of fishing for red hake in the north may have speeded the shift of its biomass to the north.

Historical and economic factors play important roles: the rise and fall of export markets and the reorganization and consolidation of industries can greatly affect which species are fished and landed where. This, it seems, is the likely reason for the unexpected dominance of relatively cool-water species in one of the more southern states of the region even though the fish community offshore is increasingly dominated by warm-water species. This could benefit some of the warm-water species moving north, which are lightly fished as yet in their newer habitats, but could impose biological costs on the trailing edge of cold-water species.

The study by Pinsky and Fogarty[1], particularly their discussion of reasons for lag and unpredicted directions of fishing response to changes in the distribution of fish populations, shows how essential it is to give explicit attention to regulatory, social, economic and historical factors when seeking scientific understanding of interactions between humans, environment and climate, even those as seemingly straightforward as fishing. ❐

Bonnie J. McCay is in the Department of Human Ecology, School of Environmental and Biological Sciences, Rutgers University, 55 Dudley Road, New Brunswick, New Jersey 08901, USA.
e-mail: mccay@aesop.rutgers.edu

References

1. Pinsky, M. L. & Fogarty, M. *Climatic Change* **115,** 883–891 (2012).
2. Nye, J. A., Link, J. S., Hare, J. A. & Overholtz, W. J. *Mar. Ecol. Progr. Ser.* **393,** 111–129 (2009).
3. Shackell, N. L., Bundy, A., Nye, J. A. & Link, J. S. *ICES J. Mar. Sci.* **69,** 1054–3139 (2012).
4. Kates, R. W. *et al. Science* **292,** 641–642 (2001).
5. Weinstein, M. D. & Turner, E. *Sustainability Science* (Springer, 2012).
6. Liu, J. *et al. Science* **317,** 1513–1516 (2007).
7. McCay, B. J., Brandt, S. & Creed, C. F. *ICES J. Mar. Sci.* **68,** 1354–1367 (2011).

ECOSYSTEM CARBON STORAGE

Squeezing the Arctic carbon balloon

The advancement of trees into Arctic tundra can increase total aboveground carbon storage. A study now shows, however, that greater plant growth also enhances belowground decomposition, resulting in a net loss of carbon from the ecosystem.

Evan S. Kane

There is more than three times as much carbon harboured in the world's soils as there is in either the atmosphere or in aboveground plant biomass, and most of this soil carbon is locked up in frozen ground at high latitudes[1]. This tremendous pool of carbon persists because carbon inputs from net primary production exceed outputs due to mineralization of organic matter to carbon dioxide. Although soil carbon accrual is only the small residual between inputs and outputs, in cold regions inputs slightly outstrip outputs because decomposition is arrested at low temperatures. As such, relatively old carbon that has been preserved for centuries is subject to mineralization when perennially frozen soil thaws[2].

Enhanced mineralization of organic soils not only releases CO_2 to the atmosphere but also increases the pool of mineral nutrients in the soil, which in turn increase the production of vegetation. Because inputs and outputs are both affected by changes in temperature, the net effects of changes in climate on total soil carbon storage have been hard to discern in boreal and Arctic ecosystems. Moreover, as perennially frozen soils thaw, the physical environment changes considerably, making it very difficult to disentangle the effects of temperature, moisture and vegetation on soil carbon accumulation. To investigate directly the effects of increased production versus increased mineralization on the soil carbon balance, Hartley *et al.*[3] conducted surveys of above- and belowground carbon pools across a transitional zone between heath and birch forest in Arctic Sweden. They were able to control for interactive effects of permafrost thaw and enhanced plant production because these Arctic soils were relatively well drained and lacked permafrost. In spite of increases in total aboveground carbon — due to increased plant production — they observed a net loss of total ecosystem carbon over the transition from tundra-heath to birch forest ecosystems, because shallow belowground carbon pools declined more than aboveground pools increased (Fig. 1).

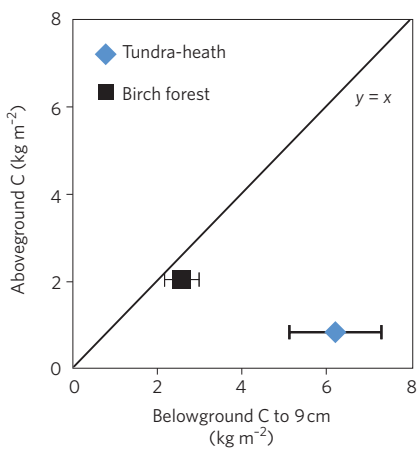

Figure 1 | Hartley *et al.*[3] show that as tundra systems give way to birch forest, more ecosystem carbon is harboured in aboveground pools, at a net loss of total ecosystem carbon. Belowground carbon pools dwarf aboveground pools, especially if one considers carbon deeper in the soil. Error bars were propagated from standard errors provided in the Supplementary Information[3] (belowground: bulk density and depth; aboveground: leaves, stems and roots). *Y* axis error bars are too small to plot.

