

for the Amazon Basin, limited to Brazil. But western Amazonia harbours extensive swamps dominated by the palm *Mauritia flexuosa* L.f., as well as innumerable smaller mires along rivers, around lakes, in stream valleys, and in minor depressions within the rainforest. *Mauritia* swamps are estimated to cover 47,140 km² in Peru⁴, and vegetation maps suggest 8,000 km² for Colombia⁵ and 4,000 km² for Ecuador⁶. Our work indicates that peat strata in these swamps are often more than a metre thick. Considerable areas of such peatlands are also thought to exist in Brazil⁷.

Small mires within the rainforest are difficult to map, because they are indistinguishable in satellite images. However, on the basis of experience from 220 km of floristic transects in Peruvian, Colombian and Ecuadorian non-inundated rainforests, we estimate that peat deposits cover about 1% of their area, totalling almost 9,000 km². If the same proportion applies in Brazil, then it has more than 40,000 km² of undocumented peatlands intermingled with 'true' rainforest. In addition, Bolivia, Venezuela and the Guyanas are likely to harbour unreported mires. Hence, we estimate that there are around 150,000 km² of peatlands throughout Amazonia.

The average net ecosystem production of peatland ecosystems has remained positive for millennia, manifested by accumulation of peat. In nutrient-poor boreal mires, summertime (5 months) net ecosystem production can be 119 g C m⁻² (ref. 8), about three times the average (1980–94) annual value (about 42 g C m⁻², "climate with CO₂") reported by Tian *et al.*¹ for the Amazon Basin. However, peat deposits can also release considerable amounts of carbon. When the water-table is exceptionally low, summertime carbon emissions from boreal peatlands can be 83 g m⁻² (ref. 8), more than twice the highest annual value (about 40 g m⁻²) of Amazonia¹. Hardly any data exist on carbon fluxes of tropical peatlands. During drought, constantly high temperatures presumably render them strong carbon emitters. As soil moisture is apparently an important controller of carbon storage in Amazonia¹, incorporating such a response into the Terrestrial Ecosystem Model would further increase carbon emissions in El Niño years. The net ecosystem production of Amazonian peatlands is hard to estimate without ecological knowledge of the systems, but it might significantly affect the total carbon budget of the basin.

Finally, the soil organic carbon density (C_s) estimate⁹ used to validate the Terrestrial Ecosystem Model¹ was based on the RADAMBRASIL survey¹⁰, which excluded peat soils and covered only Brazil. When peatlands and other Amazonian countries are also included, C_s becomes close to 12 kg C m⁻², which is 30% greater than

the value obtained with the Terrestrial Ecosystem Model¹.

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1. Tian, H. *et al. Nature* **396**, 664–667 (1998).
2. Grace, J. *et al. Science* **270**, 778–780 (1995).
3. Lappalainen, E. (ed.) *Global Peat Resources* (Int. Peat Soc., Jyväskylä, Finland, 1996).
4. *ONERN Perfil Ambiental del Peru* (Oficina Nac. de Eval. de Rec. Naturales, Lima, 1986).
5. Etter, A. *Mapa general de Ecosistemas de Colombia* (Inst. de Inv. de Rec. Biol., Alexander von Humboldt, Bogotá, 1998).
6. Winckell, A., Zebrowski, C., Sourdat, M. & Zavgorodnyaya de Costales, S. in *Geografía Básica del Ecuador*, Tomo 4, Vol. 2 (Centro Ecuatoriano de Investigación Geográfica, Quito, 1997).
7. Suszczynski, E. F. in *Proc. 7th Int. Peat Congr., Dublin* Vol. 1, 468–492 (Int. Peat Soc., Jyväskylä, Finland, 1984).
8. Alm, J. *et al. Ecology* **80**, 161–174 (1999).
9. Moraes, J. L. *et al. Soil Sci. Soc. Am.* **59**, 244–247 (1995).
10. *Projeto RADAMBRASIL Levantamento De Recursos Naturais* Vols 3–20, 22, 25 & 26 (Dept Nac. Prod. Min., Rio de Janeiro, 1973–84).

