

has a strikingly flexible life cycle. In its natural habitat of ephemeral splash pools on the rocky shores of the island of Curaçao, near the coast of Venezuela, *C. flexa* undergoes repeated transitions between unicellular and multicellular states as the splash pools evaporate and refill. During these cycles, multicellular sheets can arise clonally through serial cell division, aggregatively through assembly of independent cells, or through a mixture of both processes. The result is a form of clonal-aggregative multicellularity that blurs a boundary previously considered to be fundamental.

What conditions favour multicellularity in *C. flexa*? The level of salt is a key parameter in the evaporating splash pools. Pools with lower salinity (although they are more saline than seawater) harbour more multicellular sheets of *C. flexa* than do high-salinity ones, enabling the organism to capture more bacterial prey than it could in its free-swimming unicellular form. Further evaporation of water increases salinity, which results in the dissociation of sheets, with a subset of cells surviving in dried-out pools as dormant cells called unicellular cysts. These cysts become free-swimming once water is refilled, and the cycle continues.

The authors found that salinity also tips the balance between the aggregative path to multicellularity and the clonal one. Lower salinity and lower cell density generally favour clonality, whereas higher salinity and higher cell density favour aggregation. Therefore, rather than representing opposing evolutionary end points, clonal and aggregative multicellularity form a continuum that responds to distinct ecological conditions. In *C. flexa*, the ability to switch between modes seems to enhance robustness: clonal growth preserves cohesion and relatedness, whereas aggregation can occur only if cell density is high enough.

Ros-Rocher and colleagues' work expands scientists' view of choanoflagellate multicellularity. Although animals are confined to purely clonal development, their closest relatives display a broader range of strategies. Other lineages that are near the animal branch of the evolutionary tree but more distant than are choanoflagellates, including filastereans and ichthyosporeans, exhibit either aggregative or clonal forms of multicellularity⁴. *C. flexa* adds to the picture by providing insights about simple multicellularity among choanoflagellates. The study suggests that the ancestral state of simple multicellularity in choanoflagellates might not have been purely clonal, thereby bridging the gap between aggregative multicellularity in filastereans and clonal multicellularity in animals and choanoflagellates.

More broadly, the work highlights the importance of studying organisms in their natural contexts. The unusual life cycle of *C. flexa* becomes fully intelligible only when viewed against the backdrop of fluctuating

splash pools, where salinity, hydration and cell density change rapidly. Laboratory models, powerful as they are, can miss such ecological pressures that favour evolutionary innovation.

Given that the environmental conditions that regulate the paths to multicellularity in *C. flexa* are now established, the next challenge will be to identify the genetic pathways that respond to external cues to drive these life-cycle transitions. Such pathways might extend beyond *C. flexa* and contribute to scientists' understanding of life-cycle regulation in other eukaryotes. Addressing these questions will require genomic resources and experimental tools for non-model systems, underscoring the importance of studying diverse organisms to uncover fundamental principles of multicellularity^{5,6}.

What does this work mean for studies aiming to understand animal origins? One implication is the need for caution. The clonal multicellularity of animals might not reflect an evolutionarily conserved ancestral condition shared by all choanoflagellates, but rather one outcome among several possibilities explored by our common ancestors. The last common ancestor of animals and choanoflagellates might have had greater developmental flexibility than was appreciated previously, including

the capacity for reversible, environmentally responsive multicellular organization.

By revealing that paths to simple multicellularity are more flexible than scientists thought, Ros-Rocher and colleagues invite a reframing of one of biology's major transitions. *C. flexa* shows that rather than committing to a single strategy for multicellularity, in some environments, keeping options open might be the best strategy.

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The authors declare no competing interests.
This article was published online on 25 February 2026.

Climate science

Worst-case outcomes of moderate global warming

Rachel Warren

Moderate global warming creates a risk of climate impacts that are more severe than the most-likely impacts of high global warming. **See p.946**

The Paris agreement, an international treaty on climate change, aims to limit the rise in average global temperature to less than 2 °C above pre-industrial levels. Projections of what this level of warming would mean for human and ecological systems are generally made by running an ensemble of climate models. However, the uncertainty associated with these projections means that more-extreme outcomes cannot be ruled out.

On page 946, Bevacqua *et al.*¹ report that even if global warming is limited to 2 °C, exposure of crucial systems to climate-related hazards, such as drought and flooding, could still occur at levels that are often predicted for much higher levels of global warming. This bolsters the argument that to avoid climate-related risks to systems that are key for global food security and ecosystem functioning,

effective policy should take into account worst-case scenarios as well as average projections.