Hartley *et al.*[3] suggest that vegetation activity fosters belowground decomposition through subsidies of readily usable carbon from roots, in the form of root exudates. Root exudates can effectively create hotspots of decomposition in soils, with turnover processes being over an order of magnitude greater near roots than in bulk soil[4]. Support for their argument comes from the relative quantities of 'bomb' carbon (^{14}C) measured in CO_2 respired from the tundra-heath and birch-forested plots; this represents carbon fixed into vegetation by photosynthesis in the 1950s. Plant-respired $^{14}CO_2$ should be similar to that of the atmosphere (relatively depleted), but during peak growing season when plant-derived respiration should be the greatest, $^{14}CO_2$ respired from the birch ecosystems (plant and soil components) was more enriched (older) than $^{14}CO_2$ respired in the shoulder seasons. In contrast, $^{14}CO_2$ respired from the tundra-heath showed little seasonality. The authors suggest that this demonstrates a vegetation-mediated

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effect on the decomposition of older (and deeper) soil carbon in birch forest, although the mechanism is not well understood. For example, shrubs in the *Ericaceae* family, which are common in heath-tundra and birch forest, are particularly well adapted to low nutrient availability[5], decompose very slowly[6] and in fact have strategies for retarding decomposition and mineral nutrient cycling[7]. As such, any increased decomposition in birch forest, or slow decomposition relative to inputs in tundra-heath, may be the result of competitive interactions with *Ericaceae*, and the fungi and microorganisms associated with ericoid root activity. But exactly how the plant–soil relationships of these Arctic and boreal plant functional types are likely to respond to changes in temperature or available water is not well understood.

An increased allocation of total ecosystem carbon in aboveground pools relative to belowground pools in the Arctic, and subarctic, should be considered in the context of susceptibility to change. The change in the distribution of ecosystem carbon pools between heath-tundra and birch forest ecosystems (Fig. 1)[3] occurs at a net loss, even though only the top 9 cm of soil are considered. Although most of the CO_2 released from soils in this study was decades rather than centuries old, stores of carbon 500–1,000 years old were present in the shallow soil horizons. With combined effects of warming and vegetation change, these stores of carbon, and deeper carbon stocks that have taken thousands of years to accumulate, may become increasingly vulnerable to mineralization, as has been observed with permafrost degradation in Alaska[2]. Moreover, there is a limit to how much carbon can be stored in woody biomass, even in very productive systems, and this cap to carbon accrual is dwarfed by the deep carbon stores in Arctic soils[8]. Aboveground pools of carbon have shorter mean residence times than belowground pools and are more vulnerable to disturbances such as wildfire. This is an important additional consideration because fires in the Arctic are expected to increase if the climate continues to warm[9], and changes in ecosystem carbon allocation or fuel structure would affect the Arctic fire regime. ❐

Evan S. Kane is at the US Forest Service, Northern Research Station, 410 MacInnes Drive, Houghton, Michigan 49931, USA, and Michigan Technological University, School of Forest Resources and Environmental Sciences, 1400 Townsend Drive, Houghton, Michigan 49931, USA.
e-mail: eskane@mtu.edu

References

1. Tarnocai, C. *et al. Glob. Biogeochem. Cycles* **23**, GB2023 (2009).
2. Schuur, E. A. G. *et al. Nature* **459,** 556–559 (2009).
3. Hartley, I. P. *et al. Nature Clim. Change* **2,** 875–879 (2012).
4. Kuzyakov, Y. *Soil Biol. Biochem.* **42,** 1363–1371 (2010).
5. Cairney, J. W. G. & Meharg, A. A. *Eur. J. Soil Sci.* **54**, 735–740 (2003).
6. Cornelissen, J. H. C. *J. Ecol.* **84,** 573–582 (1996).
7. Read, D. J., Leake, J. R. & Perez-Moreno, J. *Can. J. Bot.* **82,** 1243–1263 (2004).
8. Ping, C-L. *et al. Nature Geosci.* **1,** 615–619 (2008).
9. Mack, M. C. *et al. Nature* **475,** 489–492 (2011).

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