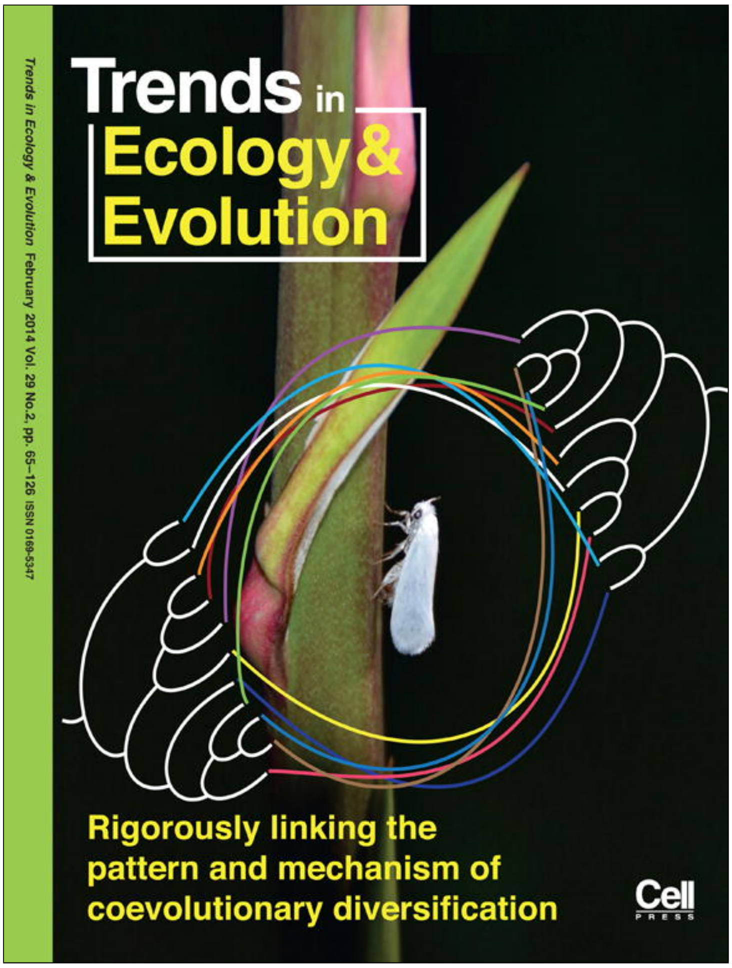
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Review

Agricultural expansion and its impacts on tropical nature

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The human population is projected to reach 11 billion this century, with the greatest increases in tropical developing nations. This growth, in concert with rising per-capita consumption, will require large increases in food and biofuel production. How will these megatrends affect tropical terrestrial and aquatic ecosystems and biodiversity? We foresee (i) major expansion and intensification of tropical agriculture, especially in Sub-Saharan Africa and South America; (ii) continuing rapid loss and alteration of tropical old-growth forests, woodlands, and semi-arid environments; (iii) a pivotal role for new roadways in determining the spatial extent of agriculture; and (iv) intensified conflicts between food production and nature conservation. Key priorities are to improve technologies and policies that promote more ecologically efficient food production while optimizing the allocation of lands to conservation and agriculture.

A tropical time bomb

Tropical ecosystems sustain much of Earth's biological diversity [1], provide myriad natural products and services to local communities [2], and play key roles in the global carbon and hydrological cycles [3,4]. Unfortunately, many tropical ecosystems are being disrupted by large-scale land-use change and other environmental alterations [5]. Such changes are an important source of greenhouse gas emissions [3,6] and are likely to have serious, if uncertain, impacts on biodiversity [5,7–9].

Tropical ecosystems will face even greater pressures in the future, especially from the expansion of agriculture [10–12]. The global footprint of agriculture is already massive: cropland encompasses an area the size of South America, and grazing lands an additional area the size of Africa [13]. Yet pressures to increase food production in coming decades will be enormous. The global population exceeded 7 billion in 2011 and is projected to approach 11 billion by the end of this century, with the population of Africa nearly quadrupling [14]. Even now, nearly 1 billion people are undernourished [15]. Beyond feeding the growing populace and eliminating hunger, rising incomes in many developing nations mean that demands for meat and dairy products are also increasing. By 2050, global food needs are expected to rise by 70–110% [10,16]. Demands for bioenergy production and bio-feedstocks for industry could also increase sharply [17,18]. These growing needs must be met by agricultural systems increasingly stressed by climate change [19].

Given the remarkable magnitude and pace of these changes, it is not inappropriate to characterize the coming era as an 'agricultural bomb'–one whose detonation will create profound challenges for human welfare and environmental conservation. The epicenter of this explosion will be in the tropics, because much of the projected growth in global population will occur in tropical nations [14], and these nations are also experiencing marked, if regionally variable, increases in living standards and per-capita food consumption [16,20]. Bioenergy production is also likely to expand far more in the tropics than elsewhere [21,22] because the climate allows year-round growth for crop production and the land is generally less expensive than in temperate countries that are further along the development pathway.

Here we assess how agricultural expansion this century will impact on tropical terrestrial and aquatic ecosystems. We highlight likely trends and some key uncertainties, and consider their implications. We also argue that improving agricultural technologies and policies will be crucial for reducing threats to tropical nature while allowing the world's food, fiber, and biofuel needs to be met more sustainably.

Major trends

Expanding agriculture

The global footprint of agriculture is likely to increase markedly this century–indeed, the global extent of cropland is currently expanding faster than at any time in the past 50 years [23]. A study that extrapolated into the future based on linear trends from the early 1960s to 2000, when global food production doubled, concluded that ~1 billion ha of additional land, mostly in developing nations, would need to be converted to agriculture by

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Box 1. Costly energy, costly food

Because intensive agriculture requires large amounts of energy, energy prices strongly influence food prices (Figure I). Modern farms are major consumers of fuel and electricity. In addition, the production of nitrogen-based fertilizers is energy demanding and their cost is strongly influenced by petroleum and natural gas prices [118]. Furthermore, lowland tropical soils, including vast expanses of the Amazon and Africa, are limited by phosphate, the minable stocks of which are declining and often located far from tropical agricultural regions [119,120]. Production, transportation, and application costs for phosphate will clearly rise with energy prices.

Global energy demands could double by 2050 [118], making energy more expensive and hindering efforts to feed billions more people with intensified agriculture. Nonetheless, technological advances for accessing petroleum and natural gas in deep-shale formations could help maintain relatively stable energy prices for the next 1–2 decades [121], assuming this can be achieved with acceptable environmental impacts. For example, the USA is projected to become the world's largest petroleum producer by 2020, surpassing Saudi Arabia, as a result of its increasing exploitation of deep-shale reserves [122]. Large reserves of unconventional petroleum and natural gas are also thought to exist in Russia, China, Venezuela, and Sub-Saharan Africa [121]. In the short to medium term, stable energy supplies could support agricultural intensification, especially if prices for key crops, such as major cereal grains and oilseeds, were to rise more quickly than do costs for energy.