Bevacqua and colleagues' approach – considering low-probability climate-risk outcomes rather than focusing on only those that are most likely – is consistent with recommendations from the Safe Landing Climates Lighthouse Activity of the World Climate Research Programme (WCRP), which aims to “identify risks from low-probability, high-impact possibilities with global-scale ramifications” (see go.nature.com/41fwi67). The authors used data from the WCRP's Coupled Model Intercomparison Project Phase 6 (CMIP6), an initiative that compares and analyses the outputs of advanced global-climate models.

For a given level of global warming, the

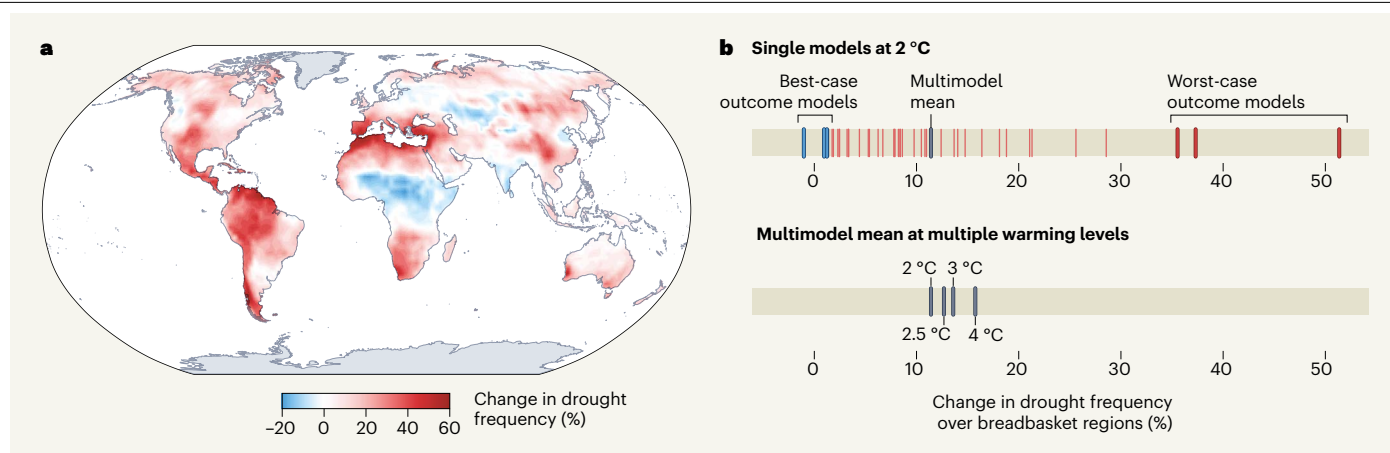


Figure 1 | Severe climate-related hazards predicted by worst-case outcomes of moderate global warming. Climate risk is generally assessed using many climate models that project various spatial patterns of climate change for a given level of global warming. Bevacqua *et al.*¹ report that these models can project severe climate risk, even if the average global temperature increases by only 2 °C, which is considered a moderate degree of global warming. This demonstrates the importance of evaluating worst-case outcomes. Using a set of advanced climate models, the researchers examined the range of

projections under various global-warming levels for three key climate-related hazards, including changes in drought frequency in breadbasket regions (those of high grain production). **a**, Projected multimodel average change in drought frequency in a 2 °C warmer world compared with pre-industrial conditions. **b**, The modelled worst-case changes in drought frequency in breadbasket regions, for 2 °C of warming, were more extreme than were the multimodel-average predictions for 2.5, 3 and 4 °C of warming. (Adapted from Fig. 3 of ref. 1.)

temperature change will exhibit regional differences, and these will vary between climate models². The CMIP6 models map variations in the spatial pattern of climate-change projections that are associated with various levels of global warming.

The authors focused on the exposure of key systems to climate-related hazards: heavy, five-day precipitation events occurring in highly populated areas; soil-moisture deficit in areas of high grain production, which form the ‘global breadbasket’; and enhancement of weather that is conducive to wildfires in forests. Previous climate-change risk assessments have tended to focus on either a global analysis, or on specific nations or geographical regions.

The authors defined a quantity called the global climatic impact-driver, which measured how much the exposure to each hazard was projected to change with a given level of global warming. This was calculated for each model separately and averaged over the models in the ensemble. The authors ranked the models by their global climatic impact-driver values, using roughly the highest and lowest 10% to indicate the worst and best potential outcomes, respectively (Fig. 1).

