The unstoppable oil palm? Oil palm is a tropical crop that presents the highest yield per hectare of oil-producing crops in the world. New high-yielding varieties could spare land for forests worldwide or could increase tropical deforestation as oil production is transferred to the tropics. The image shows land cleared for oil palm plantation in Malaysian Borneo.

CONSERVATION

A double-edged sword for tropical forests

Contrary to expectation, high-yielding tropical crops may cause forest loss in the tropics

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With a growing global population and increasing per capita consumption, reconciling agricultural production with biodiversity conservation is a major challenge to humanity (*1*). A frequently promoted solution to stem the tide of agricultural expansion is to increase crop yields, allowing global demand to be met without further tropical forest losses. Recent genome sequencing of key crops such as oil palm, eucalyptus, rubber, soybean, rice, and cocoa could facilitate substantial yield increases (*2–4*). Could such yield improvements offer a solution to both tropical forest loss and agricultural demand, or could they pose further challenges to tropical conservation?

Among the above crops, oil palm is one of the main drivers of tropical forest conversion (see the first figure) as a result of increasing demand for cosmetics, edible oil, and biofu-

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els. As global demand for oil palm continues to grow (*5*), there is concern that the massive forest conversion to oil palm observed in Southeast Asia (see the second figure) could be reproduced in Africa and Latin America.

Oil palm yield increases are already a reality. For instance, top producer Sime Darby's new "super palms" variety, which can increase yields from 4 to 10 tons/ha and was developed through molecular breeding, is expected to debut next year (*6*). Increasing yields are aligned with the Malaysian government's oil palm strategy of replacing low-yield palms with new higher-yielding varieties. Oil palm genome sequencing may also make possible the generation of seeds resistant to diseases, drought, and salinity. As a result, currently low-yielding areas would become more productive.

Intensification through yield improvement is at first glance very positive news for conservation. In theory, the global demand for palm oil could be met on less land, thus sparing land for nature (*7*). By 2050, the demand for palm oil is expected to rise substantially, leading to dramatic additional demand for land in the absence of yield improvements (*5*). Moderate yield

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improvements, from the current 4 tons/ha to 5.2 tons/ha, could lead to a global saving of 7 million ha (47% of the current global oil palm area or 7% of Indonesia's forests) that would be converted under the status quo assumptions (*5*). However, these estimates do not account for international trade and the fact that palm oil can be substituted by buyers for other vegetable oils such as soybean or rapeseed oil.

Simulations with a global trade general equilibrium model suggest that an assumed 56% increase in oil palm yield per tree in Malaysia and Indonesia has two potentially positive outcomes for biodiversity: a drop in the global price of palm oil by 4.3% and of vegetable oils generally by 2.5%, and a net increase in global forest area of ~300,000 ha (*8*). The simulations suggest that ~400,000 ha of agricultural land (equivalent to ~6% of Indonesia's oil palm area) would be taken out of production in Brazil, India, and Canada. Left uncultivated, this land could regenerate into secondary forest of conservation value.

The simulations in (*8*) also show a potential negative outcome for biodiversity: an expansion of 65,000 ha of cropland for

oil palm and 47,000 ha for pastures at the expense of tropical forests in Malaysia and Indonesia. The reason is that technological advances lead to higher returns to farmers in the region, encouraging the use of more land (8). Thus, a substantial proportion of the potential for tropical forest regeneration is negated by market effects.

A large part of the land sparing with potential for forest regeneration occurs in temperate regions, where most species are not threatened with extinction. For example, 40% of the predicted spared land is in Canada (8), presumably because high-yielding oil produced in tropical countries outcompetes crops such as rapeseed or soybean grown in temperate regions. This transfer of vegetable oil production from temperate to tropical regions as a result of international market mechanisms (9) is a worrying consequence of improving oil palm yields.