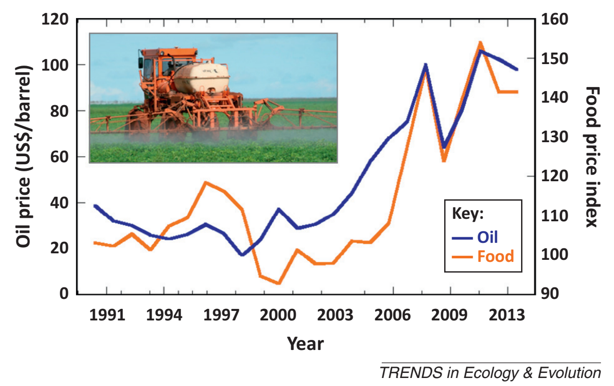

Figure I. Relation between annual oil and food prices from 1990 to 2013. Oil price was a strong predictor of food price ($F_{1,22} = 64.31$, $R^2 = 74.5\%$, $P < 0.0001$; linear regression analysis). (Data sources: US Energy Information Administration for crude oil import prices; FAOSTAT for the UN Food Price Index, which combines prices for meat, dairy, cereals, edible oils, and sugar; all values adjusted for inflation.) Inset: tractor in Brazilian soy field: copyright Greenpeace (www.greenpeace.org/forests).

2050 to meet projected demands [10]. This is a land area larger than Canada.

However, if agriculture can be made more efficient, the amount of additional land needed could be much smaller. Large areas of the tropics, including most of Africa, have relatively inefficient agriculture dominated by smallholders who lack access to modern agricultural technologies [24,25]. Such farmers frequently have large 'yield gaps'–differences between their actual and potential agricultural production [26–28]. Another projection of future agricultural trends assumed that food production could be markedly increased by closing such yield gaps, via progress in crop and animal genetics, appropriate nutrient inputs and limiting crop waste through pest management and improved transport [16]. This study optimistically suggested that yields in developing nations could double by mid-century with just 120 million ha of additional agricultural land. A key prerequisite for such large-scale intensification, however, is affordable and reliable energy supplies (Box 1).

Continental trends

As the 21st century unfolds, the greatest expansion of agriculture will almost certainly occur in South America and Sub-Saharan Africa [10,16,29], which have large land areas with unexploited agricultural potential. These include not just humid forests, such as the Amazon and Congo Basins, but also vast expanses of semi-arid land, such as the Cerrado and Pantanal regions in South America and the Miombo and Guinea savanna-woodlands of Africa.

Technological advances are underpinning much agricultural expansion in the tropics. Improving medical technologies are increasingly allowing humans to colonize areas once plagued by diseases such as malaria, sleeping sickness, and river blindness [30,31]. Agricultural expansion is also being facilitated by improved crop and soil management practices that support higher yields in humid tropical areas, which tend to have acid-infertile soils and heavy pest pressure. Major expansion of soy into the Amazon is now possible because of new soy varieties better adapted to tropical photoperiods and copious use of lime, fertilizers, and pesticides to overcome soil and pest constraints [32]. Furthermore, up to half of the Amazon [33] and much of humid Equatorial Africa [34] could potentially support oil palm, which can grow well on acid-infertile tropical soils if adequate fertilizer is applied.

Roads and agriculture

What factors will limit the future expansion of agriculture? Historical trends suggest farmers and agricultural interests will rarely be self-limiting (Box 2). Instead, other factors, such as energy prices, labor costs, water and land availability, and especially transportation networks, are more likely to determine the regional and local footprints of agriculture.

We live in an era of unprecedented expansion of roads and other transportation infrastructure in the tropics [35]. Roads are now penetrating into many of the world's last tropical wildernesses, such as the Amazon [36–38] and Congo [39,40] Basins. Valuable resources such as timber, minerals, oil, and arable land often provide the economic impetus for initial road construction. Ambitious national and regional programs to access such resources drive road expansion, both directly and indirectly [35,41]. For example, schemes to dramatically expand hydroelectric projects in the Andes-Amazon [42] and lower Mekong regions [43] will result in a proliferation of roads required for dam and powerline construction. In Sub-Saharan Africa, a massive growth of mining and other extractive industries is prompting new development corridors and associated road and rail networks [44–46].

Unfortunately, roads can also open a Pandora's box of environmental problems, including legal and illegal land colonization, land speculation, deforestation, fires (Figure 1), and overhunting [35,37–40,47]. Such problems are often exacerbated by limited governance in frontier regions [38,48]. By providing year-round access to natural resources, paved highways have particularly large-scale

Box 2. Will yield increases spare land for nature?

A hotly debated issue is the degree to which agricultural intensification and yield increases will facilitate land sparing for nature conservation (Figure I) [90,123,124]. Land sparing via intensification is a key tenet of the Green Revolution [91] and is often advocated as a strategy to preserve natural habitats for biodiversity while increasing agricultural production [92–94]. When examined at a national level, however, the land-sparing effect seems variable and strongly dependent on local context [125]. What is unclear is how much land will actually be spared if, as seems likely, agriculture in the future becomes even more industrialized and globalized [126]–whereby capital and goods move freely across borders [127], corporate land grabbing continues in developing nations [21,22], and maximizing profits remains a prime objective.

These realities suggest that increasing yields on existing farmland is a necessary, but not sufficient, condition to spare land for nature conservation [128]. Unless accompanied by improved governance [51], efforts to limit international leakage, and especially effective land-use planning and zoning [129], yield increases might simply facilitate an expansion of farming into all available lands [128,130]. In addition, yield increases will elevate the opportunity costs for nature conservation (the potential income that is lost if land is not converted to agriculture). As a result, conservation-incentive payments, such as those from international carbon-trading schemes, would have to be increased to be competitive with agriculture [51].

Figure I. Those advocating intensive agriculture argue it is the only way to feed up to 11 billion people while sparing some land for nature conservation, whereas others view diversified smallholder farming as a more sustainable and nature-friendly alternative: **(A)** industrial oil palm plantation in Sumatra, Indonesia; **(B)** clearing of native forest for industrial wood-pulp production in Sumatra; **(C)** small-scale farmers in Gabon; **(D)** aftermath of slash-and-burn farming in the central Amazon (photos reproduced, with permission, from W.F. Laurance).

impacts on forests [36], as they tend to spawn secondary roads that amplify the extent of forest conversion. For instance, the Brasília–Belém highway, completed during the early 1970s, has today evolved into a 400-km wide slash of forest destruction across the eastern Brazilian Amazon [35].

Major uncertainties

As agriculture expands, a key unknown is the degree to which biofuel production will influence land-use trends in the tropics. Under current technologies, bioethanol and biodiesel are among the few liquid fuels with high energy density that offer realistic alternatives to petroleum for the global transportation sector. If petroleum prices rise markedly in the future [49], then there could be great economic pressures to devote large land areas to biofuel-feedstock production–as much as 300 million ha by 2030, according to one estimate [21]. Biofuel production on anything approaching this scale could compete seriously with agriculture for available arable land [11,22], driving up land prices, amplifying pressures for further land clearing [50], and increasing opportunity costs for nature conservation [51].

