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Minimising the harm to biodiversity of producing more food globally ☆

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ABSTRACT

Should farming and conservation policies aim broadly to separate land for nature and land for production (land sparing) or integrate production and conservation on the same land (wildlife-friendly farming)? Most studies that try to address this question suffer from flaws in sampling design, inappropriate metrics, and/or failure to measure biodiversity baselines. We discuss how these failings can be addressed, and what existing information tells us about the key debates on this topic. The evidence available suggests that trade-offs between biodiversity and yield are prevalent. While there are some wildlife-friendly farming systems that support high species richness, a large proportion of wild species cannot survive in even the most benign farming systems. To conserve those species, protection of wild lands will remain essential. Sustainable intensification could help to facilitate sparing of such lands, provided that as much attention is given to protecting habitats as to raising yields. We discuss the general circumstances under which yield increases can facilitate land sparing, recognising that policies and social safeguards will need to be context-specific. In some situations, bringing degraded lands into production could help reduce pressure on wild lands, but much more information is needed on the biodiversity implications of using degraded lands. We conclude that restricting human requirements for land globally will be important in limiting the impacts on biodiversity of increasing food production. To achieve this, society will need to integrate explicit conservation objectives into local, regional and international policies affecting the food system.

Introduction

Human demand for food and other agricultural products is increasing rapidly (Godfray et al., 2010). Two consequences are the conversion of natural habitats to anthropogenic land uses, and the intensification of use of already-modified lands (Tilman et al., 2001; Foley et al., 2005). The switch to increasingly intensive land uses, often with detrimental impacts on wild species, has been termed the land-use cascade (Terborgh and van Schaik, 1996) (Fig. 1). From the perspective of biodiversity conservation, a key question is: for a given level of agricultural production, what allocation of area to different land uses allows the maximum level of biodiversity to persist (Green et al., 2005a)? This needs to be separated from a second key question: what policy and regulatory mechanisms are effective in influencing the allocation of land to different land-use types? Here, we focus on the first of these questions, because understanding it is a necessary precursor to devising policy solutions.

In this paper, we review different land-use strategies that have been suggested as solutions. Next, we assess the models and empirical data required to evaluate these strategies, explain why recent studies fail to provide sufficient information, and suggest how shortcomings in the existing evidence can be overcome. We discuss the most important debates and provide an initial evaluation of how different land-use strategies might be pursued in practice. We conclude with discussion of some of the wider implications for food policy of our evaluation.

A spectrum of suggested solutions

Land sparing

Land sparing (Fig. 2) involves interventions to (1) meet food demand by increasing yields (production per unit area) on existing farmed lands and (2) prevent conversion (or enable restoration) of natural or other desirable habitats (Green et al., 2005a). These two sorts of interventions are linked because in practice protection of natural habitats is likely to be ineffective if human requirements for agricultural products are not being met, while increasing yields

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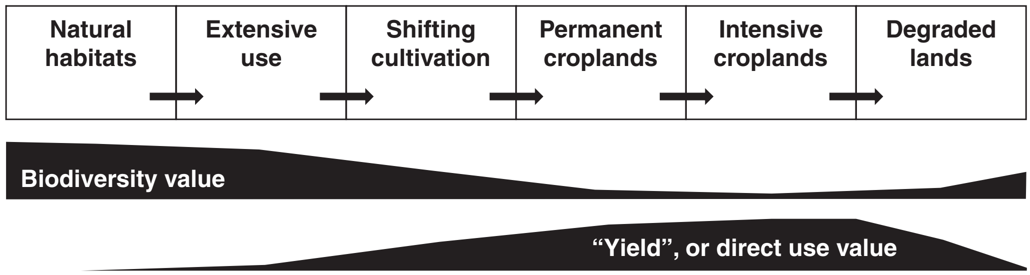

Fig. 1. Simplified diagram of the land-use cascade. Over time, people tend to intensify land use and land management, generating increasing yields and other direct benefits, while reducing populations of many wild species and often reducing indirect ecosystem benefits such as carbon storage. Unsustainably exploited land is eventually abandoned as degraded land, which has the potential to revert to some sort of natural habitat, but with the consequence that land elsewhere will have to move along the land-use cascade. Figure based loosely on Fig. 2.5 of Terborgh and Van Schaik (1996) and Fig. 1 of Grainger (2009).

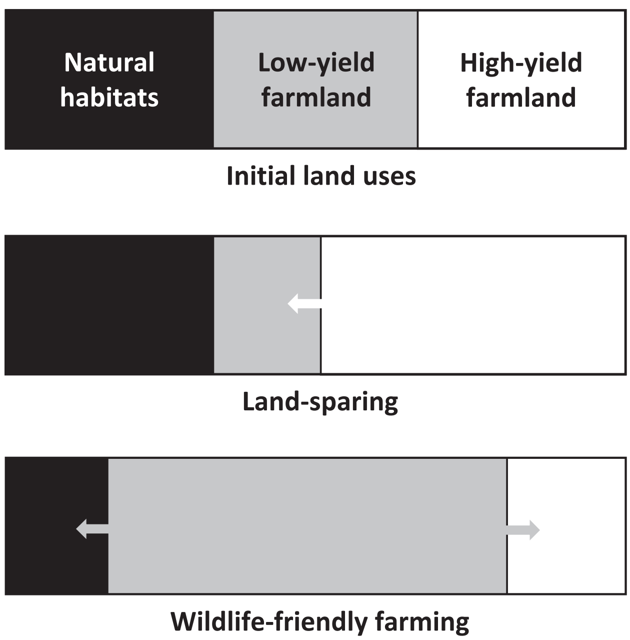

Fig. 2. Cartoon illustrating how land sparing or wildlife-friendly farming strategies could be used to meet an increase in food demand, in this example starting from a region with equal areas of natural habitats, low-yield farmland and high-yield farmland (top). Land sparing (centre) involves increasing yields in the production landscape while protecting or restoring natural habitats. Wildlife-friendly farming (bottom) involves expanding the area of low-yield farmland at the expense of natural habitats.

is unlikely to spare much land for nature unless it is coupled with constraints on land conversion (Ewers et al., 2009). Habitat conversion can be prevented in several ways, e.g. formal protected areas, community-managed reserves and conservation concessions. In situations where extensive land clearance has already taken place, restoration of habitats may be appropriate (Roberts et al., 2009). Likewise, yield increases can be achieved in many ways. "Sustainable intensification", increasing yields without compromising resources such as soils and water (Royal Society, 2009), will be needed if land degradation (leading to shortfalls in production and further pressure on natural habitats) is to be avoided. Furthermore, agricultural methods that cause negative effects on biodiversity (e.g. through pollution) outside the boundaries of the farmed landscape will diminish the potential land-sparing benefits to biodiversity of high-yield agriculture (Daly et al., 2007). High-yield agriculture need not consist of chemical-drenched, mechanically-harvested monocultures with no associated biodiversity, although it might often mean some use of chemicals, high-yielding crop varieties, mechanisation and ecologically simplified systems.

Wildlife-friendly farming

Wildlife-friendly farming (Fig. 2) involves interventions to maintain or enhance populations of wild species within production landscapes by modifying or restraining agricultural practice. Examples of wildlife-friendly interventions include agri-environment measures, some forms of agroforestry, and retention of small patches of semi-natural habitat or fallow in mosaic croplands (Benton et al., 2003; Kleijn and Sutherland, 2003; Schroth et al., 2004; Bengtsson et al., 2005; Scherr and McNeely, 2007; Scales and Marsden, 2008; Webb and Kabir, 2009). Where such interventions do not reduce yields per unit area of the production landscape, which includes any unfarmed patches, they will increase biodiversity overall. However, there is a considerable body of evidence suggesting that yield penalties are prevalent, with wildlife-friendly interventions tending to reduce actual or potential farmland yields (Donald, 2004; Green et al., 2005a,b). Populations of some wild species in production landscapes depend upon the retention of small fragments of natural habitat, which tend to reduce yields across the entire production landscape. Even for wild species that use cropland and pasture, their tendency to compete with or feed on domesticated plant species will often lower yields, as would enhancing their populations by reducing the frequency of agricultural operations that disturb soil and vegetation. If wildlife-friendly farming demands more land than high-yield farming, it will leave less land available for natural habitats, and thus might not be the best option for biodiversity overall.

