

Land for Food & Land for Nature?

Andrew Balmford, Rhys Green & Ben Phalan

Abstract: Opinions on how to limit the immense impact of agriculture on wild species are divided. Some think it best to retain as much wildlife as possible on farms, even at the cost of lowering yield (production per unit area). Others advocate the opposite: increasing yield so as to limit the area needed for farming, and then retaining larger areas under natural habitats. Still others support a mixture of the two extremes, or an intermediate approach. Here we summarize a model designed to resolve this disagreement, and review the empirical evidence available to date. We conclude that this evidence largely supports the second, so-called land-sparing approach to reconciling agriculture and biodiversity conservation, but that important questions remain over the generality of these findings for different biota and for ecosystem services, how best to increase yields while limiting environmental externalities, and whether there are effective, socially just, and practical mechanisms for coupling yield growth to habitat retention and restoration.

ANDREW BALMFORD is Professor of Conservation Science in the Department of Zoology at the University of Cambridge.

RHYS GREEN is Honorary Professor of Conservation Science in the Department of Zoology at the University of Cambridge and Principal Research Biologist at the Royal Society for the Protection of Birds.

BEN PHALAN is the Zukerman Junior Research Fellow at King's College, Cambridge University.

(*See endnotes for complete contributor biographies.)

Cultivating crops and keeping livestock have radically transformed the scale and complexity of human society, and have had greater impacts on the rest of the planet than any other human activity.¹ Crop production and permanent pasture now cover a combined 38 percent of Earth's ice-free land surface, including around half of all former temperate deciduous forests and savannas, and almost three-quarters of the world's grasslands. Continued conversion for farming is the leading cause of tropical deforestation by a considerable margin. Taken together, agriculture and related land use are responsible for 17–31 percent of all anthropogenic greenhouse gas emissions. On top of this, farming accounts for around 70 percent of human use of freshwater, and the manufacture of inorganic fertilizers is the main reason for the doubling in nitrogen fixation and resulting rise in eutrophication seen over the past century. Given the magnitude of these environmental alterations it is not surprising that agriculture threatens many more species with extinction than any other sector.²

Serious as the situation already is, it seems inescapable that the footprint of farming will increase. The expansion of the human population from about

7.4 billion today to between 9 and 10 billion, coupled with rapidly rising per capita demand for noncrop products (such as biofuels and rubber) and for animal protein (especially in newly emerging economies) mean that total agricultural demand is likely to double between 2000 and 2050.³ Demand-side interventions could help curb this growth and, insofar as hunger and undernourishment are more about food distribution and pricing than overall production, could do so without negatively impacting food security.⁴ Much could be done to reduce the 30–40 percent post-harvest loss of potentially usable food in both developing and developed countries. Food consumption in general and that of meat, dairy products, and eggs in particular could be reduced among well-off consumers.⁵ We strongly support such efforts. Nevertheless, given very limited progress on these fronts to date, we consider it likely that demand for crops and livestock will rise dramatically over the next half century.

The question that therefore arises for conservationists, and that occupies us for the rest of this essay, is how the demand for agricultural products can be met by the planet's limited supply of land at the least cost to other species. One option, widely advocated by conservationists and reflected in the European Union's €5 billion per year program of agri-environment payments to farmers, is land sharing: producing both food and wildlife in the same parts of the landscape by maintaining or restoring the conservation value of the farmed land itself, through providing nonfarmed habitat elements (such as shade trees and ponds), limiting the use of harmful chemicals, and other interventions (see the left panels of Figure 1).⁶ A very different approach, put forward by agricultural scientists in response to the observation that land-sharing interventions typically lower yields and therefore require a larger area to be farmed to achieve a given production target,⁷ is

