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commentary

Is climate change making plants go up mountains?

Paleontological evidence indicates that about 2.5 million years ago the world climate entered a period of instability. Climatic fluctuations, probably forced by cyclical changes in the earth's orbit around the sun, resulted in a series of ice ages and today we are in a period between glacial advances. Alterations in solar radiation are also thought to cause climatic variation such as the Medieval Warm Period (~950-1200 AD) and Little Ice Age (~1650-1850 AD); and major volcanic eruptions lead to short-term changes by changing atmospheric reflectance. In addition to these natural factors, climate is also increasingly thought to be influenced by human activities, an issue that is the topic of intense international discussion under the United Nations Framework Convention on Climate Change (UNFCCC) and where the scientific indicators of climate change have been under a media spotlight.

During the last century almost all environmentally important atmospheric trace gases have increased dramatically, and the consensus opinion of the Intergovernmental Panel on Climate Change (IPCC) is that there is correlation between changes in atmospheric composition and observed changes in the global climate. Major reasons are increasing use of fossil fuel energy, together with land use changes such as for food and energy production. These human activities lead to the mobilisation and volatilisation of soil and plant carbon and nitrogen stocks, increasing the flux of CO₂, CH₄ and N₂O into the atmosphere (IPCC 2007). During the last century, global mean surface temperature has increased with unprecedented speed since records began and CO₂ levels range beyond any of those of the last 650,000 years (IPCC 2007).

In a study of the altitudinal distribution of 171 western European mountain forest plant species based on an impressive database, Lenoir et al. (2008) have provided some evidence that observed increases in regional temperature are being translated into upward shifts of plant species. They compared the altitudinal distribution of their

sample between two time periods: 1905-1985 and 1986-2005, over an elevational range of 0-2600 m, and calculated an aggregate upwards shift of 64 meters from 1971 (mean year of the first interval) and 1993 (mean year of the second interval) in the core ranges of the plants investigated. As might be expected with such rapid changes in climate, trees showed less response than herbaceous species. In an additional study to investigate whether or not woody plants were also upwardly mobile, Lenoir et al. (2009) tried to demonstrate that, even if adult trees did not show a climate change signal, their seedlings were indeed responding. Both studies made attempts to eliminate confounding variables, but in doing so included some bias. They investigated the spatial core of the species' ranges, rather than the edges of distributions, where the effects of climate change are likely to be most apparent, but where there is also likely to be greater natural fluctuation. In addition they only included forest communities, which are buffered by the micro-climate created by the forest canopy and so are less likely to show short-term responses. Moreover they ruled out the effects of increasing nitrogen deposition, land-use change, invasive species and CO₂ fertilisation. On the other hand they excluded trees with a high risk of human introduction such as spruce, and in so doing lost one of the most important trees of the upper forest line.

How important is this evidence in the context of policy making? It shows that, in western European mountains at least, regional temperature increases are partly being translated into upward shifts of plant communities. However, as one would expect from an individualistic response to environmental change, the species did not behave uniformly. Mountain plants showed greater shifts than elevation generalists, as did plants with faster life history traits. Of the 171 species in the first paper (Lenoir et al. 2008) two-thirds went up but a third went down. Similarly of the tree species analysed in detail (Lenoir et al. 2009), the seedlings of 10 species showed an upward trend

and four species a downward one. With such a high proportion of species moving down, it is clear that temperature is but one of many factors influencing plant distribution; and there are different ecological demands on forest communities, such as ontogenetic niche shift and succession dynamics. Furthermore, we should also ask how important these shifts are in the big scheme of things. For example, non-reproducing populations of the Linden tree (*Tilia cordata*) in north-west England appear to have established in former warmer climates and survived for an extended period of time by vegetative propagation (Pigott and Huntley 1981). To a coppicing tree the last glacial period is only a few generations away and the overall provision of ecosystem goods and services is not likely to be overly affected as plant communities rearrange themselves to the new climate regime. At higher elevations, tree-lines have a memory of several centuries and late successional alpine vegetation responds very slowly to climate change (Körner 2003). Probably more relevant in terms of maintaining European ecosystem quality are the factors mentioned by Lenior et al. (2008, 2009) as ones they tried to control: nitrogen deposition at 6-30 kg/ha, land-use change explaining 96% of the observed ecological dynamics and human-mediated increases in the browsing deer population.

Elsewhere on the planet the effects of global warming on plant species distributions might be a bit more dramatic than in western Europe. Models of future changes in Africa suggest that forests in the central African basin and much of the unique Cape Floral Kingdom will disappear (McClellan et al. 2005) and on Kilimanjaro climate change-driven forest fires lead to a downward shift of alpine vegetation into burnt montane forest areas, interestingly showing a trend apparently opposite to climate change impacts (Hemp 2005). But the ecological impact of climate change on developing countries has not always been uppermost in the minds of the UNFCCC negotiators, as recent events at the Copenhagen meeting have shown. Nonetheless, land use change was also a major topic at Copenhagen and it is important to bear in mind that in Africa and

other tropical regions actual land use changes (and not modeled future effects of climate change), including the destruction or conversion of natural habitats, are the major drivers of landscape alteration impacting biodiversity and its underlying ecosystem services (Sala et al. 2000, Jetz et al. 2007).

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update

Feces, fungus, and the fall of megafauna

We live in strange times. For millions of years, continents and islands hosted many very large animals (e.g., mammoths, giant sloths, gorilla-sized lemurs, rhino-sized wombats), but beginning 50,000 years ago, extinctions swept away this diversity everywhere except Africa. Relative to earlier extinctions, this event was unprecedented in its selectivity against large animals. In most affected areas, the extinction postdated the arrival of modern *Homo sapiens*. This pattern and chronology implicate humans as drivers of the extinction, but the nature of their impacts (hunting, habitat alteration, introduced species, etc.) is unclear. In the Americas and Eurasia, the extinction coincided with climate and ecosystem changes that may have exacerbated human impacts. The close temporal coincidence of anthropogenic, biotic, and climatic events at the end of the Pleistocene has made it hard to test specific extinction hypotheses and has obscured the ecological repercussions of losing so many large animals.

A recent paper by Gill et al. (2009) tackles these issues with a new proxy for large animal abundance that is microscopic. Large herbivore dung is infested by a fungus, *Sporormiella*, that sheds spores that are found in sedimentary records along with the pollen and charcoal that are used to reconstruct vegetation and fire history. *Sporormiella* (and presumably large herbivore) abundance began to decline in the northeastern U.S. at the first appearance of humans (~14.8 ka), reaching trace levels by 13.7 ka. This crash in abundance precedes 1) the appearance of "non-analog" floras at 13.7 ka, 2) increased fire at 13.7 and 10.5 ka, 3) the appearance of the sophisti-

cated Clovis tools at 13.1 ka, 4) the onset of Younger Dryas cooling and 5) the final extinction of the large mammals, both ~12.9 ka.

This chronology falsifies hypotheses that link population declines to the Younger Dryas event or dietary problems associated with non-analog floras. Instead, it raises the possibility that a human-induced large herbivore crash contributed to the unusual non-analog floras and to increased fuel loads that spurred fires. The study has some minor weak spots: the ¹⁴C chronology is messy (though the relative timing of events is unlikely to change), the quantitative relationship between animal and spore abundance is complicated, and the big change in fire regime is at 10.5 ka, long after large mammals have vanished. Still, this promising approach may illuminate how our strange, large-animal depauperate ecosystems came to be, as well as the consequences of losing so many co-evolutionary partners and potential ecosystem engineers.

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