Mixed strategies

The land-sparing vs. wildlife-friendly farming dichotomy is a heuristic for thinking about trade-offs, but in reality there is a complex range of options in between. Strategies combining elements of both land sparing and wildlife-friendly farming have been suggested, e.g. the design of landscapes that incorporate high-yield farmland as well as buffers of wildlife-friendly agroforestry systems around forest fragments (Cullen et al., 2004). Such solutions might be intuitively appealing, but there has been no rigorous evaluation of their merits relative to other possible strategies. Wildlife-friendly farming and land sparing are uneasy bedfellows: pursuing either strategy can constrain overall production by reducing potential yields or making land unavailable for farming, and is likely to compromise the other.

Conceptual and analytic models

Despite the urgent need to identify the most promising ways to increase food production with least impact on wild species, there have been few attempts to combine empirical data with sound theoretical models, especially in the biodiversity-rich tropics. To evaluate which type of strategy for reconciling increased food production and biodiversity conservation is likely to be most effective, some form of model is required, together with appropriate data.

Simple trade-offs model

A useful starting point for such evaluations is the trade-offs model developed by Green et al. (2005a). This model requires a description of the relationship between population density and agricultural yield for each species (but does not depend on any prior assumption about its shape). From this function one can determine whether the total population of the species in a region (comprising both the production landscape and natural habitats) will be larger under a high-yield land-sparing strategy, under the lowest yield consistent with meeting any given target for agricultural production, or under some intermediate strategy. For example, species with a convex density-yield function (as in Fig. 3b) will have larger total populations under a land-sparing strategy, while those with a concave function (Fig. 4b) will have larger total populations with wildlife-friendly farming.

Model improvements

The simple trade-offs model captures the most fundamental elements for designing better land-use strategies. However, there is considerable potential to extend and improve the simple model to make it more realistic. More sophisticated approaches could use multiple land-use types with a number of different farming or non-farming land uses, each with a different yield. Optimisation procedures could be applied to maximise some metric of biodiversity (see below) for a specified level of production from agriculture or other land uses (e.g. Polasky et al., 2008; Nelson et al., 2009; Watts et al., 2009; Wilson et al., 2010). Spatially explicit versions of the trade-offs model could be developed to account for the effects of farmland on species' densities in unfarmed areas (e.g. because of transport of pollutants), and effects of habitat configuration (patch size and distribution) on species' dispersal and metapopulation dynamics (Opdam and Wascher, 2004; Perfecto et al., 2009).

Empirical data required

Meaningful assessments of land-use strategies require data which meet a basic minimum set of criteria (Green et al., 2005). We outline four such criteria: (1) adequate design and scale of sampling; (2) appropriate quantitative measurements of biodiversity; (3) appropriate quantitative measurements of crop yields; and (4) measurements for natural or baseline habitats, in addition to those for a range of farming systems. Despite evaluating all 113 papers that had cited Green et al. (2005) up to February 2010, we could not find any study that satisfied all four criteria. In this section, we suggest how this failure might be overcome in future studies.

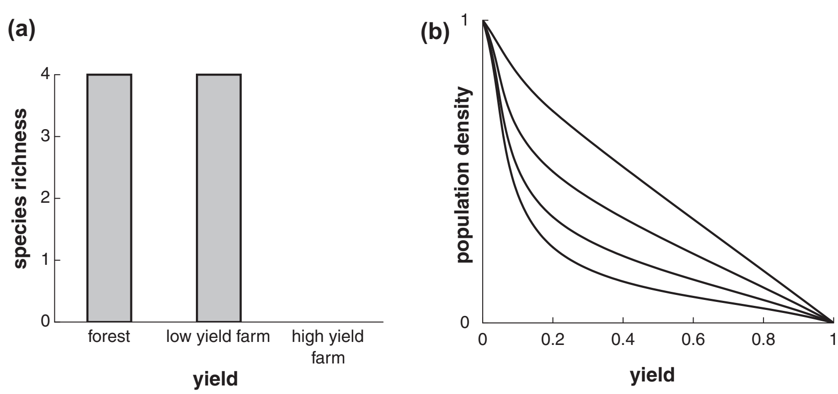

Fig. 3. Measures of presence/absence, or aggregated species richness (a), give no information on the abundance of species in different habitats (b). In this example, information on species richness suggests that wildlife-friendly farming is the best option, when in fact, populations of all four species will be higher if land sparing is adopted.

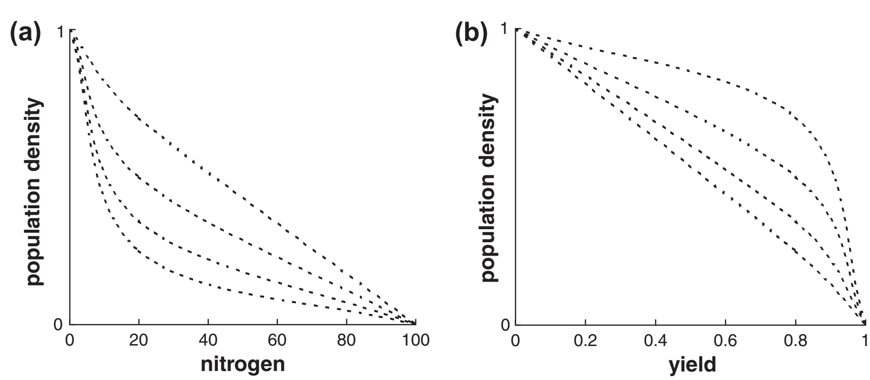

Fig. 4. Proxy measures such as nitrogen fertiliser application (a) will not give the quantitative information on yields required to assess trade-offs (b) if the relationship between nitrogen application and yield is not linear. In this example, yields saturate above a certain level of nitrogen application, and contrary to what is suggested in (a), wildlife-friendly farming will be the best option overall for this set of four species (b).

Sampling design

Frequent flaws and limitations in sampling design include: (1) lack of replication; (2) unrepresentative survey sites or no information on how representative they are; (3) sampling soon after habitat conversion, when some species committed to extinction are still present; (4) bias in sampling completeness, with modified habitats likely to be sampled more thoroughly as they tend to have less structural complexity and lower beta diversity; (5) lack of clarity on selection of the set of species studied, especially as to whether they are to be considered representative of a wider assemblage; and (6) selection of sites close to other habitats, so that local land use effects might be swamped by edge and spillover effects from adjacent land uses (Ricketts et al., 2001; Gardner et al., 2007). As well as addressing these concerns, studies need to be conducted at scales which are both biologically relevant to the focal species, and practically relevant to decision-making. Study sites that are small relative to the size of the home ranges or functional units of the focal species are unlikely to give reliable results. Similarly, study sites that are small relative to the size of farm enterprises might be inadequate unless well-replicated, and might have little bearing on strategic land-use decisions. In many cases, this will require well-spaced sample sites of the order of 1 km^2, and study areas of tens to thousands of km^2.

Quantitative biodiversity information

Simple aggregate measures of biodiversity value such as species richness, diversity indices and combined abundance do not provide sufficient information to be useful in evaluating different land-use strategies (Fig. 3). Biodiversity metrics should, at a minimum, capture information about: (1) the value of a habitat to the species using it, and (2) species' identities. A straightforward measure of the value of a land use to a species is that species' abundance or population density (Fig. 3b). At a landscape scale, measuring species' population densities in different land uses of known yield provides a measure of the value of those land uses to those species, and implicitly takes into account the local impacts of agrochemical use. However, as source-sink population studies have shown, high densities of a species can occur in habitats where reproduction and survival are insufficient for population persistence without immigration from other habitats. Other metrics could be used to allow for this, such as breeding success, or the reproductive value of individuals occupying an area (Mukherjee et al., 2002; Searcy and Shaffer, 2008), but the weaknesses of population density as a metric should be weighed against the advantage that it can be collected inexpensively for a large number of species.