However, much is uncertain about biofuels. Growing recognition of the environmental risks of biofuels could prompt helpful policy changes, such as a recent European Union directive to avoid biofuels that promote habitat destruction or are produced from crops used for food or animal feed (http://blogs.nature.com/news/2012/10/eu-reversal-on-biofuels-policy-kicks-off-fresh-battle.html). Moreover, new biofuel technologies are being developed that use plant biomass rather than simple sugars, starches, or oils from crops, which could reduce pressures on food supplies [17]. The biomass needed could come

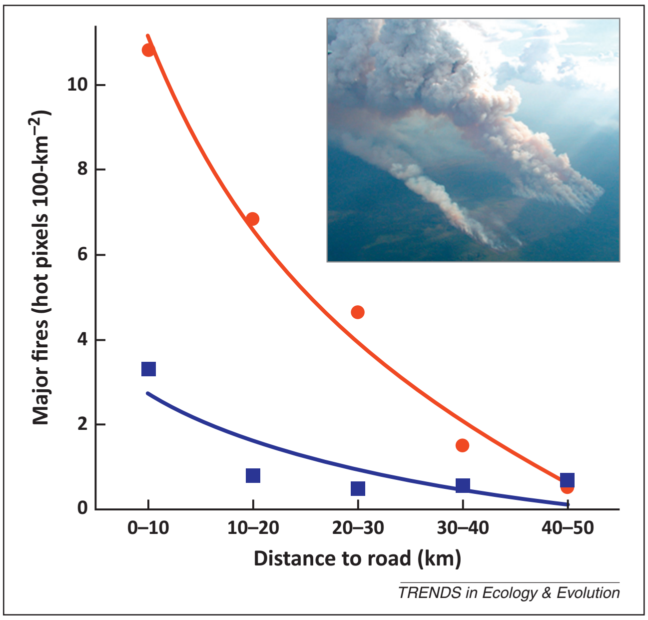

Figure 1. Roads have a major influence on patterns of land-use change. Shown are the frequencies of major deforestation fires as a function of distance from roads outside (red curve) and inside (blue curve) protected areas in the Brazilian Amazon (data from [47]). Inset: forest burning in Amazonia (photo reproduced, with permission, from M. Welling).

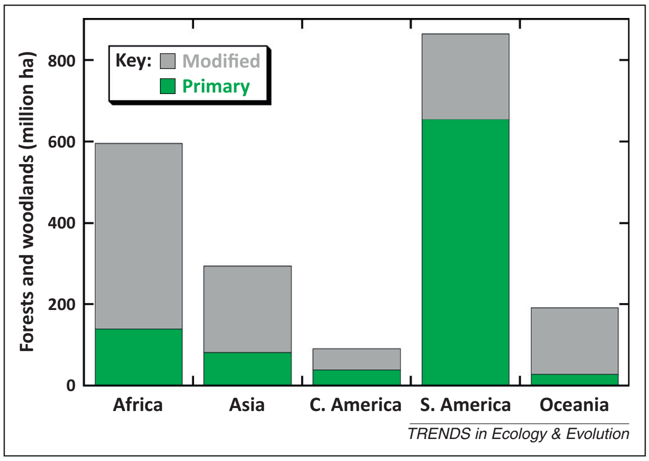

Figure 2. The decline of primary forests. Shown are the remaining areas of modified and primary (old-growth) tropical and subtropical forests and woodlands in Sub-Saharan Africa, South and Southeast Asia, Central America including the Caribbean, South America, and Oceania. Modified forests and woodlands include those that have been selectively logged, are regenerating on formerly cleared lands, or were converted to tree plantations [estimates based on UN (http://faostat.fao.org/faostat) statistics for 2010, augmented by data from relevant national experts].

partly from wood and cellulose waste [17], but might also be grown on agriculturally 'marginal' lands. In theory, global demand for food could eventually be sated, but demand for biofuels in an increasingly energy-hungry world might be effectively infinite.

A second key uncertainty is future climate change [52]. A particular concern is that shifts in the amount or seasonality of regional precipitation could strongly influence patterns of land occupancy, especially in the humid tropics where drying conditions can greatly increase forest susceptibility to fire [53]. Across the Amazon basin, for example, more-seasonal forests (which experience stronger dry seasons) are much more likely to be cleared and burned than are more humid forests [36]. Unfortunately, our capacity to project future changes in precipitation at local and regional scales, by downscaling global circulation models that simulate future climates, is poor [54]. Recent empirical data suggest that, in broad terms, drier regions are becoming drier and wetter regions wetter globally [55]. If this trend continues then it could prompt movements of people away from drier, drought-prone regions towards more humid areas of the tropics.

Impacts of agricultural change on tropical nature

Because they are so far-reaching, the environmental changes detailed above will have a wide array of impacts on tropical ecosystems and biota. Here we highlight some of the most important potential changes.

Forest loss and regeneration

Agriculture is expanding across a range of tropical ecosystems, but its impacts on forests are among the most serious from an environmental perspective. Tropical forests are still declining markedly in area [56] and the surviving forests are often modified to varying degrees. Tropical evergreen and deciduous forests originally spanned ~17 million km^2 globally and have now declined to ~11 million km^2 [9]. Forests will continue to shrink further this century, with 11–36% of forests existing in 2000 projected to disappear by 2050 [9,57]. Outside of protected areas, surviving forests will increasingly be concentrated in steep, remote, infertile, and hyper-wet areas.

Over half of the tropical or subtropical forest that persists today has been substantially altered (Figure 2). A quarter of the remaining tropical rainforest has been fragmented [58]. Many tropical forests are being logged, with one-fifth of these forests selectively logged at some level from 2000 to 2005 [59]. Additional pressures such as fuelwood harvests, hunting, and surface fires affect a large proportion of forested areas [9,60].

It has been suggested that tropical nations, as they develop economically and become increasingly urbanized, might experience land-use transitions that include a partial recovery of their lost forest cover [61,62]. However, such recovery will only occur if nations avoid or emerge from extreme poverty. In Ethiopia, Haiti, and Togo, for instance, poverty traps have forced farmers to clear their remaining forests for farming [63]. In nations where forest recovery occurs, it is often largely based on exotic tree plantations, including monocultures of rubber, eucalyptus, acacia, and oil palm. Plantations in developing nations grew by ~5300 km^2/year from 1990 to 2005, with the biggest increases in China and India [64]. In addition, many nations have large areas of regenerating (secondary) forest [9]. Older (>20-year-old) regenerating forests and those near seed sources can have fairly high conservation value [65,66] but many are being recleared before they can recover much value. In the Brazilian Amazon, for instance, one-third of formerly cleared lands sustain regenerating forests but these have a median age of less than 5 years [67].