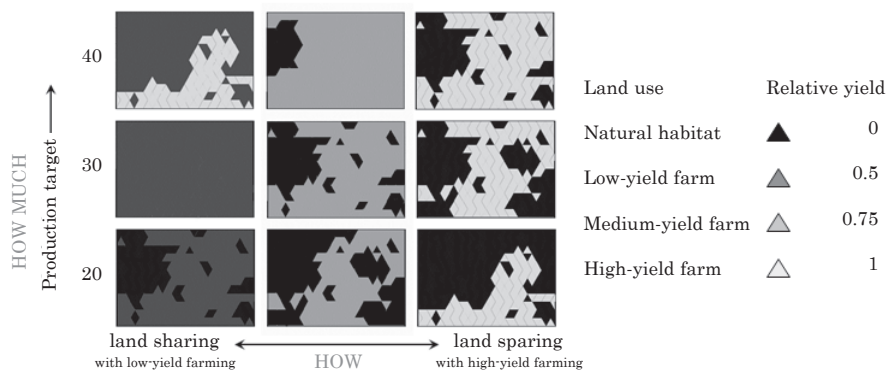
land sparing: increasing yields on farmed land while at the same time sparing remaining habitat or freeing up land for habitat restoration elsewhere (right panels, Figure 1).⁸ Thus, while land sharing focuses on enhancing biodiversity within farmland, land sparing seeks to offset the impacts of high-yield production by coupling it to conservation in nonproductive parts of the landscape. Many other options between these extremes are also possible (central panels, Figure 1).⁹

In the following sections, we summarize a simple trade-off model¹⁰ we devised for identifying which of these approaches will maximize the persistence of the native wild species inhabiting a region; we also review the empirical evidence so far available for assessing their relative merits. We then discuss a series of objections to our approach – some of which we consider to be misconceptions about the model's scope, as well as some important challenges. We end with a brief exploration of other contexts besides food production in which the land-sharing/sparing framework might usefully be applied.

Our trade-off model evaluates plausible alternative farming systems – all of which meet a region's production targets – according to their consequences for the long-term persistence of its species.¹¹ We infer the probability of long-term persistence of each species from its expected total population size in all of the region's farmed and unfarmed land combined, relative to what its population would be in the absence of farming. To make options comparable, we only consider scenarios that meet the same production target for the region (solutions occupying the same row of Figure 1). This could be achieved by farming the entire region at the lowest yield sufficient to meet the target (extreme land sharing), farming some of it at the highest achievable yield and maintaining (or restoring) the rest as

Figure 1
Schematic Illustration of Land Sharing, Land Sparing, and Mixed-Yield Landscapes

Andrew
Balmford,
Rhys Green
& Ben
Phalan



Each of the nine panels is a schematic map of a region with natural habitat (black : agricultural yield = 0 units), low-yield farmland (dark grey : yield = 0.5 units), medium-yield (mid-grey : yield = 0.75 units), and high-yield farmland (light grey : yield = 1.0 units). Region maps in the same row all produce the same quantity of agricultural products, but with different amounts of high-, medium-, and low-yield farming and with natural habitat on all land not needed to provide the production target. The three rows show results (from bottom to top) for low (120 units), medium (180), and high (240) production targets. Source : Figure prepared by authors.

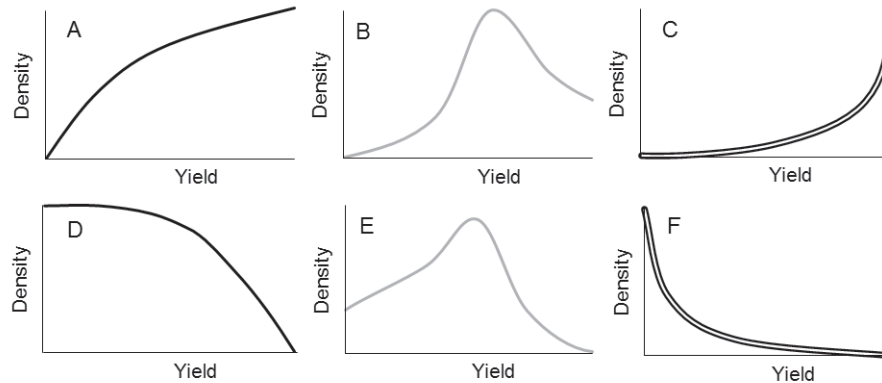
intact habitat (extreme land sparing), or by some intermediate solution.