Species' identities are important because not all species are equally threatened, nor are they interchangeable culturally and economically. A local rise in species richness can disguise a fall in conservation value, e.g. if endemics are replaced by widespread species. It is therefore essential to evaluate the impacts of different land-use strategies for each species individually and then combine results across species. Evaluations for single species are relatively straightforward. The population size and/or geographical distribution of a species can be modelled. Optimising the agricultural system for the species, at a given level of production, might then consist of maximising, or keeping within acceptable bounds, the species' population or range size, or some derived quantity like the probability of long-term persistence. Where there are several species of concern, a community-wide metric is required taking into account that optimal farming solutions may differ among species. Possibilities for such a metric depend on conservation objectives (see below), but could include the proportions of species with population sizes maintained above acceptable thresholds, or of species estimated to be committed to extinction within some specified time (e.g. Thomas et al., 2004).

Quantitative information on yield

An element often lacking from studies of the effects of agricultural systems on wild species is some quantitative measure of crop yield or economic value (but see Makowski et al., 2007). When yields are considered at all by ecologists, proxies such as management intensity indices, percentage canopy cover or nitrogen inputs are typically used (Steffan-Dewenter et al., 2007; Firbank et al., 2008). These are interesting in their own right, but direct information on nutritional or economic output is required to answer the question of how to optimise the trade-off between that and biodiversity conservation (Fig. 4). For studies at landscape scales, yield should be expressed in terms of total output per unit time per unit area averaged across the whole production landscape, including output of all crops grown, and any rotations, unproductive fallow periods or establishment times before a crop is produced. Standard currencies, such as food energy or money, are needed to combine and compare information from different crops. Food energy has the advantage that it is not affected by market fluctuations, and is directly relevant to human nutritional requirements, but is not appropriate for some kinds of crops, such as tea. For combining food and non-food products, monetary currencies are more appropriate, and permit inclusion of input costs. Measures of net profit can be considered metrics of the opportunity cost if agriculture is foregone.

Appropriate natural landscapes and baselines

In addition to quantifying biodiversity value and yield across a range of farming systems, studies need to include measurements within natural or baseline habitats (Fig. 5). Deciding what baseline to use can be a nontrivial question: they might be natural habitats, habitats elsewhere that are similar to lost natural habitats, or even restored habitats. The choice of baseline is not just a matter of aesthetics or deciding on an arbitrary "golden age", but has consequences for the less subjective issue of long-term persistence of species or populations. Suppose that it was possible to reconstruct the extent and distribution of habitats in a large area throughout a long period such as the Pleistocene. This would give an idea of the magnitude and fluctuations of species' population sizes over a period in which the effect of human land use has been slight for all but the most recent millennia. Since all species extant today have survived this long period, such an assessment would identify which species have current and modelled future abundances likely to compromise or enhance their prospects for long-term persistence. For example, if today's "farmland birds" associated with open habitats persisted for long periods in a largely forested Europe, their current population sizes might be larger than they were during much of the Pleistocene. If so, current populations might be more than adequate for long-term persistence. Birds of the Brazilian Atlantic forests, in contrast, might currently have lower populations than at any previous time (Brooks and Balmford, 1996).

Key debates

Yield differences between farming systems

There is evidence that some forms of "alternative" agriculture (an umbrella term for a wide range of non-conventional systems and practices, including organic farming) can achieve high yields (Pretty, 2005; Pretty et al., 2006; Badgley and Perfecto, 2007; Badgley et al., 2007). However, this evidence has been criticised because in most cases, alternative technologies might not have

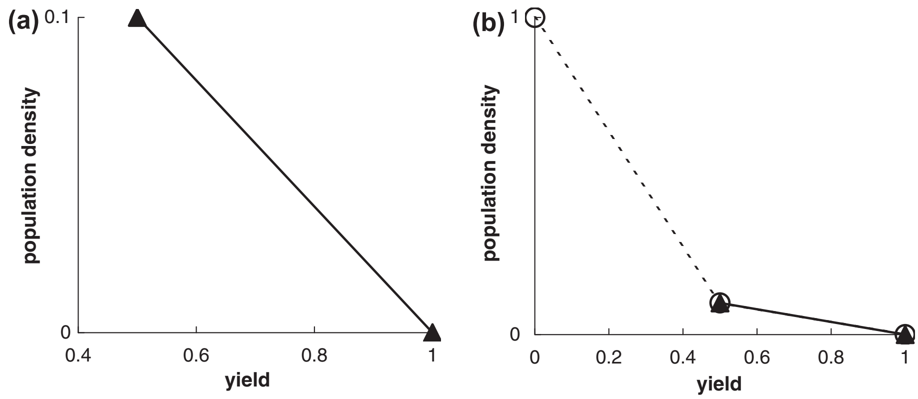

Fig. 5. Omission of baseline habitat (a) can lead to incorrect conclusions about the relationship between population density of a species and agricultural yield (b). In this example, wildlife-friendly farmland supports this species, while high-yielding farmland does not, demonstrating that wildlife-friendly farming has merit. However, baseline habitat supports a far higher population density still, and overall, a land-sparing strategy will give a larger population of the species, for any production target.

been compared against appropriate control systems: e.g. organic best practices vs. conventional best practices (Avery, 2007; Cassman, 2007; Hendrix, 2007; Phalan et al., 2007). Also, very broad definitions of "alternative" systems were used, and yields reported from organic farms do not always take into account rotations or fallow periods (Kirchmann et al., 2008). These criticisms are important, because while there is considerable scope to increase yields of developing-world farms, alternative agriculture is not necessarily the best option, and might constrain potential yields. For example, organic yields are typically lower than conventional yields in developed countries, which are closer to their potential yields (although the latter are not necessarily sustainable) (Stanhill, 1990; Mäder et al., 2002; Cassman, 2003; Lobell et al., 2009; Godfray et al., 2010).

Information needed to decide whether high-yielding alternative farming systems are wildlife-friendly is limited. Many technologies and practices are lumped under the heading "alternative", without guaranteeing that they support increased populations of wildlife (Fischer et al., 2009a). In some cases, alternative agricultural technologies might actually be detrimental to biodiversity: agroforestry or green manure systems that introduce invasive alien species, for example (Sanchez, 1999; Richardson et al., 2004). We concur with Pretty (2008) that while many alternative technologies appear to offer considerable promise, they should be evaluated according to their ability to deliver desired outcomes, rather than on the basis of ideologies.

Externalities

Objections to high-yield farming often focus on the impacts of fertilisers and pesticides (Matson and Vitousek, 2006; Fischer et al., 2008; Perfecto and Vandermeer, 2008; Pretty, 2008). These impacts can be considerable: fertiliser runoff contributes to eutrophication of freshwater ecosystems and formation of "dead zones" in shallow coastal waters (Diaz and Rosenberg, 2008; Robertson and Vitousek, 2009); pesticides have a range of impacts, from direct mortality of organisms to immunosuppression (Daly et al., 2007; Rohr et al., 2008); fossil fuels and fertilisers produce greenhouse gases including carbon dioxide and nitrous oxide, which contribute to climate change (Crutzen et al., 2008); and agrochemicals and physical disturbance contribute to edge effects on adjacent habitats (Ewers and Didham, 2008).

However, not all high-yield farming systems generate high levels of externalities. There are ways of reducing externalities: using technologies and practices such as integrated pest management, integrated nutrient management (e.g. with biochar, appropriate green manures and microfertilisation), banning the most harmful pesticides, no-till methods, replacing annuals with perennials, development of resource-efficient varieties using conventional breeding or genetic engineering, more efficient use of water, etc. (Aune et al., 2007; Scherr and McNeely, 2007; Pretty, 2008; Lal, 2008; McIntyre et al., 2009; Lele et al., 2010; Godfray et al., 2010; Guo et al., 2010). Where such practices are introduced and evaluated with the explicit aim of increasing and maintaining long term yields – "sustainable intensification" – they can contribute towards more sustainable agriculture, but there should be no assumption that they will improve the value of farmland for biodiversity. More fundamental changes, such as substituting fossil fuel with labour, for example, will depend on economic and social contexts (Wright, 2008).