Hurting hotspots

Expanding agriculture could have major impacts on biodiversity hotspots. These are 35 terrestrial biogeographic

Box 3. Extinctions and beyond

A vigorous debate in ecology concerns 'extinction debts' [131]–the degree to which species with small, fragmented populations affected by multiple stressors will vanish or persist over the next one to two centuries (e.g., [5,7,8]). This debate is overly simplistic, however, because it focuses solely on species (Figure I) while ignoring many other critical components of biodiversity.

As habitat disruption proceeds apace, many species are becoming locally extinct across large swaths of their geographic range. As this occurs they can experience marked losses of genetic, population, and geographic variation [132] that render them more vulnerable to environmental vicissitudes and random demographic events [133]. Many species–including numerous top predators and large-bodied animals that have played dominating roles in ecosystems–are almost functionally extinct [134]. For instance, the tiger, once widely distributed and having a large influence on animal and plant community structure, now clings to survival in just 7% of its original geographic range [135]. Such losses are often accompanied by wide-ranging ecological distortions [136,137] and the declines of many coevolved, ecologically dependent species [138].

Even without large-scale species extinctions, each year witnesses the loss of enormous amounts of biodiversity–evolutionary capital that has required millions of years to accumulate. The remnants of natural ecosystems are often greatly diminished, both taxonomically and functionally. In the coming century, limiting such losses while feeding up to 11 billion people will be one of the greatest challenges humanity has ever faced.

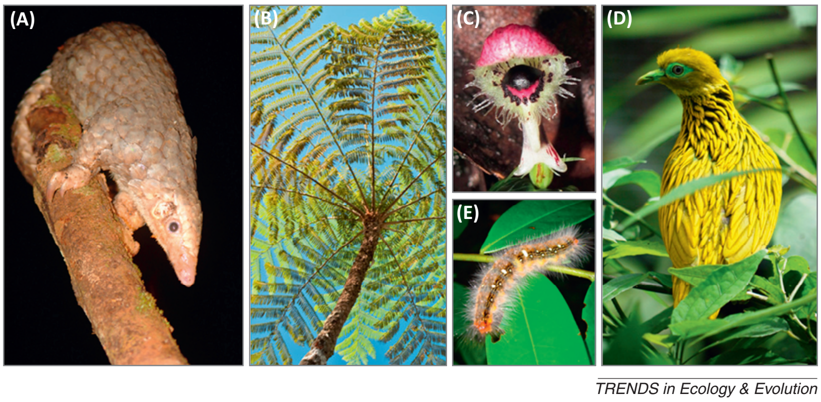

Figure I. Tropical biodiversity: **(A)** tree pangolin from Gabon; **(B)** tree fern from north Queensland; **(C)** *Corybas* orchid from Papua New Guinea; **(D)** gold dove from Fiji; **(E)** caterpillar from Suriname [photos reproduced, with permission, from W.F. Laurance (A, B, D, E) and S. Pimm Lyon (C)].

regions that sustain exceptional species richness and endemism (>1500 endemic plant species) and have suffered severe loss (>70%) of their original vegetation [1,68]. Tropical or subtropical ecosystems predominate in over half of the hotspots [68]. In addition to their many known species, hotspots evidently contain the bulk of unknown species on Earth, many of which are restricted endemics [69,70] and are likely to require undisturbed habitats for survival [71]. As such, hotspots are the world's most biologically important real estate.

Unfortunately, pressures on hotspots are likely to intensify further. Hotspots have unusually dense and rapidly growing human populations [72] that are often suffering from poverty [73] and score low on any measure of development [74]. During the 1990s, hotspot countries with the highest population growth rates and lowest human development had the greatest deforestation rates [74]. Pressing demands to increase food production, promote economic growth, and exploit natural resources could inflict high environmental costs on hotspot nations. Remaining habitats in hotspots sustain dense clumps of species, many with tiny geographic ranges whose populations are already reduced and fragmented [1,75]. Their continuing attrition could be especially perilous for biodiversity (Box 3).

Proliferation of human-dominated landscapes

As agriculture expands and intensifies, a key question is the degree to which biodiversity will persist in landscapes as they become increasingly dominated by humans [5,7]. Such landscapes can include agricultural lands, plantations, and secondary, logged, and fragmented forests. Relative to old-growth forest, biodiversity is reduced in all modified tropical forests [76], although to the smallest degree in selectively logged forests [76–78]. Larger (>100 ha) forest fragments [79] and older (>20-year-old) regrowth [65,66] can also sustain substantial biodiversity, but generally lack some ecological specialists and local endemics found only in large tracts of old growth [65,80]. Biodiversity can be moderate in some mixed-cropping and agroforestry systems [81], but is typically much reduced in plantation monocultures such as oil palm [82], rubber [83], and eucalyptus [84].

In the past, some ecologists assumed–wrongly–that modified lands will have very limited value for nature conservation (see [65,81] for more realistic views). Mosaics of disturbed and secondary habitats can provide important habitat and foraging sites for forest species, as well as stepping stones and corridors for biotic dispersal and animal migration [65,81,84–87]. Such mosaics can also be managed in some cases to benefit agriculture by promoting natural ecosystem services such as pest control and pollination [88,89]. The natural values of intensively managed farmlands and pastures are typically much lower than are those of taller and structurally more complex environments, such as logged and secondary forests, mixed plantings, and well-managed agroforestry systems [77,81].

Differing perceptions about biodiversity have complicated the debate about so-called 'land-sparing' versus 'land-sharing' strategies for agriculture. Those who advocate land sparing [90–94], in which agriculture is intensified in certain areas in order to spare lands for nature elsewhere (Box 2), tend to focus on vulnerable species that require undisturbed habitats. Advocates of land sharing, however, emphasize the role of generalist species that provide important ecosystem services [81,88,89]. Such species are favored by more benign farming approaches and multifunctional landscapes rather than intensive production systems.

Decline of freshwater ecosystems

Agricultural expansion is likely to exert particularly heavy pressures on freshwater ecosystems, whose biodiversity is even more severely threatened by human activities than that of terrestrial ecosystems [95]. Freshwater habitats sustain around one-third of all vertebrate species and 6% of global biodiversity [95,96]. Major river networks such as the Amazon, Congo, and Mekong are hotspots of species richness and sustain myriad local endemics [95].

In the tropics, large increases in water harvesting, damming, and diversion of rivers will be needed for agricultural expansion, intensification, and associated electricity needs [42,43]. Over 150 large (>2 MW) hydroelectric dams are being planned just for the Andean–Amazon region [42]. Flood plains will be prime targets for expansion of irrigated farming, especially in Africa. Many watercourses and lakes will suffer altered flows, higher temperatures, lower dissolved oxygen levels, and elevated loads of sediments, nutrients, pesticides, and other pollutants [96]. Declines of larger fishes, river migrants, and species requiring unpolluted, highly oxygenated waters and specialized microhabitats are common [96,97]. Many locally endemic fish and invertebrates are found entirely outside of protected areas [98], and relatively few protected areas encompass entire watersheds [99]. As a result, freshwater habitats are among the planet's most imperiled ecosystems.