The key to quantifying how the total population size of a species (and hence its likelihood of persistence) varies across these options is how its mean population density is related to the agricultural yield of a piece of land: a response we term its density-yield curve. Some species can be considered beneficiaries of agriculture (“winners”) because they live at consistently higher densities in farmed land than in their natural, zero-yielding habitat (panels A, B, and C in Figure 2). Given that these are likely to have larger regional populations under any form of farming than they had before the arrival of agriculture, such species are of limited conservation concern. Other species (“losers”) occur at lower densities in farmed land than in unfarmed habitat (panels D, E, and F). Their region-wide populations will thus be small-

er under some or all farming regimes than in the absence of farming. These loser species are the primary focus of our concern.

For both winners and losers, the approach to farming that maximizes their regional population size depends on the shape of their density-yield curves. Mathematical modeling shows that for those with simple concave curves (panels A and D) their total population size is greatest when the entire region is farmed at the lowest yield capable of meeting the production target (extreme land sparing). This is easiest to see for loser species (panel D), because their densities decline only slightly under low-yield farming but fall steeply under the high-yields associated with land sparing. The situation is very different for species with simple convex curves (panels C and F). For these, farming some land at maximal yield and retaining or restoring the remainder as natural habitat (extreme

Land for Food & Land for Nature? **Figure 2**
 Illustrative Density-Yield Curves for “Winner” and “Loser” Species



Illustrative density-yield curves for species whose total population sizes (on farmed and unfarmed land combined) are larger (winners, top row) or smaller (losers, bottom row) when farming is present in a region, and greatest under land sharing (A, D), intermediate-yield farming (B, E), or land sparing (C, F).

land sparing) is optimal. Again, considering loser species (panel F) helps explain why: in this case, their population densities fall sharply even under low-yield farming, whereas high-yield farming can help safeguard more of the intact habitat on which they (more or less) depend. Species with more complex curves (such as those shown in panels B and E) may have maximum population sizes under intermediate-yield strategies, though this will depend on the production target for the region.¹²

Parameterizing this model and hence evaluating the consequences of alternative farming approaches for a given set of species in a region can be challenging.¹³ It requires estimating current and likely future production targets and developing plausible land-use scenarios of how these might be met. Density-yield curves are needed for all species of interest, which should be as representative a sample of wild species as possible. Fitting density-yield curves requires data on the population density of each species across sites of known yield,

ranging from natural, baseline habitats to the highest-yielding system possible in the region, and matched for all variables (such as soil type, climate, and topography) besides agricultural inputs that might affect either yields or densities. Sites should be of a size that is relevant to major land management decisions and to the life cycles of the species concerned (see below), and they must be within sufficiently large land-use blocks that abundance estimates are not swamped by edge or spillover effects from neighboring blocks with very different yields. Choice of baseline sites can be particularly problematic, especially in regions that have lost their natural vegetation or where major elements of the Pleistocene biota are extinct. Baseline habitats suitable for survey are unfarmed areas with native vegetation typical of what could be retained or restored within the region.

The results from the land-use scenarios and density-yield curves are then combined to calculate the expected total populations of each species across farmed and non-

farmed land combined. This approach ignores possible differences in demographic processes among land-use types. Ideally, these differences would be known so that the expected whole-region population of each species could be obtained from a spatially explicit population model. However, the data this would require are only available for a handful of species. Given that the trade-off assessment is only meaningful when done in the same way for an entire suite of species, we argue our simpler density-based method is at present the only practical approach.

Given these difficulties, few studies have been able to test the land-sharing/sparing trade-off appropriately. What do the results so far show us?

