extent needed to match the amount of food and fuel produced by clearing forest. They found that, on average, the cost of adopting this approach would be well above the opportunity costs of conserving forests, at approximately US$6.50 per tonne of carbon dioxide saved (compared with their estimate of US$3.90 for the opportunity-cost approach). The cost would clearly be even higher if it turned out that agricultural yields needed to increase further to offset forest losses. However, the researchers show that even if yields needed to double, the cost (estimated at US$12 per tonne of carbon dioxide saved) would still be affordable given the current price of carbon in the European Union's Emissions Trading Scheme (about US$18 per tonne).

The magnitude of Fisher and colleagues' estimate of the cost of implementing REDD+ won't come as a complete surprise to policymakers, because some complex economic models[5,6] (which account for, among other things, price fluctuations associated with the rate of deforestation) indicate that the opportunity costs of reducing deforestation could be at least as high as the cost of implementing Fisher *et al.*'s approach. Nevertheless, Fisher and colleagues' argument[3] that the implementation of REDD+ should focus on policies that increase agricultural yields and fuel-use efficiency is a major new direction for both scientific and policy-related research on the implementation of REDD+.

It remains to be seen whether the increases in crop yields and fuel-use efficiency that they show are necessary for successful implementation are feasible. Between 1980 and 2000, more than four-fifths of new agricultural land was carved out of tropical forests, while the area of agricultural land in developed countries decreased by over 300 million hectares (ref. 7). It is likely that the pressure on tropical forests will remain, because projected increases in global agricultural yields of 1–2% will not be sufficient to keep pace with projected increases in demand for food without an increase in the area of agricultural land[7]. Furthermore, agricultural intensification has not, historically, reduced cropland expansion, except where countries have imported significant quantities of cereals and implemented strong land-protection programmes[8]. Successful implementation of REDD+ will thus require a dramatic departure from the recent trend of agricultural expansion into tropical and sub-tropical forests.

It will also require all tropical countries with significant areas of forest to take part in the scheme. Otherwise, participating countries that are unable to meet their own demands for agricultural products could simply import food from tropical countries not taking part, displacing emissions there. That said, importing agricultural products from other REDD+ nations or developed countries could still result in leakage if these countries are unable to increase agricultural yields sufficiently to meet demand — and importing food from developed countries would also have the considerable disadvantage of coming at a higher cost.

Future research will therefore need to assess how the mounting global demand for agricultural products from a growing and increasingly wealthy population can continue to be met whilst also conserving the world's remaining forests. Close consideration will need to be given to the costs (in terms of the prices of food, fuel, fodder and carbon) of doing so, as well as the potential impacts on human welfare. For example, restrictions on access to land to conserve forests could leave part of the rural population in developing countries landless and with reduced livelihood opportunities.

Fisher and colleagues[3] show that agricultural intensification policies are needed for the successful implementation of REDD+, and that these policies probably cost more than simply paying people to conserve forests. But in practice, it may well be that both policies are required to increase agricultural supply from existing farmland while also ensuring that the livelihoods of those who would otherwise rely on the forests are maintained[9]. It remains to be seen whether the increase in funding that this would require would make REDD+ unpalatable for the rich, developed countries that fund it. ❐

Luca Tacconi is at the Crawford School of Economics and Government, The Australian National University, Lennox Crossing, Canberra, Australian Capital Territory 0200, Australia.
e-mail: luca.tacconi@anu.edu.au

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ECOLOGY

Dishing the dirt on carbon cycling

The roles that microorganisms play in carbon storage are not fully understood. Now modelling results show that the activity of a single group of soil fungi may significantly enhance ecosystem carbon-storage capacity.