Pressures on protected areas

In the face of massive environmental changes, protected areas are a cornerstone of efforts to sustain biodiversity and natural ecosystem processes. Approximately 6.6% of all tropical and subtropical forests are now in strictly protected areas (IUCN categories I–IV) and the total approaches 19% if multiple-use reserves (IUCN categories V–VI) are included [100]. Sizeable indigenous lands, especially in the Brazilian Amazon, also help to protect some forests [41,101]. Protection of drier tropical habitats, including grasslands, savannas, and shrublands, is somewhat lower, with 5.9% in strictly protected areas and 12.5% in all reserve categories [100]. Although the tropical protected-area system has grown markedly in the past quarter century, it is still inadequate because many threatened and locally endemic species fall entirely outside of protected areas [98].

As the human populace expands, tropical protected areas face growing threats. Funding for reserve management is limited [102] and many reserves are imperiled by illegal encroachment, logging, and hunting [103–105]. Many are also becoming isolated from their surrounding habitats [106]. In this context, agricultural expansion and intensification near reserves tend to erode biodiversity, because they diminish the quality of the matrix of surrounding habitats for wildlife use and movement [81,85,88] while intensifying harmful edge and spillover effects [79]. Anthropogenic threats inside and outside tropical reserves are often strongly correlated, suggesting that reserves will partially mirror their surrounding environments [104]. As their surrounding habitats become increasingly modified, reserves and their biodiversity will become increasingly imperiled.

Key challenges ahead

Over the course of the 21st century, humanity will face unprecedented environmental and societal challenges, many of which will play out in the tropics. Here we highlight some urgent priorities and opportunities for confronting these challenges.

First, food needs to be produced where people live, and that means increasing production in the tropics, where the greatest population growth is occurring. The good news is that there are large yield gaps in the tropics and thus considerable potential to increase crop production [27,28]. The bad news is that ongoing gains in crop yields are not keeping pace with population growth and income-driven increases in food demand [107,108]. The shift from small-scale, biologically more diverse farms to large-scale industrial agriculture is often portrayed as a threat to tropical nature. However, evidence from temperate regions suggests that industrial agriculture can produce more food while using land, water, fertilizers, pesticides, and energy much more efficiently [109,110], and this model is also likely to hold in the tropics.

Second, raising crop yields in tropical developing nations involves surmounting many obstacles. These include building local capacity and institutions needed to improve agricultural practices [24]; developing needed infrastructure for irrigation, energy, and crop transportation; and, most of all, increasing agricultural efficiency. In an increasingly resource-limited world, yield increases must be achieved with greater efficiencies for fossil fuels, pesticides, mineral fertilizers, water, and land. In promoting such changes, adaptable, multifaceted approaches are vital [24]. Given the great array of societies, crops, and farming systems across the tropics, there is no 'one size fits all' approach for achieving yield increases.

Third, too much food is being wasted. Worldwide, approximately one-third of the food produced for human consumption–$\sim$1.3 billion tons, on a fresh-weight basis–is lost [111]. Although great quantities of food are discarded in industrial nations, food losses in developing nations mostly occur after harvest, while food is being stored, transported, or processed. Reducing such losses, which can range from 10% to 40% of total food production [111,112], is a key priority for increasing agricultural efficiency and food security in the tropics.

Fourth, even with increasing yields, the tropics are likely to experience a massive increase in the footprint of agriculture. This will affect not only forests but also woodland, savanna, grassland, and wetland ecosystems. In this context, effective spatial planning and regulation of chaotic or opportunistic agricultural expansion are crucial. Of particular importance is managing the dramatic growth

Box 4. Roads and the agricultural footprint

In the tropics, as elsewhere, new roads are a major proximate cause of land-use change [35]. Spatial patterns of agricultural expansion are being strongly influenced by the burgeoning exploitation of timber, minerals, petroleum, and other natural resources, which provide a major economic impetus for road building. Some areas that are marginal as farming or grazing lands, such as those in remote areas or that have inadequate rainfall or infertile soils, are being exploited for this reason [48,139].

From an environmental perspective, roads that penetrate into remaining intact forests are the biggest peril, because they often promote large-scale forest loss and degradation [35,37,38]. Deforestation is exceedingly contagious spatially, such that the probability that a land parcel will be cleared rises dramatically if it is adjacent to an area that has already been cleared [140,141]. For this reason, the first cut into a forest is critical; if it occurs, then other cuts are likely to follow.

Nonetheless, high-quality roads that link existing agricultural areas with markets might actually reduce overall deforestation. Such roads can act as 'magnets' that attract farmers to areas that are already human dominated, and away from vulnerable frontier regions [111,142]. Such roads could promote greater agricultural efficiency while benefitting farmers economically.

As the 21st century progresses, proactively planning and zoning new roads will be vital for limiting the footprint and impacts of agriculture [113]. Such efforts will help to ensure that biologically critical lands are spared for nature conservation.

of transportation infrastructure, which has a major impact on the pattern and pace of agricultural expansion (Box 4). The most urgent priorities, in our view, are limiting road expansion into the world's last surviving tropical wildernesses [113] and slowing the rapid disruption of habitats adjoining nature reserves [104].

Fifth, even under optimistic scenarios for yield increases, vast expanses of tropical land will be exploited by smallholders and those using mixed-production systems. This creates abundant opportunities to use principles of landscape design [114], agroecology [81,88], and ecological intensification [115] to enhance conservation and food production in multi-use landscapes. External subsidies, including those from eco-certification of agricultural products and international carbon trading, could help to offset the costs of such practices [116].

Sixth, we must recognize that decision making in tropical countries is changing. Across the tropics, moves to community-based resource management are placing local needs for employment and products ahead of global demands to protect nature. 'Crony capitalists' (those with close personal or family ties to governments) have a growing influence on political processes, and short-term benefits are taking precedence over long-term sustainability. In Indonesia, for instance, the emergence of democracy and decentralization of natural resource decisions has given local political expediency greater influence than national conservation laws [117]. Environmental strategies must adapt to these changing realities.

Seventh, we must stop behaving as if burgeoning human population growth is a *fait accompli*. Population increases will be most dramatic and destabilizing in parts of Asia and especially in Africa. For instance, the population of Nigeria–which already suffers from weak governance and poor living standards–is expected to increase by 500% this century [14]. These stark projections highlight an urgent need for aid and investments in family planning and educational opportunities for younger women, along with sustainable economic development.

Finally, we must anticipate not only greater social, economic, and environmental stresses this century but also greater instability. The best-laid plans for sustainability can be derailed by limiting resources, social instability and conflicts, and the tyranny of unintended consequences. Because complex, interconnected production systems are often vulnerable to collapse, techno-optimism needs to be tempered by clear-eyed planning that prioritizes social and environmental resilience.