Published studies have parameterized density-yield curves of large numbers of species in only three regions: Southwest Ghana (for birds and trees), Northern India (birds and trees), and Southern Uganda (birds) (see Table 1).¹⁴ All show remarkably similar results across taxa and across regions (Figure 3). In every case, there are more loser species than winners, and most losers would have larger total population sizes under land sparing than under a land-sharing (or any intermediate-yielding) strategy. These outcomes are more marked for trees (not shown) than for birds, and for species with small global ranges that are more likely to be of conservation concern (compare the left and right panels in Figure 3). The preponderance of losers and, among those, of species that fare better with land sparing than land sharing increases as production targets rise (moving from left to right within the panels in Figure 3). Importantly, however, most loser species benefit from land sparing even if production targets are below current levels. Hence, even if – by tackling food waste, population growth, and diet – demand were somehow to fall, land sparing would still

be the least bad option for most loser species in the taxa studied. Addressing the needs of loser species that are associated with low-yield farming will require careful attention in land-use planning,¹⁵ but for each of the groups examined so far, and in each region, the conservation status of most species would be better under high-yield farming coupled with retention of remaining nonfarmed habitat.

A handful of other studies have addressed the land-sharing/sparing question using different analytical frameworks and abundance-based measures of the persistence of species (Table 1).¹⁶ In the Colombian Andes, simulations show that total populations of most bird and dung beetle species would be larger under land sparing than in land-sharing landscapes that produce the same quantity of agricultural goods. In the United Kingdom, overall butterfly abundance is expected to be greater for a combination of conventionally farmed land and grassland reserves than with organic farming (unless the yield of organic farming is exceptionally high). Studies on birds in Argentina, Sabah, and Thailand have reached the same general conclusion: more species would persist under land sparing than land sharing.

Results from a roughly equal number of analyses are interpreted as supporting either intermediate strategies or land sharing (Table 1).¹⁷ Mostly, these authors do not perceive there to be a trade-off between improving the wildlife value of farmed habitats and maximizing retention of natural habitats; but none of these studies compare sparing and sharing while keeping overall land areas and production targets constant, so they do not have a strong basis from which to conclude there is no trade-off. Most important, none of these studies calculate population-wide consequences of different land-use strategies for individual species. Our view is that summary metrics such as species richness

Andrew
Balmford,
Rhys Green
& Ben
Phalan

Land for Table 1

Food & Land for Nature? Examples of Studies Addressing the Question of How to Reconcile Agricultural Production with Biodiversity Conservation