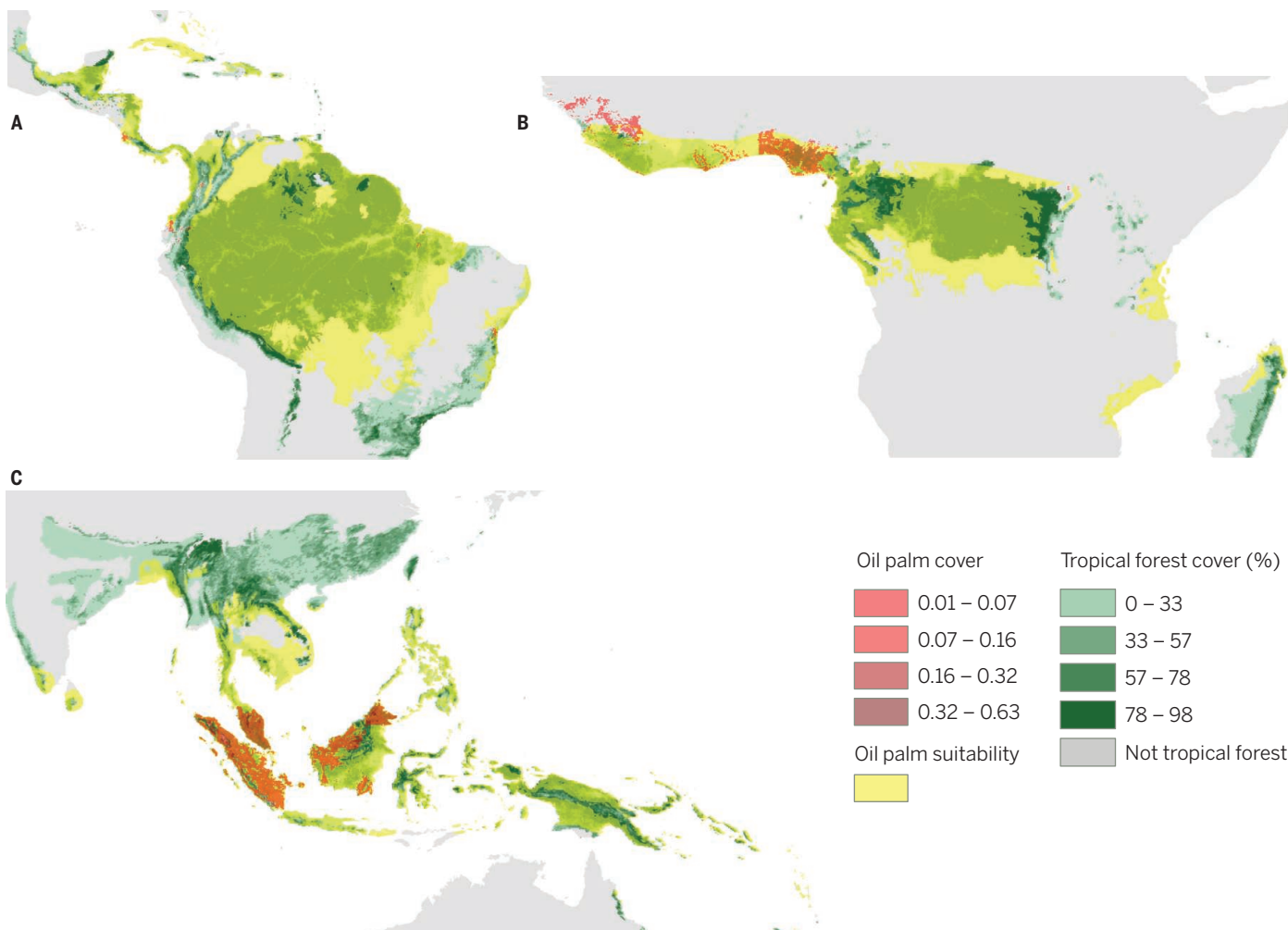As the demand for palm oil continues to increase, yield improvements could also present further challenges to conservation by allowing expansion of oil palm to countries where little oil palm is currently grown. In both Africa and Latin America, vast tracts of land highly suitable for oil palm production are still covered by tropical forests (see the second figure). Lower yields of African and Latin American varieties and higher production costs have so far prevented an explosive expansion of oil palm production in these regions. Having exploited the most suitable land for oil palm in Southeast Asia, oil palm companies are now investing in Africa (10). Availability of high-yielding varieties more suitable for difficult growing conditions is likely to accelerate this trend.

The global interconnectedness of oil palm production requires a large-scale, predictive approach to conservation planning (7). For instance, African governments could control the expansion of new oil palm varieties by dividing land into areas available for oil palm conversion (such as degraded land), those that are key for local livelihoods and require community-level management, and those allocated mainly for conservation. Landscape-scale planning could help to reconcile the economic benefits of the new varieties with ecosystem service provision (such as flood protection and carbon sequestration), improving the livelihoods of local people, and minimizing biodiversity losses.

Global initiatives can also help to realize the potential social and conservation benefits of land spared through oil palm yield improvements. Such initiatives may include the introduction of strong safeguards by governments to prevent further expansion of oil palm cropland into forests and into communal agricultural areas important for local food security. Certification schemes such as the Roundtable for Sustainable Palm Oil (RSPO) should be strengthened through the inclusion of stricter environmental criteria and greater consumer pressure for change. This would give companies an incentive to respond to biodiversity concerns (10).

The case of oil palm resonates with other crops driving tropical deforestation

Oil palm cover		Tropical forest cover (%)	
	0.01 – 0.07		0 – 33
	0.07 – 0.16		33 – 57
	0.16 – 0.32		57 – 78
	0.32 – 0.63		78 – 98
Oil palm suitability			Not tropical forest

Rapid expansion. Oil palm has been one of the main drivers of deforestation in the tropical forests of Southeast Asia. New high-yielding varieties could promote expansion in Africa and Latin America by increasing its productivity there. The maps overlay extant tropical forests, in 2005, distribution of oil palm covering more than 1% of the landscape in 2000 (14), and oil palm yield potential > 0 [based on oil palm suitability maps from (15)] in (**A**) Latin America, (**B**) Africa, and (**C**) Southeast Asia.