Jennifer M. Talbot and Kathleen K. Treseder

Over the past 15 years, there has been an explosion of research in the field of microbial ecology. This work has revealed that microbes are extremely diverse, metabolize carbon and nutrients in a number of different ways, and perform a whole suite of unexpected processes in soils[1]. Yet models that explore how the terrestrial carbon cycle is linked to climate continue to treat the activity of soil microorganisms as a single 'black box' through which soil carbon is converted into either atmospheric carbon dioxide or a poorly defined pool of recalcitrant carbon in a single step[2]. Writing in *Ecology Letters*, Orwin and colleagues[3] present a modelling study that bridges this divide and shows that a single metabolic strategy of one microbial group — the uptake of organic nutrients by mycorrhizal fungi — alters carbon retention in an ecosystem to an extent that calls the reliability of all other ecosystem models into question.

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Fungi are critical to the movement of carbon through ecosystems. They are the main decomposers of dead plant, animal and microbial biomass and can provide plants with essential nutrients. Different types or 'functional groups' of soil fungi can differ dramatically in their metabolic strategies. Some free-living fungi break down carbon compounds in plant litter and convert them into resources for growth. By contrast, mycorrhizal fungi, which form symbioses with plant roots, acquire the majority of their carbon directly from plants, but scavenge for nutrients such as nitrogen and phosphorus in the soil. Until the 1980s, mycorrhizal fungi were thought to use inorganic forms of these nutrients, such as ammonium and phosphate. However, over the past three decades evidence has accumulated that shows they can also obtain nutrients from organic compounds such as amino acids. The extent to which they do so is still a matter of debate[4,5], in part because it is difficult to quantify the process in the field.

Orwin and colleagues[3] do not attempt to resolve this debate. Rather, they explore the possible consequences of organic nutrient uptake by mycorrhizal fungi for ecosystem-level carbon cycling. Using current soil biogeochemical models as a starting point, the researchers designed a model that divides the single 'microbial pool' of previous models into different functional groups — mycorrhizal fungi, free-living fungi, bacteria, grazers and predators — and simulates their growth, turnover and nutrient uptake individually (Fig. 1). They used this model to explore the effect that organic nutrient uptake by mycorrhizal fungi has on the pools and fluxes of carbon in plants and soils under different soil-fertility and litter-quality regimes.

When mycorrhizal fungi were allowed to access organic nutrients in plant litter and soil, they supplied their host plants with more nutrients, which led to faster rates of photosynthesis. The resulting increase in plant productivity enhanced carbon allocation to mycorrhizal symbionts, boosting soil-carbon content by up to 14%. The simulated increases in soil-carbon stocks were of a similar magnitude to the changes induced by lowering the 'quality' (or digestibility) of plant litter considerably. This result is surprising because litter quality is one of the most important controls of terrestrial carbon storage[6]. Accordingly, it is possible that organic nutrient uptake by mycorrhizal fungi plays a major role in regulating terrestrial ecosystem carbon storage.

Owing to the limited understanding of soil processes, the researchers' model necessarily makes a number of assumptions. For example, it assumes that mycorrhizal fungi, bacteria and free-living fungi are equal competitors for organic nutrients, which may not be the case in all soil environments. Bacteria and free-living fungi may be more efficient than mycorrhizal fungi at producing extracellular enzymes that break down organic nutrients. Alternatively, mycorrhizal fungi's access to plant carbon may allow them to out-compete other microbes for organic nutrients when external forms of carbon (such as litter carbon) are low. Furthermore, the model does not allow mycorrhizal fungi to use carbon from organic nutrients for their metabolism, which may occur in the field. This process would diminish soil-carbon stocks, potentially offsetting the enhanced storage predicted by the model[7].