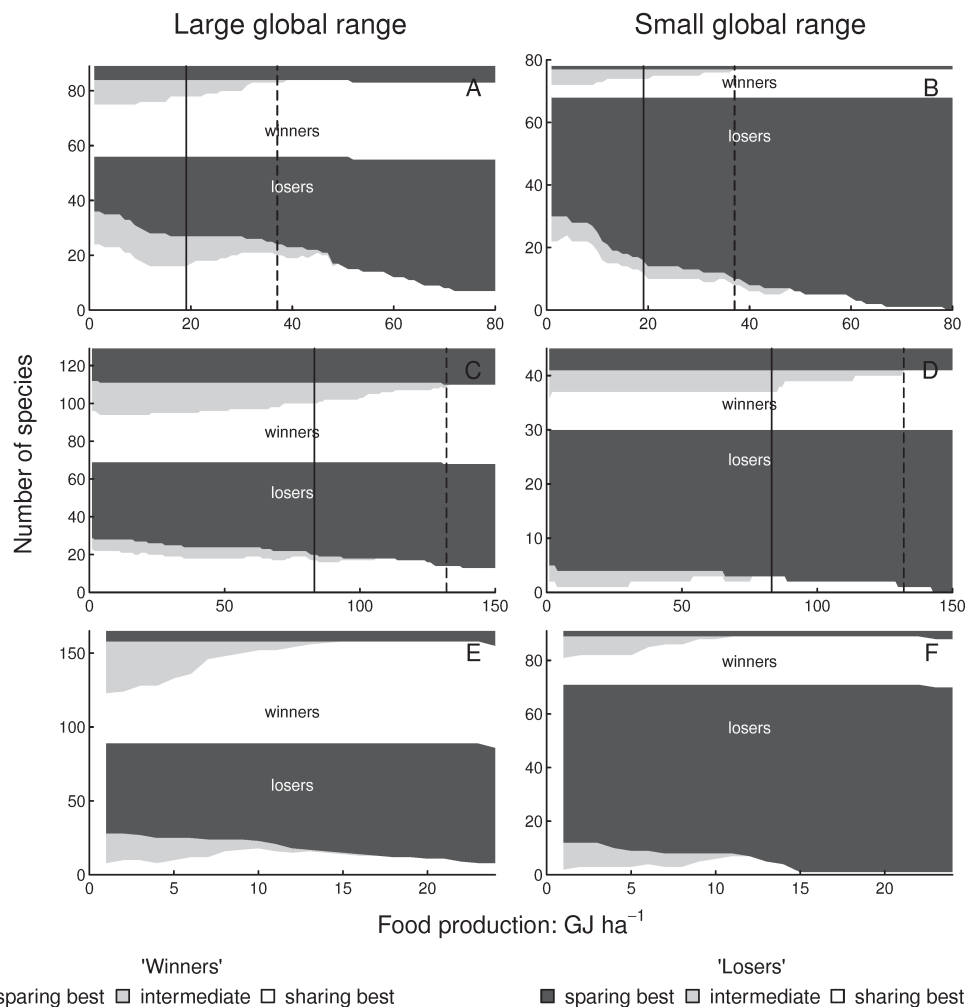
Location	Agricultural System	Include Baseline	Measure Abundance or Density	Calculate Total Population Effects	Quantify Yields	Taxa	Primary Strategy Supported
Uganda ¹⁸	Multiple crops	X	X	X	X	Birds	Sparing
Ghana, India ¹⁹	Multiple crops	X	X	X	X	Birds, trees	Sparing
Thailand ²⁰	Oil palm	X	X			Birds	Sparing
Sabah ²¹	Oil palm	X	X			Birds	Sparing
Colombia ²²	Livestock	X	X	(X)	(X)	Birds, dung beetles	Sparing (unless <500m from contiguous forest)
Argentina ²³	Arable, livestock	X	(X)		X	Birds	Sparing
Amazon ²⁴	Mainly livestock	(X)	(X)			Birds	Sparing
United Kingdom ²⁵	Arable, livestock	X	X	(X)	X	Butterflies	Sparing (but depends on yield ratio & nature of spared land)
Costa Rica ²⁶	Coffee	X	(X)		(X)	Birds	“Small-scale” sparing
United States ²⁷	Arable	X	(X)			Plants	“Small-scale” sparing
United Kingdom ²⁸	Arable		(X)		X	Eight plant & animal taxa	Depends on taxon & yield contrast
Argentina ²⁹	Pasture	X	X		X	Birds	Intermediate
U.S. Great Plains ³⁰	Arable, some livestock	X	X			Birds	Intermediate
New South Wales, Australia ³¹	Arable, livestock	X	(X)			Bats	Intermediate
Western Ghats ³²	Areca nut	X				Birds	Sharing
South-eastern Australia ³³	Livestock	X			X	Plants	Sharing
Sulawesi ³⁴	Cocoa				X	Nine plant, fungus & animal taxa	Sharing/intermediate
Mexico ³⁵	Coffee	(X)			X	Birds	No trade-off

Columns give assessments of whether the studies include an appropriate baseline, measure the abundance or density of individual species, estimate the effect of alternative approaches on total population sizes (on farmland and natural habitat combined), and quantify yields. We have included our interpretation of the primary strategy supported by the authors of each study. Ticks in parentheses refer to studies that partly meet the criterion (for example, by measuring an attribute but not including it in the main analysis). Source: Table built by authors from the sources cited.

