

mianserin (Fig. 1c), a potent antagonist at insect octopamine receptors *in vitro*^{4,5} and active in honeybees *in vivo*⁷.

The effective doses in this study were at least three orders of magnitude larger than endogenous levels in the brain⁸. Direct application to the brain might have allowed the use of lower doses, but would probably not have been compatible with a bioassay with unrestrained bees. Another possible side effect of this bioassay was that control bees did not discriminate between nestmates and non-nestmates as well as they normally do², perhaps because of the smaller group size.

Nestmate recognition is thought to require an individual to form a mental template based on learned (presumably olfactory) recognition cues of itself or its close relatives; the similarity of a conspecific's recognition cues to those represented by the template is then used to assess relatedness. We suggest that a higher octopamine concentration improves nestmate recognition by acting as a neuromodulator in the brain and increasing attention to relevant olfactory stimuli, so that fewer recognition mistakes are made. This is consistent with the finding that differences between treated and control bees resulted in both decreased aggression towards nestmates and increased aggression towards non-nestmates. It is also consistent with previous findings for bees that octopamine increases the rate of antennal scanning⁹, improves performance on an olfactory learning test⁴, and decreases the threshold of response for behavioural stimuli in other systems¹⁰. Octopamine levels in the bee brain increase with age⁸, and older bees are more defensive than younger bees. These results demonstrate that kin recognition, with widespread occurrence and compelling adaptive significance, offers promising experimental material for neuroethological analysis.

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Parameters for global ecosystem models

Tian *et al.*¹ have used their process-based ecosystem model to estimate the net CO₂ exchanges, also called net ecosystem productivity, for the years 1980–94. They deduced a large interannual variability ranging between –0.2 (from land to atmosphere) and +0.7 petagrams of carbon (Pg C) per year, the variability being mostly a function of soil moisture, which in turn is largely regulated by precipitation and temperature. These values were derived by including the modelled effects of increasing atmospheric levels of CO₂. The above numbers are the differences between net primary productivity and heterotrophic respiration. Over the given time period for the CO₂ feedback case, these values were 5.0 (±0.3) and 4.8 (±0.1) Pg C per year, respectively. The calculated net ecosystem productivity was thus a small fraction, between –4% and +14%, of the net primary productivity, with an average over the 15-year period of +4%.

We wish to point out that another carbon-release process, involving the emissions of isoprene (C₅H₈) and other volatile organic compounds (VOCs) from the Amazon vegetation to the atmosphere, must be taken into account. Guenther *et al.*² have estimated a global VOC emission of 1.15 Pg C per year, corresponding to an average global fraction of 2.4% of the net primary productivity. With the relatively larger VOC contributions from deciduous forests, this fraction will be of the order of 3% for tropical forests. The oxidation of isoprene to CO₂ does not occur promptly, but involves many reactions in which compounds such as CO and oxidized hydrocarbons are formed; these compounds have lifetimes of the order of days to a month (in the case of CO). The neglect of VOC emissions can lead to a substantial underestimate of the ultimate release of carbon from the tropical ecosystems to the atmosphere.

In our research in the forested regions of Surinam during March 1998 (refs 3,4), we used a proton-transfer-reaction mass spectrometer on an aircraft to detect VOCs. We measured not only high concentrations of short-lived (hours) isoprene averaging 2.8 nmol mol⁻¹, but also high concentrations of

up to 13.5 nmol mol⁻¹ of various VOC compounds with a positive ion mass of 43 atomic mass units such as propan-2-ol, as well as formic acid and acetic acid with average molar ratios approaching 10 nmol mol⁻¹.

In agreement with Guenther *et al.*², we conclude that a proper forest-ecosystem carbon budget analysis must take into account the emissions of VOCs as well as of CO₂. Not only are direct emissions of VOCs from intact vegetation important, but leaf wounding is a significant additional source of VOCs³; herbivores consume (and thus wound) about 40% of tropical forest above-ground net foliar production⁶. Research is greatly needed to make better estimates of these emissions and the processes affecting them in order to expand the model of Tian *et al.*¹. This is also important for an understanding of the air chemistry above the tropical forests and its influence on global chemistry^{7,8}.

The occurrence of fires is an additional factor that must be taken into account. 'Dry' years, during which emissions of CO₂ are highest owing to low soil humidity¹, are also years of more extensive fires in the tropics, further increasing the interannual variability of carbon release.

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We agree that the Terrestrial Ecosystem Model analyses by Tian *et al.*¹ of carbon fluxes of Amazonian ecosystems represent a methodological improvement compared with extrapolation from site-specific estimates², especially with regard to spatial resolution. However, the resolution of a model cannot be finer than that of the input data, and Tian *et al.* disregard one important group of ecosystems: peatlands. This is understandable, as the literature grossly underestimates the extent of peatlands in Amazonia. Our estimate is 150,000 km², ten times more than previously reported.

A global peat resource assessment³ erroneously implied a mire area of 15,000 km²

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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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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