revealed that the α-subunit’s carboxy-termi
nal tail is essential for receptor binding. 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–FSHα 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 determined, 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 structure does further our understanding of the key–lock mechanism by which glyco-protein 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–FSHα 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.

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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 soil. The dangers of treating soil organic carbon as a single pool were highlighted by Davidson et al., 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. have now re-analysed Giar dina 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 Ryan, 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 have seemed to show that decomposition is insensitive to temperature. The reasons for this are unclear, but as Davidson et al. 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’ analysis 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 forecast 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 analysis now appears incorrect, it was useful in provoking a deeper examination of the temperature sensitivity of the decomposition of soil organic carbon, and has led to a greater appreciation of the importance of stable organic carbon fractions in influencing climate change.

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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 selection. The phenomenon continues to exercise evolutionary biologists today, with the latest salvo coming from Skelhorn and Rowe. 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 use. 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. But this conclusion will need to be re-examined in light of the ingenious experiments reported by Skelhorn and Rowe. 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 supposition. 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