Expressed per unit of output, low-yield farming can also have high externalities. Probably the biggest externality of farming, at least as far as biodiversity is concerned, is habitat loss. Comparisons per unit of output, rather than per unit of area, are needed to know whether other externalities such as greenhouse gas emissions are greater from alternative than conventional farming systems (Olesen et al., 2006). Full accounting of externalities is essential to assess, for example, whether the net costs of replacing carbon- and biodiversity-rich forests with low-yielding farms outweigh those of sparing forests and increasing yields on existing croplands with the aid of fossil fuel inputs (Crutzen et al., 2008; Burney et al., 2010). Externalities can be included in land-use models either as components of cost, which need to be minimised overall, or as constraints (e.g. by not accepting any solution that exceeds a certain threshold of nitrogen runoff or greenhouse gas emissions).

Heterogeneity and scale

Although it might be tempting to think that wildlife-friendly farming and land sparing are the same thing at different scales, this is not the case (Fig. 6). For example, agri-environment buffer strips might be viewed as land sparing at a field scale, but at scales relevant to most species, this is wildlife-friendly farming. An important question, therefore, is: what is the most appropriate scale (grain size) at which to implement land sparing? Should different land uses be aggregated in large blocks, small blocks, or blocks of varying size? The answer is likely to depend on the species in question. Ideally, areas of conserved habitat should be (1) sufficiently large to support viable populations, whether independently or as part of metapopulations; (2) sufficiently large to provide areas of "core" habitat, free from harmful edge effects; and (3) sufficiently small and dispersed to represent the full range of species. These

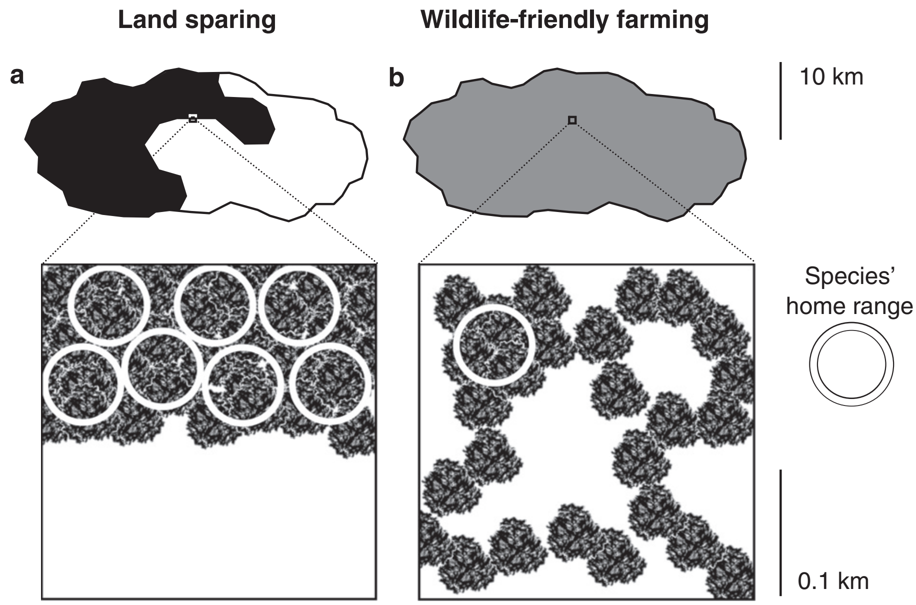

Fig. 6. Land sparing and wildlife-friendly farming are not simply the same thing at different scales. The maps show two land-use scenarios (a and b) for a region that was originally forested. In both scenarios, farming produces the same total agricultural output. In scenario (a) the region is divided between intact forest (black) and a high-yield farming landscape (white) in which no forest patches are retained. In scenario (b) the whole region is allocated to a lower yield wildlife-friendly farming landscape (grey) in which small forest patches are present (one possible form of wildlife-friendly farming). The squares enlarge a small, representative part of the region under each scenario: tree symbols represent forest vegetation, and white represents crops. The yield per unit area of cultivated land is the same in both scenarios, but the yield per unit area of the farming landscape is lower in (b) because of the retention of unproductive forest patches. The white circles represent the minimum contiguous area required to support the home range of a forest species intolerant of modified habitat. Although the overall agricultural production in each scenario is the same, scenario (a) supports a greater total population of this species than (b). The ratio of population size in the enlarged squares is typical of that for the region as a whole. The smaller the minimum contiguous area requirement of the species, the smaller the difference between the two strategies, but only if species' range requirements were vanishingly small would the land sparing and wildlife-friendly farming scenarios be equivalent.

requirements suggest that if extinctions are to be avoided, some very large areas of habitat will need to be protected within each biome (Peres, 2005). Smaller patches might augment these large patches, if there is evidence that they would be effective in capturing beta diversity, providing stepping stones for dispersal or increasing opportunities for people to interact with nature.

Some argue that wildlife-friendly farming is desirable because it maximises habitat heterogeneity (Fischer et al., 2008). We question this assumption. Wildlife-friendly farming often promotes small-scale heterogeneity as perceived by humans, but it might often compromise: (1) heterogeneity at larger scales, and (2) heterogeneity as perceived by many wild species (Lim et al., 2008). For example, a landscape converted to a mosaic of agroforestry plots might appear to be more heterogeneous than one in which there are large monoculture plantations and large forest reserves, but the latter landscape might be more effective in conserving globally scarce habitats and species, thus adding to global heterogeneity. To herbivorous and canopy-dwelling insects, which make up the bulk of animal species, the heterogeneity of host plants in a "homogeneous" block of natural forest could well provide niches for many more species than the smaller number of plants in an apparently "heterogeneous" agricultural mosaic landscape.

Fischer et al. (2008) argue that land sparing involves the separation of humans and nature. In this, they hint at concerns that land sparing will deprive people of contact with wild species and further exaggerate the disconnect between people and nature (Miller, 2005). We share this concern, but wildlife-friendly farming is not the only possible solution, for several reasons: (1) providing access to nature might equally, or better, be achieved by a network of accessible and well-interpreted reserves of natural habitats; (2) protecting ecosystems in a relatively intact state will help to counter the "shifting baseline" syndrome, whereby generations become accustomed to increasingly modified and impoverished landscapes; (3) more than half of the world's human population now lives in urban areas, and that proportion is rising (United Nations, 2007): perhaps urban parks would be a more efficient way of providing people with access to nature than extensive agricultural land-uses?

Species dispersal and connectivity

Vandermeer and Perfecto (2007) argue that wildlife-friendly farming can act as a benign matrix to allow animals to disperse between habitat patches. Manning et al. (2006) warn of extinction lags in land-sparing landscapes. Some wildlife-friendly farming systems are locally more benign for a range of species than some high-yield systems, and can be more permeable to dispersing organisms. However, many of the species at most risk of extinction are restricted to the interior of natural habitats. Increasing the area of core habitat could benefit the populations and even dispersal abilities of these most vulnerable species more than modifying the matrix (Falcy and Estades, 2007). As with other aspects of this debate, quantitative information is required to assess the merits of these alternative ways of enhancing dispersal and metapopulation dynamics – whether by ensuring a relatively benign matrix, by maintaining corridors or stepping stones of relatively intact habitat, or by conserving large source populations. The extinction risk of fragmented populations is a function of the extinction risk within fragments and the colonisation rate between fragments. To conclude, as Perfecto et al. (2009) do, that we can do nothing about the extinction risk in fragments, and should therefore focus on enhancing dispersal, is simply incorrect. Certainly, the matrix matters; but focusing primarily on habitat area and quality could still be a more effective conservation strategy (Hodgson et al., 2009).