Tian et al. reply — Our model-based analysis of the effects of interannual climate variability and increasing atmospheric CO₂ concentration on carbon storage in Amazonian ecosystems focused on CO₂ exchanges between the atmosphere and undisturbed forests and other upland ecosystems of the region¹. Crutzen *et al.* urge us to add the emissions of isoprene and other volatile organic compounds (VOCs) to our analysis. They argue that ignoring these emissions could lead to an overestimation of annual net carbon storage (net ecosystem production) in the Amazon Basin.

We did not include VOCs in our Terrestrial Ecosystem Model because not enough is known about their production, such as controls on rates, and tree species involved². The parameterization of CO₂ uptake (gross primary production) in the model is based on an estimate of the sum of net primary production and plant respiration, and does not include allocation of carbon to support the production of VOCs. Because we make no allowances in the model for CO₂ uptake by plants to support the production of VOCs, we make no allowances for emissions associated with VOCs. The estimates of net ecosystem production in our current version of the model are therefore independent of VOC emissions, and should not be corrected downwards for them.

However, the future development of the Terrestrial Ecosystem Model will certainly include the addition of VOCs because of their importance in tropospheric chemistry. Because the model is subject to mass balance constraints, we expect that our estimates of both gross primary production and net primary production will increase to accommodate the addition of VOC fluxes.

Schulman *et al.* suggest that we consider carbon fluxes between the atmosphere and peatlands in our calculations of net ecosystem production for the Amazon Basin.

They state that these ecosystems cover a large area, and they assume that tropical peatlands are likely to be at least as responsive to climate changes as their boreal counterparts. From our review of the literature on the areal extent of peatlands in Amazonia^{3,4}, we conclude that Schulman *et al.*'s estimate of peatland area in the basin, 150,000 km², is reasonable. If we combine the total peatland area of Amazonia with the boreal peatland flux rates cited by Schulman *et al.*, the resulting basin-wide fluxes are small. A carbon storage rate (positive net ecosystem production) of 119 g C m⁻² yr⁻¹ translates to an annual basin-wide storage of about 0.02 Pg C, and a carbon loss rate (negative net ecosystem production) of 83 g C m⁻² yr⁻¹ translates to an annual basin-wide release of about 0.01 Pg C. For interannual climate variability to have a significant effect on the net ecosystem production of Amazonia through peatlands, these ecosystems would have to be much more sensitive than boreal peatlands to climate shifts.

There is evidence that this is not the case. The literature on peatlands in warm climates indicates that, because of the poor quality of their organic matter, decomposition rates in these ecosystems are low under both aerobic and anaerobic conditions⁵. This is not true for boreal peatlands, where the low temperatures that prevail for most of the year slow the decay of plant litter. Slow decay leads to a build-up of relatively high-quality organic matter that decomposes rapidly under warmer and drier conditions. Because tropical peatlands may be less sensitive than boreal peatlands to interannual climate variability, and because the area of peatlands is relatively small in Amazonia, we conclude that the net ecosystem production of the Amazon Basin is little influenced by the effects of year-to-year variability on carbon storage in its peatlands.

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1. Tian, H. *et al. Nature* **396**, 664–667 (1998).
2. Lerdau, M., Guenther, A. & Monson, R. *Bioscience* **47**, 373–383 (1997).
3. Junk, W. J. in *Mires: Swamp, Bog, Fen and Moor* (ed. Gore, A. J. P.) 269–294 (Elsevier, Amsterdam, 1983).
4. Junk, W. J. in *Transport of Carbon and Minerals in Major World Rivers* (eds Degens, E. T. H., Kempe, S. & Herrera, R.) 267–283 (Mitt. Geol.-Palaont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd, Hamburg, 1985).
5. Bridgman, S. D. & Richardson, C. J. *Soil Biol. Biochem.* **24**, 1089–1099 (1992).