than just an increase in temperature: changes in soil water and nutrient availability will occur, and these can influence decomposition. The observation of apparent insensitivity of soil decomposition to temperature is sometimes termed acclimatization to suggest a gradual biological adaptation of soil organisms to a higher temperature. Knorr and colleagues' analysis¹ shows that biological adaptation does not have to be invoked — such results can simply be a consequence of using a model that ignores the dominance of large, slowly changing pools of organic matter.

As a final twist, Knorr *et al.* predict that, over a timescale of decades to centuries, the dominant slow pools will be more sensitive to temperature than the faster pools (Fig. 1b), causing a larger positive feedback in response to global warming than previously thought. The feedback suggested by current models is already very significant; for instance, one forecast⁶ is that organic carbon will accumulate in soil as a result of CO₂ fertilization until the middle of the twenty-first century and then decline as the effect of rising temperature

on decomposition becomes dominant.

Although Giardina and Ryan's analysis² now appears incorrect, it was useful in provoking a deeper examination of the temperature sensitivity of the decomposition of soil organic carbon^{11,14}, and has led to a greater appreciation of the importance of stable organic carbon fractions in influencing climate change. ■

David Powlson is in the Agriculture and Environment Division, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK.
e-mail: david.powlson@bbsrc.ac.uk

1. Knorr, W., Prentice, I. C., House, J. I. & Holland, E. A. *Nature* **433**, 298–301 (2005).
2. Giardina, C. P. & Ryan, M. G. *Nature* **404**, 858–861 (2000).
3. Batjes, N. H. *Eur. J. Soil Sci.* **47**, 151–163 (1996).
4. Jenkinson, D. S., Adams, D. E. & Wild, A. *Nature* **351**, 304–306 (1991).
5. Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. *Nature* **408**, 184–187 (2000).
6. Jones, C. *et al. Glob. Change Biol.* **11**, 154–166 (2005).
7. Grace, J. & Rayment, M. *Nature* **404**, 819–820 (2000).
8. Jenkinson, D. S. *Phil. Trans. R. Soc. Lond. B* **329**, 361–369 (1990).
9. *The Role of Land Carbon Sinks in Mitigating Global Climate Change* Policy doc. 10/01 (Royal Society, London, 2001).
10. Smith, P. *et al. Geoderma* **81**, 153–225 (1997).
11. Davidson, E. A., Trumbore, S. E. & Amundson, R. *Nature* **408**, 789–790 (2000).
12. Oechel, W. C. *et al. Nature* **406**, 978–981 (2000).
13. Luo, Y., Wan, S., Hui, D. & Wallace, L. L. *Nature* **413**, 622–625 (2001).
14. Ågren, G. I. & Bosatta, E. *Soil Biol. Biochem.* **34**, 129–132 (2002).

Evolution

A taste for mimicry

Graeme D. Ruxton and Michael P. Speed

Looking inedible is a great way to deter predators, but the warning signs must be learnt first. It seems that unpalatable species employ some unexpected strategies to make the education a quick one.

Darwin saw mimicry — strong visual resemblances between unrelated species — as an excellent test case for his theories of natural selection¹. The phenomenon continues to exercise evolutionary biologists today, with the latest salvo coming from Skelhorn and Rowe². Writing in *Proceedings of the Royal Society*, they find that mimicry can work in an unexpected way to provide safeguards against predators.

Mimicry generally occurs in two forms, Batesian and Müllerian. Batesian mimicry is essentially parasitic: a prey species evolves to look like a species that is unattractive to predators (because it is poisonous, for example), and in so doing degrades the effectiveness of the signals used by the inedible species to warn off predators. By contrast, Müllerian mimicry involves two unpalatable species, and is thought to be mutualistic because the two species share the mortality costs incurred when naive predators sample them before learning to avoid the warning signal they both use³. Butterflies are among the commonest examples of Müllerian mimicry; a possible example is shown in Figure 1 (overleaf).

Müllerian mimicry has become highly contentious, with a body of mainly theoretical work arguing that systems identified previously as Müllerian might in fact be parasitic rather than mutualistic^{4,5}. But this conclusion will need to be re-examined in light of the ingenious experiments reported by Skelhorn and Rowe². An (often implicit) assumption of previous work on Müllerian mimicry has been that the two species are unappealing to predators because they have the same defence — the same toxin, say. However, there is no logical or observational foundation for this supposition⁶. Skelhorn and Rowe now demonstrate that Müllerian mimicry can provide highly effective protection from predation when the two species concerned have different defences.

The authors' experiments involved giving domestic chicks coloured food crumbs flavoured with aversive chemicals. All the crumbs were coloured identically, but some were flavoured with quinine, some with an equally bitter solution of Bitrex (a preparation designed to discourage people from biting their nails) and some with a blend of