Concluding remarks

Human societies are remarkably adaptable but, as the 21st century progresses, we are moving ever farther into uncharted territory. Tropical ecosystems are crucial for global biodiversity and provide vital ecosystem services, but are facing unprecedented pressures. The already-massive global footprint of agriculture is expanding rapidly, especially in Sub-Saharan Africa and South America. Its impacts on terrestrial and aquatic ecosystems will be intense and increasingly pervasive.

Pressing demands to ramp up food production are creating manifold challenges for agriculture. A huge question is the degree to which demands can be met from yield increases on existing crop and grazing lands versus expanding the spatial extent of agriculture. There are great needs to produce food more efficiently, to reduce food waste, and to optimize the resiliency of agriculture and food production. Across much of the tropics, large gaps exist between agricultural best practice and on-the-ground reality, and these gaps must be surmounted.

Although we can clearly see daunting challenges ahead, much remains uncertain. How much land will be devoted to biofuels? How will climate change impact on agriculture? How many species will be lost to extinction? Despite these deep unknowns, we can still identify urgent priorities to protect tropical nature–limiting destructive road expansion into the last surviving wildernesses; protecting nature reserves and their imperiled surrounding habitats; and working actively to slow burgeoning population growth, especially where current population trajectories are likely to elevate human suffering and environmental harm.

Ultimately, what is clear is that the goals of a well-nourished global population and healthy ecosystems are inextricably linked. Nations with high poverty and poor governance typically have the worst environmental conditions [73,74]. To avoid environmental calamity, we must achieve ambitious goals for agriculture while limiting the threats to tropical nature.

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References

1 Myers, N. *et al.* (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858
2 Grimes, A. *et al.* (1994) Valuing the rain forest: the economic value of nontimber forest products in Ecuador. *Ambio* 23, 405–410

3 Fearnside, P.M. (2000) Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Clim. Change* 46, 115–158
4 Avissar, R. and Werth, D. (2005) Global hydroclimatological teleconnections resulting from tropical deforestation. *J. Hydrometeorol.* 6, 134–145
5 Laurance, W.F. (2007) Have we overstated the tropical biodiversity crisis? *Trends Ecol. Evol.* 22, 65–70
6 DeFries, R. *et al.* (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 90s. *Proc. Natl. Acad. Sci. U.S.A.* 99, 14256–14261
7 Wright, S.J. and Muller-Landau, H.C. (2006) The future of tropical forest species. *Biotropica* 38, 287–301
8 Bradshaw, C.J.A. *et al.* (2009) Tropical turmoil – a biodiversity tragedy in progress. *Front. Ecol. Environ.* 7, 79–87
9 Wright, S.J. (2010) The future of tropical forest species. *Ann. N. Y. Acad. Sci.* 1195, 1–27
10 Tilman, D. *et al.* (2001) Forecasting agriculturally driven global environmental change. *Science* 292, 281–284
11 Gibbs, H.K. *et al.* (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl. Acad. Sci. U.S.A.* 107, 16732–16737
12 Dobrovolski, R. *et al.* (2011) Agricultural expansion and the fate of global conservation priorities. *Biodivers. Conserv.* 20, 2445–2459
13 Foley, J.A. *et al.* (2005) Global consequences of land use. *Science* 309, 570–574
14 United Nations (2013) *World Population Prospects: The 2012 Revision*, United Nations Population Division
15 United Nations Food and Agricultural Organization (2011) *The State of Food Insecurity in the World 2011*, United Nations Food and Agricultural Organization
16 Bruinsma, J. (2009) *The Resource Outlook to 2050: Expert Meeting on How to Feed the World*, United Nations Food and Agricultural Organization
17 Scharlemann, J. and Laurance, W.F. (2008) How green are biofuels? *Science* 319, 52–53
18 Fargione, J. *et al.* (2008) Land clearing and the biofuel carbon debt. *Science* 319, 1235–1238
19 Nelson, G.C. *et al.* (2009) *Climate Change: Impact on Agriculture and Costs of Adaptation*, International Food Policy Research Institute
20 Kastner, T. *et al.* (2012) Global changes in diets and the consequences for land requirements for food. *Proc. Natl. Acad. Sci. U.S.A.* 109, 6868–6872
21 Rights and Resources Initiative (2008) *Seeing People Through the Trees: Scaling up Efforts to Advance Rights and Address Poverty, Conflict and Climate Change*, Rights and Resources Initiative
22 von Braun, J. and Meinzen-Dick, R. (2009) *'Land Grabbing' by Foreign Investors in Developing Countries: Risks and Opportunities*, International Food Policy Research Institute
23 Grassni, P. *et al.* (2013) Distinguishing between yield advances and yield plateaus in historical crop production trend. *Nat. Commun.* http://dx.doi.org/10.1038/ncomms3918
24 Sayer, J. and Cassman, K.G. (2013) Agricultural innovation to protect the environment. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8345–8348
25 Masters, W.A. *et al.* (2013) Urbanization and farm size in Asia and Africa: implications for food security and agricultural research. *Global Food Secur.* 2, 156–165
26 Tilman, D. *et al.* (2002) Agricultural sustainability and intensive production practices. *Nature* 418, 671–677
27 Mueller, N.D. *et al.* (2012) Closing yield gaps through nutrient and water management. *Nature* 490, 254–257
28 Carberry, P.S. *et al.* (2013) Scope for improving eco-efficiency varies among diverse cropping systems. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8381–8386
29 World Bank (2009) *Awakening Africa's Sleeping Giant: Prospects for Commercial Agriculture in the Guinea Savannah Zone and Beyond*, World Bank
30 Molyneux, D.H. (2004) 'Neglected' diseases but unrecognized successes–challenges and opportunities for infectious disease control. *Lancet* 364, 380–383
31 Hotez, P.J. *et al.* (2009) Rescuing the bottom billion through control of neglected tropical diseases. *Lancet* 373, 1570–1575
32 Warnken, P.F. (1999) *The Development and Growth of the Soybean Industry in Brazil*, Iowa State University Press
33 Butler, R.A. and Laurance, W.F. (2009) Is oil palm the next emerging threat to the Amazon? *Trop. Conserv. Sci.* 2, 1–10
34 Greenpeace (2012) *Palm Oil's New Frontier*, Greenpeace International
35 Laurance, W.F. *et al.* (2009) Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24, 659–669
36 Laurance, W.F. *et al.* (2002) Predictors of deforestation in the Brazilian Amazon. *J. Biogeogr.* 29, 737–748
37 Laurance, W.F. *et al.* (2001) The future of the Brazilian Amazon. *Science* 291, 438–439
38 Fearnside, P.M. (2006) Containing destruction from Brazil's Amazon highways: now is the time to give weight to the environment in decision-making. *Environ. Conserv.* 33, 181–183
39 Laurance, W.F. *et al.* (2006) Impacts of roads and hunting on central-African rainforest mammals. *Conserv. Biol.* 20, 1251–1261
40 Blake, S. *et al.* (2007) Forest elephant crisis in the Congo Basin. *PLoS Biol.* 5, e111
41 Killeen, T.J. (2007) *A Perfect Storm in the Amazon Wilderness: Development and Conservation in the Context of the Initiative for the Integration of the Regional Infrastructure of South America (IIRSA)*, Conservation International
42 Finer, M. and Jenkins, C.N. (2012) Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes–Amazon connectivity. *PLoS ONE* 7, e35126
43 Grumbine, R.E. *et al.* (2012) Mekong hydropower: drivers of change and governance challenges. *Front. Ecol. Environ.* 10, 91–98
44 Mitchell, J. (2008) The Maputo Development Corridor: a case study of the SDI process in Mpumalanga. *Dev. South. Afr.* 15, 757–769
45 Weng, L. *et al.* (2013) Mineral industries, growth corridors and agricultural development in Africa. *Global Food Secur.* 2, 195–202
46 Edwards, D.P. *et al.* (2013) Mining and the African environment. *Conserv. Lett.* http://dx.doi.org/10.1111/conl.12076
47 Adeney, J.M. *et al.* (2009) Reserves protect against deforestation fires in the Amazon. *PLoS ONE* 4, e5014
48 Fearnside, P.M. (1986) Settlement in Rondônia and the token role of science and technology in Brazil's Amazonian development planning. *Interciencia* 11, 229–236
49 Hirsch, R.L. (2005) The inevitable peaking of world oil production. *Atlantic Council Bull.* 16, 1–9
50 Laurance, W.F. (2007) Switch to corn promotes Amazon deforestation. *Science* 318, 1721
51 Phelps, J. *et al.* (2013) Agricultural intensification escalates future conservation costs. *Proc. Natl. Acad. Sci. U.S.A.* 110, 7601–7606
52 Vermeulen, S.J. *et al.* (2013) Addressing uncertainty in adaptation planning for agriculture. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8357–8362
53 Brodie, J. *et al.* (2012) Climate change and tropical biodiversity: a new focus. *Trends Ecol. Evol.* 23, 145–150
54 Vera, C. *et al.* (2006) Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. *Geophys. Res. Lett.* 33, L13707
55 Durack, P.J. *et al.* (2012) Ocean satellites reveal strong global water cycle intensification during 1950 to 2000. *Science* 336, 455–458
56 Hansen, M.C. *et al.* (2013) High-resolution global maps of 21st century forest cover change. *Science* 342, 850–853
57 Millennium Ecosystem Assessment (2005) *Millennium Ecosystem Assessment Ecosystems and Human Well-being: Synthesis*, Island Press
58 Wade, T.G. *et al.* (2003) Distribution and causes of global forest fragmentation. *Conserv. Ecol.* 7, 7
59 Asner, G.P. *et al.* (2009) A contemporary assessment of change in humid tropical forests. *Conserv. Biol.* 23, 1386–1395
60 Peres, C.A. *et al.* (2006) Detecting anthropogenic disturbance in tropical forests. *Trends Ecol. Evol.* 21, 227–229
61 Rudel, T.K. (2005) *Tropical Forests: Regional Paths of Destruction and Regeneration in the Late Twentieth Century*, Columbia University Press
62 Lambin, E.F. and Meyfroidt, P. (2010) Land use transitions: socio-ecological feedback versus socio-economic change. *Land Use Policy* 27, 108–118