The authors showed that even for 2 °C of warming, extremely adverse outcomes cannot be ruled out. For the climate-impact drivers considered, the worst-case outcomes for 2 °C of global warming include several that are more extreme than the average projections for 3 °C, or even 4 °C. This indicates that a precautionary approach, limiting the level of warming to well below 2 °C, is needed to avoid these extreme outcomes with high confidence.

Policy-makers for climate-change mitigation

and adaptation should not just be aware of the most probable outcome associated with a particular level of global warming, but also of the less likely, more-extreme outcomes that need to be avoided. Uncertainties in global climate sensitivity – the predicted change in global temperature caused by a doubling of the concentration of atmospheric carbon dioxide relative to pre-industrial times – have received attention from policymakers³, who need to know the probability that global warming can be constrained if emissions reach net zero by certain dates, or if cumulative emissions are kept within certain limits.

Uncertainties in projections of exposure to climate-related hazards have received less attention. Good-quality regional or national climate-change risk assessments generally include error margins, reflecting the uncertainty in regional climate projection. To improve risk management and adaptation planning, risk assessments should also focus on the potential for extreme outcomes in particularly exposed areas.

Bevacqua and colleagues’ work highlights the need to consider extreme outcomes for climate risk by making a direct comparison of averages and extremes at various levels of global warming. It also shows that it is crucial to focus the quantification of the exposure of key socio-ecological systems to climatic hazards in the most important locations, here defined by their contribution to global food security or ecosystem functioning.

Assessments from the Intergovernmental Panel on Climate Change have synthesized data on the climate-related risk associated with various levels of global warming into a diagram known as burning embers⁴. This has been used to indicate how risks that are

associated with extreme weather events grow with warming⁵. In these assessments, the risks associated with various levels of warming are colour-coded to indicate low, moderate, high and very high levels of risk. This colour-coding is based on the strength of the underlying evidence in literature and on the magnitude, likelihood, permanence and importance of the risk – the research from Bevacqua *et al.* could be used to inform future burning embers diagrams.

A body of research that takes into account the impact of the most extreme 10% of climate-risk predictions would highlight risks that might otherwise be overlooked. A first step would be to apply Bevacqua and colleagues’ methodology to other crucial systems, such as oceans, low-lying coastal regions, human health and physical infrastructure, which would provide valuable information. Furthermore, although the authors assessed the exposure of key socio-ecological systems, such as population centres and forests, to climate hazards, they did not consider the vulnerability or adaptive capacity of those systems. To do so would be another valuable extension of their work.

The United Nations Environment Programme estimates that under current policies, global warming will reach 2.8 °C (ref. 6). It is therefore essential to accelerate climate-change mitigation efforts to prevent outcomes that are as, or even more, extreme than those identified by Bevacqua and colleagues. This will require rapid reductions in greenhouse-gas emissions this decade, so that global CO₂ emissions reach net zero in the early 2050s⁷. Key actions that are necessary to deliver this include transitioning from fossil fuels to low- or zero-carbon energy sources,

widespread electrification, energy conservation and the removal of some CO₂ from the atmosphere.

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The author declares no competing interests.

Ancient DNA

Dogs have deep roots in ice-age Europe

Mikkel-Holger S. Sinding & Lauren M. Hennelly

Two studies report the oldest dog genomes ever to be sequenced, representing leaps in scientists' understanding of the animal's origins. See p.986 & p.995

Dogs have a special place in human history. They were the first animals to be domesticated and are commonly found in our homes today. But where did dogs come from? What were the earliest dogs like? Despite numerous resourceful studies across disciplines, the enigmatic origin of these animals is still unclear. Writing in *Nature*, Bergström *et al.*¹ and Marsh *et al.*² break this barrier, getting closer in time to the origin of dogs than ever before and charting their early evolution in western Eurasia.