Orwin and colleagues' study[3] focused on two groups of mycorrhizal fungi: ericoid and ectomycorrhizal, because these are known to use organic nutrients[8]. Future models could be improved by including arbuscular mycorrhizal fungi, the most common type of mycorrhizal symbiosis. Evidence is accumulating that these fungi can access organic nutrients in soil[9]. They also produce glomalin, a molecule that is resistant to decay and may contribute to soil-carbon storage[10]. Arbuscular mycorrhizal associations are dominant

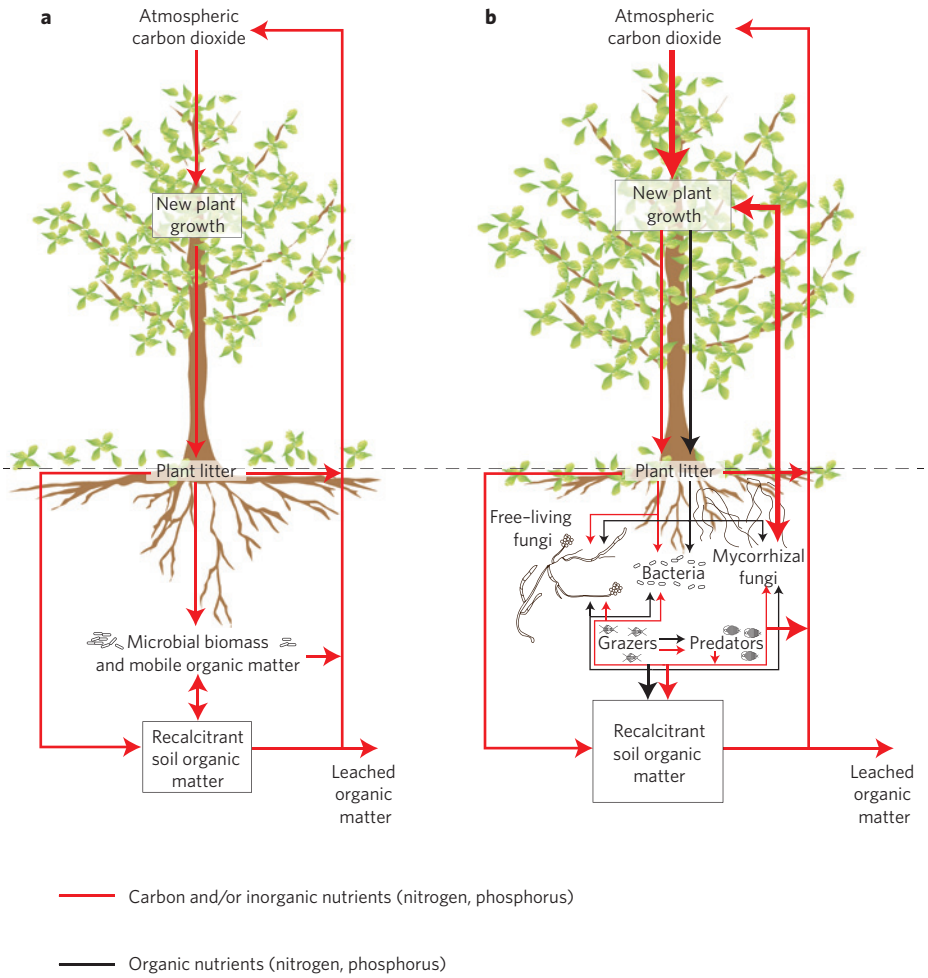

Figure 1 | Schematic of models used to study carbon cycling in soils. **a**, Conventional models treat soil microbes as a single 'black box' through which carbon and inorganic nutrients flow from plant litter to slowly decaying (recalcitrant) soil organic matter, with a portion of the carbon transferred to the atmosphere as respired carbon dioxide. **b**, In contrast, the model used by Orwin and colleagues[3] simulates the activities of individual groups of microbes, including uptake of organic nutrients by mycorrhizal fungi and direct transfer of carbon from plants to mycorrhizal fungi. Their results show that organic nutrient uptake by mycorrhizal fungi increases the amount of carbon stored in soils on a landscape-scale by increasing nutrient transfer to plants, which in turn enhances plant growth and thereby increases both plant-litter inputs to the soil and carbon flows to mycorrhizal fungi.

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in grasslands, which have some of the highest rates of carbon fixation on Earth, suggesting that they might have an even more important role in the carbon cycle than ericoid and ectomycorrhizal fungi.