Conservation and environmental objectives

The identification of land-use strategies that can best meet the needs of both humans and other species depends to some extent on conservation objectives. While we have so far emphasised species persistence and avoiding global extinctions (Ricketts et al., 2005; Noss, 2010), other possible objectives include maintaining a range of ecosystem functions and services, such as water quality, cultural value and carbon storage, and their resilience in the face of change (Scherr and McNeely, 2007; Fischer et al., 2008; Fisher et al., 2009). Such objectives can be difficult to define in practice, because our understanding of the roles species play in ecosystems is limited, and because the resilience of ecosystems is difficult to predict. However, some ecosystem function-based objectives can be defined readily, e.g. carbon storage (Wade et al., 2010). For other objectives, maintaining viable populations of most species is a pragmatic, if imperfect proxy for ecosystem function. Trade-offs as well as synergies between different conservation objectives are likely to occur. For example, maximising pollination services might demand a fine mosaic of farms and natural habitat areas, which would be an unsuitable landscape configuration for the conservation of edge-sensitive habitat specialists (although here, a more appropriate objective would be maximising overall long-term production from the landscape rather than pollination services per se). As the number of objectives increases, trade-offs become almost inevitable (Pilgrim et al., 2010). Working towards truly multifunctional landscapes will require us to identify and navigate those trade-offs (Rodríguez et al., 2006).

Fischer et al. (2008) argue that ecosystem resilience is accorded priority in wildlife-friendly farming schemes, while maximum efficiency in the present moment is the priority of land sparing. We disagree that this is necessarily so. Maximising local resilience over the short-term by promoting wildlife-friendly farming could well reduce resilience at larger temporal and spatial scales (e.g. if it involves clearing more forests for agriculture). There is a need for more explicit recognition of this potential trade-off. We can work towards this by including explicit objectives for resilience, ecosystem functions and ecosystem services in land-use models (Fischer et al., 2009b).

Poverty, food sovereignty and other social questions

Some in the conservation and development communities argue that traditional peasant systems of low-input, low-yielding agriculture are both wildlife-friendly and "pro-poor" (Perfecto and Vandermeer, 2008; Perfecto et al., 2009). Others argue that developing countries need technology transfer: the sharing of the most up to date scientific knowledge that can enable them to enhance crop production (Wambugu, 1999). There are practical social risks with either extreme: rejecting scientific advances in favour of "indigenous knowledge" risks denying farmers access to technologies that could lift them out of poverty (Cross et al., 2009), while the practice of technology transfer can result in even greater disadvantage to poor farmers relative to wealthy elites (Durosomo, 1993).

An emerging theme in the discourse on developing-world agriculture is that of "food sovereignty": the principle that farmers should themselves be able to define their own food production systems (Rosset, 2008). This is sometimes associated with the presumption that a wildlife-friendly farming strategy is best for both wildlife and for those concerned with food sovereignty (Perfecto et al., 2009). That might be true in some situations, but the evidence is not compelling; there might equally be cases where both social and conservation objectives are better served by land sparing, or where the two sets of objectives are in conflict. Given the flexibility and variety of social institutions (Ostrom, 2007), one approach is to assess potential solutions from a biophysical perspective initially, before evaluating and developing equitable ways to achieve them. An alternative approach would be to identify the range of solutions admissible in particular socio-economic contexts, within the constraints imposed by land ownership patterns and political systems, and evaluate their potential biodiversity value and impacts.

From evidence to practice

Capacity of different farming systems to support biodiversity

Although species richness and other simple aggregate metrics are insufficiently informative to help assess the biodiversity value of modified habitats, they are commonly used for that purpose (e.g. Perfecto et al., 2005; Dorrough et al., 2007; Wallis De Vries et al., 2007; Steffan-Dewenter et al., 2007; Attwood et al., 2008; Firbank et al., 2008). What is required is information on the abundances of individually identified species in relation to crop yield. In the absence of that information, a somewhat informative, though still crude, metric is the proportion of species found in natural habitats but not in wildlife-friendly farmland (although this is likely to be underestimated as a consequence of sampling biases, and because it ignores species' abundances and source-sink dynamics: Barlow et al., 2010; see below). Evidence from modified tropical forest landscapes suggests that many species (typically around half of those found in natural habitats) do not occur in wildlife-friendly farmland (Daily et al., 2001; Green et al., 2005a; Gardner et al., 2010). For such species, conservation in wildlife-friendly farmland is simply not possible.

The true number of species dependent on natural habitats is likely to be even higher. Because of source-sink dynamics and extinction lags, some of the species found in agricultural landscapes or habitat fragments are unlikely to persist in the long term without immigration from nearby natural habitats (Brooks et al., 1999). Mature shade-bearing trees, for example, might survive for decades in complex agroforestry systems, but if unable to reproduce, they will eventually disappear. Evidence suggests that over time, farmers of agroforestry systems tend to favour a smaller number of fast-growing, often exotic "useful" shade trees, whilst killing and preventing the regeneration of unfavoured species (Sonwa et al., 2007; Anand et al., 2008; Ambinakudige and Sathish, 2009; Cassano et al., 2009). A further issue is that of shifting baselines. The reference systems against which modified landscapes are compared have themselves often been modified by human activities, so that comparisons might underestimate the difference between species' abundances in wildlife-friendly farmland and those in very well conserved or rehabilitated natural habitat (Gardner et al., 2009).

There is considerable evidence that the species persisting in wildlife-friendly farmland are not random subsets of species. For birds, large-bodied species, understorey species, forest specialists and restricted-range species are those least able to survive habitat conversion, even to wildlife-friendly agroforestry (Thiollay, 1995; Petit and Petit, 2003; Waltert et al., 2004, 2005; Abrahamczyk et al., 2008). Similarly, in butterflies, the species unable to survive in agroforestry systems are those with the smallest geographic ranges (Bobo et al., 2006). These patterns suggest that increasing the area of wildlife-friendly farmland leads to biotic homogenisation, as local endemics and habitat specialists are replaced by more widespread species (McKinney and Lockwood, 1999).

What role for wildlife-friendly farming?

Initiatives which improve the wildlife value of farmland without limiting yield increases are to be welcomed (Rosenzweig, 2003). In such cases, wildlife-friendly farming could form part of a land-sparing strategy. Unfortunately, however, evidence suggests that yield penalties are prevalent (Green et al., 2005a,b; Kirchmann et al., 2008), and thus that such opportunities are probably rare. That said, there are some possibilities to reduce excess impacts on biodiversity without lowering yields (e.g. through integrated pest management with reduced use of pesticides): developing and mainstreaming such practices remains an important challenge for agro-ecologists.

There is also an argument for "sparing" wildlife-friendly farmland in cases where, even if low-yielding, farmland has comparable biodiversity value to natural habitats. An example might be extensive grazing lands in Europe, where cattle act as surrogates for extinct aurochsen (Marris, 2009). Such land use might be an option for biodiversity conservation in some situations, whilst producing some meat without dependence on cultivated feeds. On the other hand, there is a question whether conservation objectives might be better served by land sparing coupled with restoration of large areas of habitat where reintroductions of native ungulates and top predators might take place (Soulé, 2010).

Permanence is an important issue for both wildlife-friendly farming and land-sparing strategies. Agricultural systems are dynamic and change over time, influenced by social, economic and environmental conditions: thus, the biodiversity benefits of wildlife-friendly farming are fragile unless protected by strong institutions. Likewise, guaranteeing the long term conservation of "spared" habitats can be a challenge, and also requires strong institutions coupled with the genuine involvement of local communities.

Conditions under which policies to increase yields could facilitate land sparing

In general, yield increases cannot be depended upon to result in land sparing without active measures to protect natural habitats (Rudel et al., 2009). However, there are some circumstances under which yield-increasing technologies can facilitate land sparing: (1) If new technologies are more appropriate for established (or abandoned) farmland than for conversion frontiers, farmers might be attracted to consolidate production on already-cleared land rather than carrying out further habitat conversion; (2) If high-yield farming is labour-intensive, it can draw labourers away from frontiers of habitat conversion; and (3) If demand for food and other agricultural products is relatively inelastic, as is the case with staples, and is not distorted by subsidies, then high-yield farming reduces the area required to meet that demand (Angelsen and Kaimowitz, 2001; Wunder, 2004; Ewers et al., 2009).