Between roughly 10,000 and 4,000 years ago, agriculture spread across Europe. In an impressive effort, Bergström and colleagues (page 986) analysed and directly compared genome-wide data from more than 200 ancient canids, finding dozens of dogs (*Canis lupus familiaris*) that lived in Europe before and after this defining transition in human history. For humans, the shift to farming was accompanied by large-scale immigration from southwest Asia and, in many places, a major shift in human genetic groups^{3,4}. Remarkably, Bergström *et al.* find that this was not the case for early dogs: the ancestry of the ancient dogs that were associated with farmers can be traced back to dogs that lived more than 14,000 years ago and were linked to hunter-gatherer populations. This suggests that there was genetic continuity for dogs in ancient Europe, rather than a sharp population shift like that found in humans. In this fascinating case, human history and dog history differ; by contrast, in Asia⁵ and the Americas⁶, dog history mostly reflects the history of human mobility and cultural transitions. Although

there have clearly been genetic contributions from other dog populations over time, the oldest ancestry of modern European dogs can be traced to the earliest known dogs in western Eurasia.

In the second study, Marsh and colleagues (page 995) report the oldest dog genome that has been sequenced so far, dating to almost 16,000 years ago, from Anatolia in south-western Asia. Using this genome and a newly sequenced one from a dog that lived around 14,000 years ago in Great Britain, Marsh *et al.* illuminate the early history of dogs in Europe. These two ancient genomes belong to one of two major dog lineages – the western Eurasian lineage – suggesting that it can be traced back to almost 16,000 years ago. A stunning finding is that these two ancient dogs, separated by more than 3,000 kilometres, were closely related genetically. This suggests that the population from which they both originated had quickly expanded across vast distances, and that dogs must have been passed on among diverse cultures and groups of people.

Together, Marsh *et al.* and Bergström *et al.* provide insights into dog domestication by positioning the oldest dog genomes in place and time in human and dog history. In the past few years, analyses of numerous ancient genomes from Eurasia and North America have shown that, by around 10,000 years ago, dogs were already widely distributed and had diversified into distinct genetic groups^{7,8}. Evidently, dog domestication pre-dates this and probably originated in Eurasia, the centre of this diversification. Of modern dogs, those in eastern Asia have the greatest genetic diversity, so it was long assumed that this was where dogs originated⁹. However, no dog remains more than

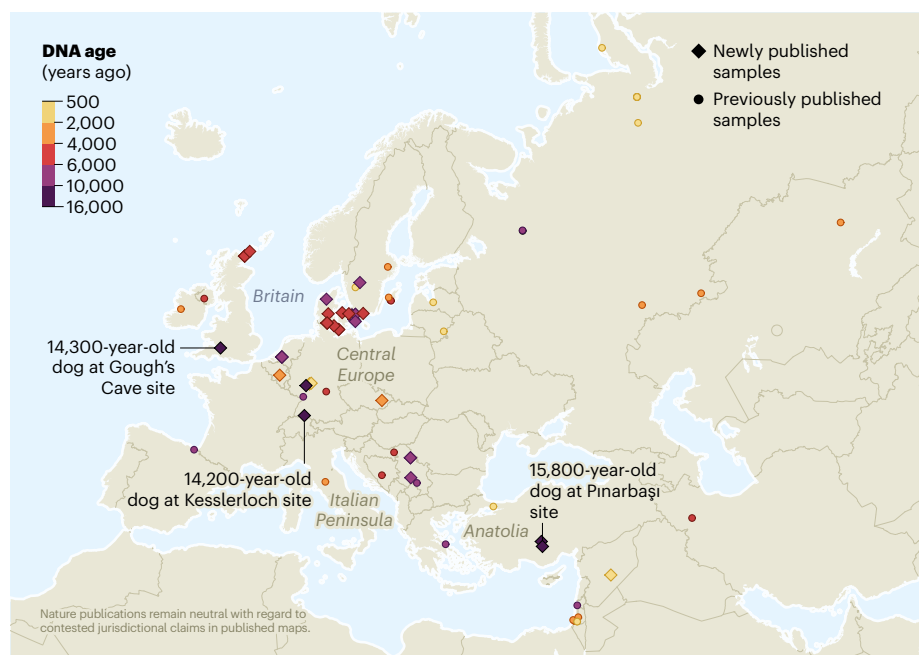


Figure 1 | Ancient dog genomes. The map of Eurasia shows the locations and ages of ancient dog (*Canis lupus familiaris*) genomes that were analysed by Bergström *et al.*¹ and Marsh *et al.*² (some sites have more than one sample). Among them are the oldest dog genomes ever to be sequenced, located in the region of Anatolia (around 15,800 years old), the island of Britain (around 14,300 years old) and present-day Switzerland (around 14,200 years old). Genetic analyses reveal that an ancient dog population was distributed widely across western Eurasia before the introduction of agriculture, and that much of the ancestry of modern western dogs can be traced to this population.