Orwin and colleagues' study[3] potentially has important implications for modelling the balance of carbon between the biosphere and the atmosphere. Global climate models are the most powerful tools we have at our disposal for predicting the impact of a changing carbon cycle on ecosystems and human societies. It is imperative that these models are both accurate and as precise as possible, as they influence the actions we take to mitigate climate change. The team's results indicate that modifying climate models by incorporating the diverse functions of different microbial groups into their coding could have significant consequences for simulations of the soil-carbon balance, and thus potentially for predictions of future atmospheric carbon dioxide concentrations.

We are not yet, however, at a stage where it is clear that such modifications would improve model predictions of the global carbon balance: more work is needed to understand and quantify the effects that microbial functions — including organic nutrient uptake — have on carbon cycling. An important first step will be to test how different groups of microbes and their activities contribute to carbon cycling in the field, in a way that can be used to validate Orwin and colleagues' model at a regional scale. ❐

Jennifer M. Talbot and Kathleen K. Treseder are at the Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92617-2525, USA.
e-mail: jtalbot@uci.edu; treseder@uci.edu

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POLICY

Trade's growing footprint

The production of traded goods accounts for a significant proportion of global greenhouse-gas emissions. Now analysis reveals that emissions embodied in imports from developing countries have out-stripped emission reductions made by developed countries at home over the past 20 years.

Carolyn Fischer

The question of the burden that different countries should bear in reducing greenhouse-gas emissions is at the heart of international negotiations to tackle climate change. The 1992 *United Nations Framework Convention on Climate Change* established the principle of 'common but differentiated responsibilities', acknowledging that developed countries bear more responsibility than developing countries for historical emissions, and that emissions from developing countries will need to grow to facilitate their development. Shortly after the convention was adopted, the World Trade Organization was established, enshrining rules and obligations for liberalized trade. Since then, global trade has expanded and shifted, with emerging economies becoming major exporters of manufactured goods, rather than just raw materials and agricultural commodities[1]. Writing in *Proceedings of the National Academy of Sciences*, Peters and colleagues[2] show that these changes make it even more difficult to answer the question of who should be responsible for reducing greenhouse-gas emissions — not least because emissions embodied in imports from developing countries over the past 20 years exceed the emission reductions that developed countries have made within their own territories.

Under the 1997 Kyoto Protocol, developed countries agreed to legally binding emission-reduction targets for 2012. These commitments apply only to greenhouse-gas emissions produced within each country's own territories. By this 'territorial' accounting system, developed countries have stabilized their carbon dioxide emissions since 1990, while emissions from developing countries have doubled[2]. However, this system does not account for the flows of trade between countries and thus overlooks the fact that developed countries are net importers of emissions, while emerging economies are net exporters[3,4].

Peters and colleagues[2] identify important trends in the role that international trade has played in emissions growth at global, regional and country scales. Using a time series of global trade data, they calculated net emission transfers between almost 100 different countries — that is, the emissions generated in a country to produce exported goods and services minus the emissions that are generated elsewhere to produce the goods and services that it imports. Adjusting each country's territorial emissions by this amount, they created inventories that reflect the emissions associated with consumption in each country (Fig. 1).

The analysis shows that net emission transfers from developing to developed countries have been growing steadily, at an average rate of 17% per year. Furthermore, for developed countries as a whole, these transfers exceed the reductions in territorial emissions achieved since 1990. Overall, growth in emission transfers to developed countries through international trade equates to 14% of the growth in global carbon dioxide emissions since 1990. China has played a striking role in these trends: emissions associated with imports from China accounted for 75% of the growth in developed countries' consumption-based emissions. Moreover, Chinese emissions accounted for 55% of the growth in global carbon dioxide emissions from 1990 to 2008, with one-third of this contribution due to exports.

Analysis by sector reveals that energy-intensive industries such as cement and steel production, which are often targeted in climate policies, are not the main source of 'carbon leakage' from developed to developing countries. Trade in these sectors has grown in

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