In addition to concerns about whether yield increases spare land, it cannot be assumed that such land will be kept as natural habitat. In the absence of deliberate protection measures, it is often likely to be used for other purposes. Also, while "abandoned" or "degraded" farmland might often offer some potential for increasing food production with fewer negative impacts on biodiversity than converting natural habitats, there are large uncertainties surrounding the definition, extent and production potential of such lands (Plieninger and Gaertner, 2010). Developing them for food production would in some cases have substantial negative impacts on biodiversity (e.g. Edwards et al., 2011).

Wider food policy implications

Our assessment suggests that the physical footprint of food production should be at the forefront of the debate about "ethical" food (Lang, 2010). If minimising the amount of land used is of paramount importance for biodiversity, wildlife-friendly production methods might be less desirable than high-yield farming, even if the former supports greater biodiversity on the farmland itself. Further information is needed to understand whether this is true in specific contexts, but where it is, an adjustment of incentives will be required. In some circumstances, price premiums and subsidies which currently go towards wildlife-friendly farming certification or agri-environment schemes might be more effectively spent on large-scale habitat protection and restoration. Thoughtful application of "biodiversity banking" schemes is one way in which this could be developed (Burgin, 2008). A key insight is that sustainable intensification need not involve maintaining high levels of in-field biodiversity for it to be part of an effective conservation strategy.

Demand-side measures could also play an important role in reducing the physical footprint of food. A switch towards diets based on foods which use less land could help to create opportunities for stabilising and even reducing land demand for crops, as could reducing food waste (Godfray et al., 2010). As previously noted, explicit measures are needed to ensure that "spared" land is allocated to nature conservation rather than, say, to the production of biofuels or luxury foods and fibres, and land sparing seems most likely to succeed where food and conservation policy are well co-ordinated. We do not seek to downplay the risks of high-yield agriculture, but if locally "sustainable" food systems do not add up to a global food system capable of feeding humanity, whilst also leaving enough space for wild species, then radical solutions must be considered.

Conclusion

The data needed to inform decisions about the extent and scale at which to separate or integrate food production and biodiversity conservation are surprisingly scarce. Conceptualising the problem in terms of trade-offs focuses attention on the real threats to biodiversity from an expanding food system. Based on available evidence, and taking a global perspective, we cautiously advocate better integration of food policy and conservation policy to limit the amount of land used for food production, and to maintain or increase the area of natural habitats. We recognise that translating that broad strategy into local and regional policy objectives will depend greatly on the local context. In some situations, reducing food waste and unnecessary demand for land-hungry crops might be as important as increasing yields. In other contexts, sustainable intensification is needed to ensure sufficient food production whilst avoiding a sprawl of low-yield farming at the expense of wild lands. Careful assessments are needed of the biodiversity implications of using degraded lands. If yield increases are harnessed not just to increase production, but to enable greater levels of habitat protection, they could help much of the planet's biodiversity to survive the coming century of unprecedented human pressure.

Ultimately, neither wildlife-friendly farming nor land sparing is a complete solution: they will only delay and not avert biodiversity loss unless humans are able to limit their requirements for land. Biodiversity conservation will fail if we expect it to be achieved solely as a by-product of other policies such as sustainable intensification. It can however succeed, if explicit objectives, and steps needed to deliver them, are integrated throughout local, regional and international policies affecting the food system.

References

Abrahamczyk, S., Kessler, M., Dwi Putra, D., Waltert, M., Tscharntke, T., 2008. The value of differently managed cacao plantations for forest bird conservation in Sulawesi, Indonesia. Bird Cons. Int. 18, 349–362.

Ambinakudige, S., Sathish, B., 2009. Comparing tree diversity and composition in coffee farms and sacred forests in the Western Ghats of India. Biodivers. Conserv. 18, 987–1000.

Anand, M.O., Krishnaswamy, J., Das, A., 2008. Proximity to forests drives bird conservation value of coffee plantations: implications for certification. Ecol. Appl. 18, 1754–1763.