Figure 3

The Breakdown of Bird Species According to the Farming Strategy that Maximizes Their Total Population Size, in Relation to Production Target

Andrew Balmford, Rhys Green & Ben Phalan



GJ ha⁻¹ = Gigajoules per hectare. Data are for Southwestern Ghana (top row), Northern India (middle), and Southern Uganda (bottom), shown separately for species with global ranges above (left) and below (right) three million square kilometers. Within each panel, winner species are plotted above losers and are split by whether their populations are greatest under land sparing (dark grey), intermediate-yield farming (light grey), or land sharing (white). The vertical lines indicate estimated production targets for 2007 (solid) and 2050 (dashed). Source: Ben Phalan, Malvika Onial, Andrew Balmford, and Rhys E. Green, "Reconciling Food Production and Biodiversity Conservation: Land Sparing and Land Sharing Compared," *Science* 333 (6047) (2011): 1289 – 1291; and Mark F. Hulme, Juliet A. Vickery, Rhys E. Green, Ben Phalan, Dan E. Chamberlain, Derek E. Pomeroy, Dianah Nalwanga, David Mushabe, Raymond Katebeka, Simon Bolwig, and Philip W. Atkinson, "Conserving the Birds of Uganda's Banana-Coffee Arc: Land Sparing and Land Sharing Compared," *PLoS ONE* 8 (2) (2013): e54597.

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should not be used to draw conclusions about the relative merits of sharing and sparing for biodiversity.³⁶ A site's species richness includes species traveling between or reliant on other land-use types, and is affected by time-lags between habitat loss and relaxation to extinction.³⁷ Simple richness scores also do not include information about species' identities. When an area of natural habitat is converted to agriculture, species richness may be maintained, but perhaps only through the replacement of narrowly distributed, disturbance-sensitive species by widespread generalists. We found evidence of this in the Ghana study, where the overall species richness of birds in low- and intermediate-yielding farm mosaics was similar to that in baseline sites, even though the abundance of most narrowly distributed and forest species was far lower in farmland.³⁸ All of these effects mean richness measures are likely to give an inflated view of the relative conservation value of farmland.

Our assessment of the literature is therefore that all studies that have assessed both yields and their population-wide consequences for individual species across sites ranging from zero-yielding baselines right through to high-yield farming have concluded that land sparing would enable more species to persist than would land sharing. This conclusion makes intuitive sense. As biologists know, most species are specialists. It is therefore unsurprising that very many of them are highly sensitive to substantial habitat modification (as happens under conversion even to low-yield farming). That said, the studies that have used what we consider appropriate methods are few and have covered a limited range of regions, biomes, and taxonomic groups. More data are clearly needed for groups other than birds, for predominantly open biomes,³⁹ and in areas whose biota have potentially been purged of many sensitive spe-

cies by repeated exposure to natural disturbance events such as glaciation. To address this, our group is currently involved in projects to evaluate land-sparing and land-sharing outcomes for a range of taxa in Kazakhstan, the Pampas, Poland, and Yucatán.

Alongside these gaps in knowledge about the sensitivity of populations to changes in the yield of the land they are living on, several other issues about the merits and demerits of the land-sharing/sparing framework have been raised.⁴⁰ Here we examine nine issues, starting with what we believe to be five misconceptions.

1. *Land sparing only needs to be considered if agricultural demand grows dramatically in the future, and this can be avoided.* Analyses to date suggest the relative advantage to wild species of land sparing compared with land sharing increases as production targets rise (Figure 3). However, these analyses also indicate that sparing would be preferable in terms of maximizing species persistence even if demand were to shrink substantially below present-day levels. Whichever strategy is pursued, the overall impact of farming on wild species will be less negative the more that demand for agricultural products can be curbed – through cutting waste, limiting consumption of animal protein, and lowering demand for biofuels.