63 Ewers, R.M. (2006) Interaction effects between economic development and forest cover determine deforestation rates. *Global Environ. Change* 16, 161–169
64 United Nations Food and Agricultural Organization (2005) *Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management*, United Nations Food and Agricultural Organization
65 Chazdon, R.L. *et al.* (2009) The potential for species conservation in tropical secondary forests. *Conserv. Biol.* 23, 1406–1417
66 Dent, D.H. and Wright, S.J. (2009) The future of tropical species in secondary forests: a quantitative review. *Biol. Conserv.* 142, 2833–2843
67 Almeida, C.A. *et al.* (2010) Estimativa de área de vegetação secundária na Amazônia Legal Brasileira. *Acta Amazonica* 40, 289–302
68 Mittermeier, R.A. *et al.* (2005) *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecosystems*, University of Chicago Press
69 Joppa, L.N. *et al.* (2011) Biodiversity hotspots house most undiscovered plant species. *Proc. Natl. Acad. Sci. U.S.A.* 108, 13171–13176
70 Scheffers, B.R. *et al.* (2012) What we know and don't know about Earth's missing biodiversity. *Trends Ecol. Evol.* 27, 501–510
71 Giam, X. *et al.* (2011) Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. *Proc. R. Soc. B* 279, 67–76
72 Cincotta, R.P. *et al.* (2000) Human population in the biodiversity hotspots. *Nature* 404, 990–992
73 Fisher, B. and Christopher, T. (2007) Poverty and biodiversity: measuring the overlap of human poverty and the biodiversity hotspots. *Ecol. Econ.* 62, 93–101
74 Jha, S. and Bawa, K.S. (2006) Population growth, human development, and deforestation in biodiversity hotspots. *Conserv. Biol.* 20, 906–912
75 Pimm, S.L. and Raven, P.R. (2000) Biodiversity: extinction by numbers. *Nature* 403, 843–845
76 Gibson, L. *et al.* (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381
77 Edwards, D.P. *et al.* (2011) Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proc. R. Soc. B* 278, 82–90
78 Putz, F.E. *et al.* (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conserv. Lett.* 5, 296–303
79 Laurance, W.F. *et al.* (2011) The fate of Amazonian forest fragments: a 32-year investigation. *Biol. Conserv.* 144, 56–67
80 Barlow, J. *et al.* (2010) Measuring the conservation value of tropical primary forests: the effect of occasional species on estimates of biodiversity uniqueness. *PLoS ONE* 5, e9609
81 Perfecto, I. and Vandermeer, J. (2010) The agroecological matrix as alternative to the land-sparing/agricultural intensification model. *Proc. Natl. Acad. Sci. U.S.A.* 107, 5786–5791
82 Fitzherbert, E.B. *et al.* (2008) How will oil palm expansion affect biodiversity? *Trends Ecol. Evol.* 23, 538–545
83 Ziegler, A.D. *et al.* (2009) The rubber juggernaut. *Science* 324, 1024–1025
84 Barlow, J. *et al.* (2007) Quantifying the biodiversity value of tropical primary, secondary and plantation forests. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18555–18560
85 Laurance, W.F. (1991) Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv. Biol.* 5, 79–89
86 Blake, J.G. and Loiselle, B.A. (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *Auk* 118, 304–326
87 Pereira, H.M. and Daily, G.C. (2006) Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87, 1877–1885
88 Vandermeer, J. *et al.* (2010) Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *BioScience* 60, 527–537
89 Boreux, V. *et al.* (2013) Interactive effects among ecosystem services and management practices on crop production: pollination in coffee agroforestry systems. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8387–8392
90 Green, R.E. *et al.* (2005) Farming and the fate of wild nature. *Science* 307, 550–555
91 Borlaug, N. (2007) Feeding a hungry world. *Science* 318, 359
92 Edwards, D.P. *et al.* (2010) Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. *Conserv. Lett.* 3, 236–242
93 Phalan, B. *et al.* (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333, 1289–1291
94 Stevenson, J. *et al.* (2013) Green Revolution research saved an estimated 18 to 27 million hectares from being brought into agricultural production. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8363–8368
95 Sala, O.E. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774
96 Dudgeon, D. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182
97 Egea-Serrano, A. *et al.* (2012) Understanding the impact of chemicals on amphibians: a meta-analytic review. *Ecol. Evol.* 2, 1382–1397
98 Rodrigues, A.S.L. *et al.* (2004) Global gap analysis: priority regions for expanding the global protected-area network. *BioScience* 54, 1092–1100
99 Saunders, D.L. *et al.* (2002) Freshwater protected areas: strategies for conservation. *Conserv. Biol.* 16, 30–41
100 Jenkins, C.N. and Joppa, L. (2009) Expansion of the global terrestrial protected area system. *Biol. Conserv.* 142, 2166–2174
101 Nepstad, D. *et al.* (2006) Inhibition of Amazon deforestation and fire by parks and indigenous lands. *Conserv. Biol.* 20, 65–73
102 Bruner, A.G. *et al.* (2004) Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. *BioScience* 54, 1119–1126
103 Curran, L.M. *et al.* (2004) Lowland forest loss in protected areas of Indonesian Borneo. *Science* 303, 1000–1003
104 Laurance, W.F. *et al.* (2012) Averting biodiversity collapse in tropical forest protected areas. *Nature* 489, 290–294
105 Harrison, R.D. (2011) Emptying the forest: hunting and the extirpation of wildlife from tropical nature reserves. *BioScience* 61, 919–924
106 DeFries, R. *et al.* (2004) Increasing isolation of protected areas in tropical forests over the last twenty years. *Ecol. Appl.* 15, 19–26
107 Cassman, K.G. *et al.* (2010) Crop yield potential, yield trends, and global food security in a changing climate. In *Handbook of Climate Change and Agroecosystems* (Rosenzweig, C. and Hillel, D., eds), pp. 37–51, Imperial College Press
108 Ray, D.K. *et al.* (2013) Yield trends are insufficient to double global crop production by 2050. *PLoS ONE* 8, e66428
109 De Wit, C.T. (1992) Resource use efficiency in agriculture. *Agric. Syst.* 40, 125–151
110 Grassini, P. and Cassman, K.G. (2012) High yield maize with large net energy yield and low global warming potential. *Proc. Natl. Acad. Sci. U.S.A.* 109, 1074–1079
111 United Nations Food and Agricultural Organization (2013) *Global Food Losses and Food Waste: Extent Causes and Prevention*, United Nations Food and Agricultural Organization
112 World Bank (2011) *Missing Food: The Case of Postharvest Grain Losses in Sub-Saharan Africa*, World Bank
113 Laurance, W.F. and Balmford, A. (2013) A global map for road building. *Nature* 495, 308–309
114 Sayer, J. *et al.* (2013) Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. *Proc. Natl. Acad. Sci. U.S.A.* 110, 8349–8356
115 Bommarco, R. *et al.* (2013) Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238
116 van Ittersum, M.K. *et al.* (2008) Integrated assessment of agricultural systems: a component-based framework for the European Union (SEAMLESS). *Agric. Syst.* 96, 150–165
117 Barr, C.M. and Sayer, J.A. (2012) The political economy of reforestation and forest restoration in Asia–Pacific: critical issues for REDD+. *Biol. Conserv.* 154, 9–19
118 Foresight (2011) *Executive Summary: The Future of Food and Farming*, Government Office for Science
119 Fearnside, P.M. (2002) Can pasture intensification discourage deforestation in the Amazon and Pantanal regions of Brazil? In *Deforestation and Land Use in the Amazon* (Wood, C.H. and Porro, R., eds), pp. 299–314, University of Florida Press