Angelsen, A., Kaimowitz, D., 2001. Agricultural Technologies and Tropical Deforestation. CABI, Wallingford.
Attwood, S.J., Maron, M., House, A.P.N., Zammit, C., 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecol. Biogeogr. 17, 585–599.
Aune, J.B., Doumbia, M., Berthe, A., 2007. Microfertilizing sorghum and pearl millet in Mali. Outlook Agric. 36, 199–203.
Avery, A., 2007. 'Organic Abundance' report: fatally flawed. Renew. Agr. Food Syst. 22, 321–323.
Badgley, C., Perfecto, I., 2007. Can organic agriculture feed the world? Renew. Agr. Food Syst. 22, 80–85.
Badgley, C., Moghtader, J., Quintero, E., Zakem, E., Chappell, M.J., Aviles-Vazquez, K., Samulon, A., Perfecto, I., 2007. Organic agriculture and the global food supply. Renew. Agr. Food Syst. 22, 86–108.
Barlow, J., Gardner, T.A., Louzada, J., Peres, C.A., 2010. Measuring the conservation value of tropical primary forests: the effect of occasional species on estimates of biodiversity uniqueness. PLoS ONE 5, e9609.
Bengtsson, J., Ahnström, J., Weibull, A., 2005. The effects of organic agriculture on biodiversity and abundance. a meta-analysis. J. Appl. Ecol. 42, 261–269.
Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188.
Bobo, K.S., Waltert, M., Fermon, H., Njokagbor, J., Mühlenberg, M., 2006. From forest to farmland: butterfly diversity and habitat associations along a gradient of forest conversion in southwestern Cameroon. J. Insect Conserv. 10, 29–42.
Brooks, T., Balmford, A., 1996. Atlantic forest extinctions. Nature 380, 115.
Brooks, T.M., Pimm, S.L., Oyugi, J.O., 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13, 1140–1150.
Burgin, S., 2008. BioBanking: an environmental scientist's view of the role of biodiversity banking offsets in conservation. Biodivers. Conserv. 17, 807–816.
Burney, J.A., Davis, S.J., Lobell, D.B., 2010. Greenhouse gas mitigation by agricultural intensification. Proc. Natl. Acad. Sci. USA 107, 12052–12057.
Cassano, C.R., Schroth, G., Faria, D., Delabie, J.H.C., Bede, L., 2009. Landscape and farm scale management to enhance biodiversity conservation in the cocoa producing region of southern Bahia, Brazil. Biodivers. Conserv. 18, 577–603.
Cassman, K.G., 2003. Meeting cereal demand while protecting natural resources and improving environmental quality. Annu. Rev. Environ. Resour. 28, 315–358.
Cassman, K.G., 2007. Can organic agriculture feed the world—science to the rescue? Renew. Agr. Food Syst. 22, 83–84.
Cross, P., Edwards, R.T., Opondo, M., Nyeko, P., Edwards-Jones, G., 2009. Does farm worker health vary between localised and globalised food supply systems? Environ. Int. 35, 1004–1014.
Crutzen, P.J., Mosier, A.R., Smith, K.A., Winiwarter, W., 2008. N_2O release from agro-biofuel production negates global warming reduction by replacing fossil fuels. Atmos. Chem. Phys. 8, 389–395.
Cullen, L., Lima, J.F., Beltrame, T.P., 2004. Agroforestry buffer zones and stepping stones: tools for the conservation of fragmented landscapes in the Brazilian Atlantic forest. In: Schroth, G. et al. (Eds.), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, pp. 415–430.
Daily, G.C., Ehrlich, P.R., Sanchez-Azofeifa, G.A., 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecol. Appl. 11, 1–13.
Daly, G.L., Lei, Y.D., Teixeira, C., Muir, D.C.G., Castillo, L.E., Wania, F., 2007. Accumulation of current-use pesticides in neotropical montane forests. Environ. Sci. Technol. 41, 1118–1123.
Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–929.
Donald, P.F., 2004. Biodiversity impacts of some agricultural commodity production systems. Conserv. Biol. 18, 17–37.
Dorrough, J., Moll, J., Crosthwaite, J., 2007. Can intensification of temperate Australian livestock production systems save land for native biodiversity? Agr. Ecosyst. Environ. 121, 222–232.
Durosomo, B., 1993. Technology adoption and Sub-Sahara African agriculture: the sustainable development option. Agr. Human Values 10, 58–70.
Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A., Hamer, K.C., Wilcove, D.S., 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proc. Roy. Soc. B 278, 82–90.
Ewers, R.M., Didham, R.K., 2008. Pervasive impact of large-scale edge effects on a beetle community. Proc. Natl. Acad. Sci. USA 105, 5426–5429.
Ewers, R.M., Scharlemann, J.P.W., Balmford, A., Green, R.E., 2009. Do increases in agricultural yield spare land for nature? Glob Change Biol. 15, 1716–1726.
Falcy, M.R., Estades, C.F., 2007. Effectiveness of corridors relative to enlargement of habitat patches. Conserv. Biol. 21, 1341–1346.
Firbank, L.G., Petit, S., Smart, S., Blain, A., Fuller, R.J., 2008. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. Philos. Trans. Roy. Soc. B 363, 777–787.
Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J., Tallis, H., 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? Front. Ecol. Environ. 6, 380–385.
Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J., Tallis, H., 2009a. Fostering constructive debate: a reply to Chappell et al. Front. Ecol. Environ. 7, **184.
Fischer, J., Peterson, G.D., Gardner, T.A., Gordon, L.J., Fazey, I., Elmqvist, T., Felton, A., Folke, C., Dovers, S., 2009b. Integrating resilience thinking and optimisation for conservation. Trends Ecol. Evol. 24, 549–554.
Fisher, B., Turner, R.K., Morling, P., 2009. Defining and classifying ecosystem services for decision making. Ecol. Econ. 68, 643–653.
Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574.
Grainger, A., 2009. Measuring the planet to fill terrestrial data gaps. Proc. Natl. Acad. Sci. USA 106, 20557–20558.
Gardner, T.A., Barlow, J., Parry, L.W., Peres, C.A., 2007. Predicting the uncertain future of tropical forest species in a data vacuum. Biotropica 39, 25–30.
Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582.
Gardner, T.A., Barlow, J., Sodhi, N.S., Peres, C.A., 2010. A multi-region assessment of tropical forest biodiversity in a human-modified world. Biol. Conserv. 143, 2293–2300.
Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. Science 327, 812–818.
Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005a. Farming and the fate of wild nature. Science 307, 550–555.
Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005b. The future of farming and conservation: response. Science 308, 1257.
Guo, J.H., Liu, X.J., Zhang, Y., Shen, J.L., Han, W.X., Zhang, W.F., Christie, P., Goulding, K.W.T., Vitousek, P.M., Zhang, F.S., 2010. Significant acidification in major Chinese croplands. Science 327, 1008–1010.
Hendrix, J., 2007. Editorial response by Jim Hendrix. Renew. Agr. Food Syst. 22, 84–85.
Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. J. Appl. Ecol. 46, 964–969.
Kirchmann, H., Bergström, L., Kätterer, T., Andrén, O., Andersson, R., 2008. Can organic crop production feed the world? In: Kirchmann, H., Bergström, L. (Eds.), Organic Crop Production – Ambitions and Limitations. Springer, Berlin, pp. 39–72.
Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40, 947–969.
Lal, R., 2008. Food insecurity's dirty secret. Science 322, 673–674.
Lang, T., 2010. From 'value-for-money' to 'values-for-money'? Ethical food and policy in Europe. Environ. Plann. A 42, 1814–1832.
Lele, U., Pretty, J., Terry, E., Trigo, E., Klousia, M., 2010. Transforming agricultural research for development. Global Forum for Agricultural Research, Montpellier.
Lim, M.L.M., Sodhi, N.S., Endler, J.A., 2008. Conservation with sense. Science 319, 281b.
Lobell, D.B., Cassman, K.G., Field, C.B., 2009. Crop yield gaps: their importance, magnitudes, and causes. Annu. Rev. Environ. Resour. 34, 179–204.
Mäder, P., Fließbach, A., Dubois, D., Gunst, L., Fried, P., Niggli, U., 2002. Soil fertility and biodiversity in organic farming. Science 296, 1694–1697.
Makowski, D., Dore, T., Gasquez, J., Munier-Jolain, N., 2007. Modelling land use strategies to optimise crop production and protection of ecologically important weed species. Weed Res. 47, 202–211.
Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures–implications for conservation. Biol. Conserv. 132, 311–321.
Marris, E., 2009. Reflecting the past. Nature 462, 30.
Matson, P.A., Vitousek, P.M., 2006. Agricultural intensification: will land spared from farming be land spared for nature? Conserv. Biol. 20, 709–710.
McIntyre, B.D., Herren, H.R., Wakhungu, J., Watson, R.T., 2009. International Assessment of Agricultural Knowledge, Science and Technology for Development (IAASTD): Global Report. Island Press, Washington.
McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14, 450–453.
Miller, J.R., 2005. Biodiversity conservation and the extinction of experience. Trends Ecol. Evol. 20, 430–434.
Mukherjee, A., Borad, C.K., Parasharya, B.M., 2002. Breeding performance of the Indian sarus crane in the agricultural landscape of western India. Biol. Conserv. 105, 263–269.
Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Chan, K.M., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front. Ecol. Environ. 7, 4–11.
Noss, R.F., 2010. Local priorities can be too parochial for biodiversity. Nature 463, 424.
Olesen, J.E., Schelde, K., Weiske, A., Weisbjerg, M.R., Asman, W.A.H., Djurhuus, J., 2006. Modelling greenhouse gas emissions from European conventional and organic dairy farms. Agr. Ecosyst. Environ. 112, 207–220.
Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol. Conserv. 117, 285–297.
Ostrom, E., 2007. A diagnostic approach for going beyond panaceas. Proc. Natl. Acad. Sci. USA 104, 15181–15187.

Peres, C.A., 2005. Why we need megareserves in Amazonia. Conserv. Biol. 19, 728–733.

Perfecto, I., Vandermeer, J., 2008. Biodiversity conservation in tropical agroecosystems: a new conservation paradigm. Ann. NY Acad. Sci. 1134, 173–200.

Perfecto, I., Vandermeer, J., Mas, A., Pinto, L.S., 2005. Biodiversity, yield, and shade coffee certification. Ecol. Econ. 54, 435–446.

Perfecto, I., Vandermeer, J., Wright, A., 2009. Nature's Matrix: Linking Agriculture, Conservation and Food Sovereignty. Earthscan, London.

Petit, L.J., Petit, D.R., 2003. Evaluating the importance of human-modified lands for Neotropical bird conservation. Conserv. Biol. 17, 687–694.

Phalan, B., Rodrigues, A.S.L., Balmford, A., Green, R.E., Ewers, R.M., 2007. Comment on 'Resource-conserving agriculture increases yields in developing countries'. Environ. Sci. Technol. 41, 1054–1055.

Pilgrim, E.S., Macleod, C.J., Blackwell, M.S., Bol, R., Hogan, D.V., Chadwick, D.R., Cardenas, L., Misselbrook, T.H., Haygarth, P.M., Brazier, R.E., Hobbs, P., Hodgson, C., Jarvis, S., Dungait, J., Murray, P.J., Firbank, L.G., 2010. Interactions among agricultural production and other ecosystem services delivered from European temperate grassland systems. Adv. Agron. 109, 117–154.

Plieninger, T., Gaertner, M. 2010. Harnessing degraded lands for biodiversity conservation. J. Nat. Conserv., doi:10.1016/j.jnc.2010.04.001.

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biol. Conserv. 141, 1505–1524.