2. *It is unclear at what spatial grain size sharing becomes sparing.* Individual farms and fields in land-sharing landscapes will often comprise a mix of crop and noncrop elements (such as trees and ponds). Some authors have argued that because these might resemble at a very fine scale the region-wide mosaics of farmland and natural habitat blocks envisioned under land sparing, land sharing is therefore a special case of sparing.⁴¹ We contend this is not helpful, because overall approaches to agriculture should be evaluated at the scale at which major land-use decisions are made, which we suggest is typically that of landholdings

through to regions, rather than individual hedgerows and trees. At this scale – that of entire panels in Figure 1 – the structure of sharing and sparing landscapes and their ability to support the species evaluated so far (such as birds) are very different. Large blocks of forest or wetland in land-sparing landscapes may support viable populations of sensitive species while a similar total area of trees or wetland comprising small woodlots or ponds does not.⁴² A related point is whether there is an upper limit to the grain size at which land sparing might be beneficial. Here we agree with others that sparing at very large scales – say, entire states or countries – would not be appropriate.⁴³ Assigning extremely large areas entirely to agriculture and others entirely to habitat protection would compromise livelihoods and food security, risk the extinction of many narrowly distributed specialists whose ranges fell entirely within farmland, and be exceptionally difficult to implement.

3. *Intermediate-yielding approaches might be optimal but are not considered by the trade-off model.* Our model considers species with density-yield curves of any shape, including those where densities peak at intermediate yields (see panels B and E in Figure 2). Some – but not all⁴⁴ – of this last group of species would have their largest population sizes when yields are below maximum but above the minimum needed to meet production targets. However, studies to date indicate such species are relatively infrequent, especially among losers. More commonly found are species with highest population densities at yields that are lower than the minimum required to meet production targets. Where sparing of natural habitats would be insufficient to conserve such species, sparing of very low-yielding farmland (permitted by increasing yields elsewhere) might be needed.

4. *Land sparing reduces landscape heterogeneity.*⁴⁵ Farmland that is low-yielding be-

cause of the inclusion of many noncrop elements is likely to be more heterogeneous than high-yielding farmland and may therefore contain more species. However, the extra species will often be quite widespread generalists. More significant, when viewed at a larger scale, land-sharing landscapes have smaller blocks of nonfarmed habitat than equally productive land-sparing landscapes (compare panels within rows in Figure 3). Because many natural habitats are highly heterogeneous within themselves, they provide many niches not found at all within farmed land, and thus, land-sparing landscapes can generally support many more specialists than is possible under land sharing.

5. *Land sparing is especially vulnerable to the effects of increasing demand.* Rising demand for agricultural goods is bad for biodiversity regardless of which approach to farming is adopted: it will increase pressure both to expand farmland at the expense of natural habitat and to raise yields within existing farmland. But it is not evident that land sparing is more likely to stimulate demand growth than is land sharing. On the one hand, if high-yield farming techniques lower prices of agricultural commodities for which demand is elastic, then demand is likely to increase, and if high yields boost agricultural wages, they may increase rural demand in particular.⁴⁶ On the other hand, these effects are less likely for staple goods (for which demand is relatively price-inelastic). Perhaps most important, land sparing is not just about yield growth but about setting land aside for conservation (see below). Such restrictions on agricultural expansion will tend to raise prices and hence limit demand growth under land sparing. Whatever the balance of these effects, it is clear that increasing demand will compromise biodiversity under any strategy, reinforcing the point that restricting demand growth – by tackling waste reduction and excessive consumption – must re-

Andrew
Balmford,
Rhys Green
& Ben
Phalan

main a high priority for conservation, and a necessary condition for the long-term success of either sparing or sharing.

We consider the previous points to have arisen from misunderstandings about the idea of land sparing. However, there are several other areas where additional work is required.