Left column (continuation):

for which genetic improvements have recently been achieved. For instance, new high-yielding genetically modified varieties of eucalyptus are being considered for use by Brazil, raising concerns that the new varieties will encourage further expansion of plantations and pose biosafety risks through gene flow (11). Although the oil palm varieties under current consideration are not genetically modified, common patterns exist in their implications for tropical land use. Genome sequencing and variety improvement are also likely to affect the land use dynamics of many other tropical crops. A consortium that includes Mars Inc. and the University of California has sequenced the cacao genome and is working on sequencing almost 100 other neglected African crops (12). The new varieties could be capable of pest and disease resistance, drought tolerance, and higher yield quality. These new traits could improve livelihoods but may also lead to crop expansion in previously unsuitable areas.

As the oil palm example shows, there is a danger that improvements in tropical crop yields will further transfer agricultural production from temperate to tropical regions, leading to more tropical deforestation and thereby limiting the social and ecological benefits of high-yielding varieties. To help governments to prepare for the indirect effects of the new crop varieties, scientists need to relate globally interconnected land use dynamics to local conservation actions (13). This requires the development of models of the drivers of environmental change that incorporate feedbacks at a range of scales. These models will help governments to preempt and plan for the unintended negative consequences of technical advances. ∎

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IMMUNOLOGY

A neighborhood watch upholds local immune protection

T cells that reside in peripheral tissue create conditions that enable local and broad responses to infection

By **Francis R. Carbone** and **Thomas Gebhardt**

"Memory" T cells are "antigen-experienced" cells that are generated during a prior infection. Capable of migrating through extra-lymphoid regions of the body (*1*), they are poised to mount a swift and strong response when they next recognize the pathogen. The description of effector memory T cells (T_{EM}) built on this notion (*2*), and by extension, peripheral immunity was thought to rely extensively on T_{EM} cell recruitment from blood to extra-lymphoid tissues such as the gut and skin. Nevertheless, recent attention has turned to memory T cells that permanently reside in the periphery, with little or no representation in the wider circulation. These "tissue-resident" memory T cells (T_{RM}) are more effective in controlling peripheral infection than their circulating counterparts (*3*). On pages 93, 98, and 101 of this issue, Iijima and Iwasaki (*4*), Schenkel *et al.* (*5*), and Ariotti *et al.* (*6*), respectively, probe the mechanistic underpinnings of the persistence and protective function of tissue-resident memory T cells.

Whereas most studies on tissue-resident memory cells have featured the CD8 T_{RM} cell subtype, Iijima and Iwasaki examine the CD4 T_{RM} cells remaining in mouse mucosa after the clearance of vaginal infection with herpes simplex virus. Those CD4 T_{RM} cells were not replenished from the blood and do not freely migrate. Instead, they were found in aggregates surrounding macrophages, forming a distinct microanatomical structure that the authors call a "memory lymphocyte cluster." The main driver of cluster formation appears to be a combination of the cytokine interferon-γ (IFN-γ), which is released by the CD4 T_{RM} cells, and chemokines [predominantly chemokine (C-C motif) ligand 5] produced by macrophages that are central to cluster formation (see the figure). Importantly, ablation of the macrophages or disruption of the chemokine network resulted in dissolution of clusters, disappearance of CD4 T_{RM} cells, and concomitant loss of local immune protection.

What drives the IFN-γ expression in memory lymphocyte clusters is left undefined, although Iijima and Iwasaki speculate that residual antigen may be involved despite the absence of detectable virus. Although CD4 T_{RM} cells and CD8 T_{RM} cells share important commonalities, there are key differences that support this idea. Both subsets demonstrate parallel modulation of molecules required for tissue egress, such

> *"Tissue-resident memory T cells may be the immune cells of choice in designing strategies to stop pathogens before they establish a meaningful infection."*

as the sphingosine-1-phosphate receptor 1 and C-C chemokine receptor type 7 (*7*, *8*). However, memory lymphocyte clusters are not required for CD8 T_{RM} cell retention, especially at body surfaces where these cells can be widely dispersed within the epithelium (*9*, *10*). More importantly, CD8 T_{RM} cells can form and persist in the absence of prior localized infection (*11*). Differences in the requirements for long-term peripheral persistence between CD4 T_{RM} cells and CD8 T_{RM} cells were highlighted in an earlier study that showed that only CD8 T_{RM} cells remained in vaginal mucosa after nonspecific recruitment (*12*). By contrast, their CD4 counterparts were not maintained under those same conditions, now explained by the absence of memory cluster formation without prior infection (*4*). Whether this reflects an underlying antigen-dependent basis for CD4 T_{RM} cell retention, in contrast to a cell-intrinsic CD8 T_{RM} developmental process (*7*, *8*), remains unknown.

Schenkel *et al.* and Ariotti *et al.* focus on the effector mechanisms involved in infection control by CD8 T_{RM} cells. A rapid CD8 T_{RM} cell–dependent recruitment of circulating memory T cells to sites of viral infection has been described as a consequence of im-