120 Sanchez, P.A. (2002) Soil fertility and hunger in Africa. *Science* 295, 2019–2020
121 Jaffe, A.M. *et al.* (2011) *The Status of World Oil Reserves: Conventional and Unconventional Resources in the Future Supply Mix*, James A. Baker III Institute for Public Policy, Rice University
122 International Energy Agency (2012) *World Energy Outlook*, International Energy Agency
123 Fischer, J. *et al.* (2008) Should agricultural policies encourage land-sparing or wildlife-friendly farming? *Front. Ecol. Environ.* 6, 380–385
124 Tscharnke, T. *et al.* (2012) Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59
125 Ewers, R.M. *et al.* (2009) Do increases in agricultural yield spare land for nature? *Global Change Biol.* 15, 1716–1726
126 Lambin, E.F. and Meyfroidt, P. (2011) Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci. U.S.A.* 108, 3465–3472
127 Lenzen, M. *et al.* (2012) International trade drives biodiversity threats in developing nations. *Nature* 486, 109–112
128 Macedo, M.N. *et al.* (2012) Decoupling of deforestation and soy production in the southern Amazon during the late 2000s. *Proc. Natl. Acad. Sci. U.S.A.* 109, 1341–1346
129 Balmford, A. *et al.* (2012) What conservationists need to know about farming. *Proc. R. Soc. B* 279, 2714–2724
130 Angelsen, A. and Kaimowitz, D. (2001) *Agricultural Technologies and Tropical Deforestation*, CABI Publishing
131 Tilman, D. *et al.* (1994) Habitat destruction and the extinction debt. *Nature* 371, 365–366
132 Ceballos, G. and Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science* 296, 904–906
133 Franklin, I.R. and Frankham, R. (1998) How large must populations be to retain evolutionary potential? *Anim. Conserv.* 1, 69–73
134 Estes, J.A. *et al.* (2011) Trophic downgrading of the Planet Earth. *Science* 333, 301–306
135 Dinerstein, E. *et al.* (2007) The fate of wild tigers. *BioScience* 57, 508–514
136 Terborgh, J. *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* 294, 1923–1926
137 Wright, S.J. *et al.* (2007) The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* 39, 289–291
138 Koh, L.P. *et al.* (2004) Species coextinctions and the biodiversity crisis. *Science* 305, 1632–1634
139 Smith, N.J.H. (1982) *The TransAmazon Colonization Scheme*, University of California Press
140 Boakes, E.H. *et al.* (2012) Extreme contagion in global habitat clearance. *Proc. R. Soc. B* 277, 1081–1085
141 Robalino, J.A. and Pfaff, A. (2012) Contagious development: neighbor interactions in deforestation. *J. Dev. Econ.* 97, 427–436
142 Weinhold, D. and Reis, E. (2008) Transportation costs and the spatial distribution of land use in the Brazilian Amazon. *Global Environ. Change* 18, 54–68