Pretty, J., 2005. Sustainability in agriculture: recent progress and emergent challenges. In: Hester, R., Harrison, R. (Eds.), Sustainability in Agriculture. Royal Society of Chemistry, Cambridge, pp. 1–15.

Pretty, J., 2008. Agricultural sustainability: concepts, principles and evidence. Philos. Trans. Roy. Soc. B 363, 447–465.

Pretty, J.N., Noble, A.D., Bossio, D., Dixon, J., Hine, R.E., Penning de Vries, F.W.T., Morison, J.I.L., 2006. Resource-conserving agriculture increases yields in developing countries. Environ. Sci. Technol. 40, 1114–1119.

Richardson, D.M., Binggeli, P., Schroth, G., 2004. Invasive agroforestry trees: problems and solutions. In: Schroth, G. et al. (Eds.), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, pp. 371–396.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Fay, J.P., 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conserv. Biol. 15, 378–388.

Ricketts, T.H., Dinerstein, E., Boucher, T., Brooks, T.M., Butchart, S.H.M., Hoffmann, M., Lamoreux, J.F., Morrison, J., Parr, M., Pilgrim, J.D., Rodrigues, A.S.L., Sechrest, W., Wallace, G.E., Berlin, K., Bielby, J., Burgess, N.D., Church, D.R., Cox, N., Knox, D., Loucks, C., Luck, G.W., Master, L.L., Moore, R., Naidoo, R., Ridgely, R., Schatz, G.E., Shire, G., Strand, H., Wettengel, W., Wikramanayake, E., 2005. Pinpointing and preventing imminent extinctions. Proc. Natl. Acad. Sci. USA 102, 18497–18501.

Roberts, L., Stone, R., Sugden, A., 2009. The rise of restoration ecology. Science 325, 555.

Robertson, G.P., Vitousek, P.M., 2009. Nitrogen in agriculture: balancing the cost of an essential resource. Annu. Rev. Environ. Resour. 34, 97–125.

Rodríguez, J.P., Beard Jr, T.D., Bennett, E.M., Cumming, G.S., Cork, S., Agard, J., Dobson, A.P., Peterson, G.D., 2006. Trade-offs across space, time, and ecosystem services. Ecol. Soc. 11, 28 (online).

Rohr, J.R., Schotthoefer, A.M., Raffel, T.R., Carrick, H.J., Halstead, N., Hoverman, J.T., Johnson, C.M., Johnson, L.B., Lieske, C., Piwoni, M.D., Schoff, P.K., Beasley, V.R., 2008. Agrochemicals increase trematode infections in a declining amphibian species. Nature 455, 1235–1239.

Rosenzweig, M.L., 2003. Reconciliation ecology and the future of species diversity. Oryx 37, 194–205.

Rosset, P., 2008. Food sovereignty and the contemporary food crisis. Development 51, 460–463.

Royal Society, 2009. Reaping the Benefits: Science and the Sustainable Intensification of Global Agriculture. London.

Rudel, T.K., Schneider, L., Uriarte, M., Turner, B.L., DeFries, R., Lawrence, D., Geoghegan, J., Hecht, S., Ickowitz, A., Lambin, E.F., Birkenholtz, T., Baptista, S., Grau, R., 2009. Agricultural intensification and changes in cultivated areas, 1970–2005. Proc. Natl. Acad. Sci. USA 106, 20675–20680.

Sanchez, P., 1999. Improved fallows come of age in the tropics. Agroforest. Syst. 47, 3–12.

Scales, B.R., Marsden, S.J., 2008. Biodiversity in small-scale tropical agroforests: a review of species richness and abundance shifts and the factors influencing them. Environ. Conserv. 35, 160–172.

Scherr, S.J., McNeely, J.A., 2007. Farming with Nature. Island Press, Washington.

Schroth, G., Da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Lasconcelos, H.L., Izac, A.M.N., 2004. Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington.

Searcy, C.A., Shaffer, H.B., 2008. Calculating biologically accurate mitigation credits: insights from the California Tiger Salamander. Conserv. Biol. 22, 997–1005.

Sonwa, D., Nkongmeneck, B., Weise, S., Tchatat, M., Adesina, A., Janssens, M., 2007. Diversity of plants in cocoa agroforests in the humid forest zone of Southern Cameroon. Biodivers. Conserv. 16, 2385–2400.

Soulé, M.E., 2010. Conservation relevance of ecological cascades. In: Terborgh, J., Estes, J.A. (Eds.), Trophic Cascades: Predators. Prey, and the Changing Dynamics of Nature. Island Press, Washington, pp. 337–351.

Stanhill, G., 1990. The comparative productivity of organic agriculture. Agr. Ecosyst. Environ. 30, 1–26.

Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M.M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S.R., Guhardja, E., Harteveld, M., Hertel, D., Hohn, P., Kappas, M., Kohler, S., Leuschner, C., Maertens, M., Marggraf, R., Migge-Kleian, S., Mogea, J., Pitopang, R., Schaefer, M., Schwarze, S., Sporn, S.G., Steingrebe, A., Tjitrosoedirdjo, S.S., Tjitrosoemito, S., Twele, A., Weber, R., Woltmann, L., Zeller, M., Tscharntke, T., 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proc. Natl. Acad. Sci. USA 104, 4973–4978.

Terborgh, J., van Schaik, C., 1996. Minimizing species loss: the imperative of protection. In: Kramer, R. et al. (Eds.), Last stand: Protected Areas and the Defense of Tropical Biodiversity. Oxford University Press, New York, pp. 15–35.

Thiollay, J.M., 1995. The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. Conserv. Biol. 9, 335–353.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281–284.

United Nations, 2007. State of World Population 2007. <http://esa.un.org/unpp/index.asp>.

Vandermeer, J., Perfecto, I., 2007. The agricultural matrix and a future paradigm for conservation. Conserv. Biol. 21, 274–277.

Wade, A.S.I., Asase, A., Hadley, P., Mason, J., Ofori-Frimpong, K., Preece, D., Spring, N., Norris, K., 2010. Management strategies for maximizing carbon storage and tree species diversity in cocoa-growing landscapes. Agr. Ecosyst. Environ. 138, 324–334.

Wallis De Vries, M.F., Parkinson, A.E., Dulphy, J.P., Sayer, M., Diana, E., 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. Grass Forage Sci. 62, 185–197.

Waltert, M., Mardiastuti, A.N.I., Mühlenberg, M., 2004. Effects of land use on bird species richness in Sulawesi, Indonesia. Conserv. Biol. 18, 1339–1346.

Waltert, M., Bobo, K.S., Sainge, N.M., Fermon, H., Mühlenberg, M., 2005. From forest to farmland: habitat effects on Afrotropical forest bird diversity. Ecol. Appl. 15, 1351–1366.

Wambugu, F., 1999. Why Africa needs agricultural biotech. Nature 400, 15–16.

Watts, M.E., Ball, I.R., Stewart, R.S., Klein, C.J., Wilson, K., Steinback, C., Lourival, R., Kircher, L., Possingham, H.P., 2009. Marxan with zones: software for optimal conservation based land- and sea-use zoning. Environ. Modell. Soft. 24, 1513–1521.

Webb, E., Kabir, M.E., 2009. Home gardening for tropical biodiversity conservation. Conserv. Biol. 23, 1641–1644.

Wilson, K.A., Meijaard, E., Drummond, S., Grantham, H.S., Boitani, L., Catullo, G., Christie, L., Dennis, R., Dutton, I., Falcucci, A., Maiorano, L., Possingham, H.P., Rondinini, C., Turner, W., Venter, O., Watts, M., 2010. Conserving biodiversity in production landscapes. Ecol. Appl. 20, 1721–1732.

Wright, J., 2008. Sustainable Agriculture and Food Security in an Era of Oil Scarcity. Earthscan, London.

Wunder, S., 2004. Policy options for stabilising the forest frontier: a global perspective. In: Gerold, G. et al. (Eds.), Land Use, Nature Conservation and the Stability of Rainforest Margins in Southeast Asia. Springer-Verlag, Berlin, pp. 3–25.