6. *Identifying mechanisms for linking the sparing of natural habitats to high-yield farming.* Land sparing comprises two interdependent elements: raising yields on agricultural land and at the same time either decreasing conversion of natural lands to agriculture or freeing up former farmland for habitat restoration. Ensuring yield growth and habitat conservation are coupled is essential for land sparing to succeed. Insofar as demand is fixed, increasing yields can spare land directly, even in the absence of additional interventions. Statistical analyses and economic modeling of historical changes in yields and land cover show that such passive land sparing does occur, sometimes to a greater degree than expected.⁴⁷ This is more likely when demand for products is inelastic, where yield growth is directed away from conversion frontiers, and where yield-improving practices use up labor or capital⁴⁸ – suggestions that have important implications for which crops, areas, and technologies land-sparing strategies might most effectively target. However, we believe additional, explicit interventions are needed to tie within-farm yield growth much more closely to land sparing elsewhere. Possibilities include:

- Command-and-control measures, such as land-use planning and regulation, that simultaneously restrict the footprint of farming and protect or restore natural habitats;⁴⁹
- Use of public funds to provide financial incentives to landowners or cooperatives to spare large blocks of their land through

agricultural subsidies and taxes, Payment for Ecosystem Service schemes, and other means;⁵⁰

- Strategic deployment – away from frontiers of habitat conversion or in exchange for conservation agreements – of investments capable of enhancing yields, such as new or improved roads or irrigation,⁵¹ agricultural extension officers, and micro-finance; and
- Market-based approaches such as certification or preferential access to markets or credit for crops produced from land-sparing landscapes.⁵²

Much work is now needed to develop, test, and refine these and other ideas in order to assemble a toolbox of practical methods for implementing land sparing.

7. *Increasing yields while lowering the externalities of farming.* High-yield farming need not consist of vast monocultures dependent on such high inputs of pesticides, fertilizers, mechanization, and irrigation that they jeopardize agriculture and biodiversity both on farms and elsewhere. As conservationists interested in land sparing, we back calls for sustainable intensification, in which negative impacts of yield increases are avoided or minimized.⁵³ Of course, finding ways of lowering negative environmental impacts per unit of agricultural production is also central to land sparing. Many different but often complementary approaches are possible.⁵⁴ A great variety of new developments deploying both conventional breeding and new genetic technologies (including genetic modification, or GM) have enormous potential to raise attainable yields through 1) improving the ability of crops to acquire water and minerals and use them efficiently; 2) increasing their tolerance to drought and to salinization; and 3) enhancing their defenses against pests and diseases. Radical innovations – such as the prospect of transfer-

ring C₄ metabolism into C₃ grasses, and of perennializing currently annual crops – offer the promise of substantially lowering the inputs to agriculture. But alongside these highly technical developments much can be done – especially in sub-Saharan Africa – to narrow existing yield gaps by adopting practices that are already widespread elsewhere, such as using improved seed varieties and modest amounts of inorganic fertilizer. Promoting agriculturally important ecosystem services such as pollination and pest control will also raise overall yields, provided these services more than offset the production lost on the land needed for their maintenance. Integrated pest management, organic methods, co-culture, drip irrigation, and precision application of fertilizers and pesticides can all help to lower inputs. In our view the key to bringing about sustainable intensification is to avoid dogma and instead explore the likely effects of all promising options – on yield but, critically, also on net negative externalities per unit of production, on prices and livelihoods, and in terms of likelihood of uptake by farmers.

8. *Refining our understanding of how land-use patterns affect long-term persistence of populations.* Our trade-off model is simple and could be developed in several ways so that it more fully captures the demographic consequences of alternative land-use configurations.⁵⁵ In particular, it could usefully include edge effects: both of farmed environments on adjacent natural habitat patches and effects in the opposite direction. Likewise it could incorporate the configuration of habitat patches across the landscape and the permeability of farmland to dispersing individuals, and hence address issues of interpatch connectivity and metapopulation dynamics. Our group is attempting some of these refinements, but there are no *a priori* reasons to expect them to alter our findings in a consistent direction. For example, while edge effects will reduce

the biodiversity value of all natural habitat patches, they will do so disproportionately in small fragments with high-edge-to-area ratios, increasing the relative advantage of land-sparing landscapes (with larger habitat blocks) for retaining habitat-interior specialists. Likewise, while high-yield practices may make farmland more hostile to species associated with natural habitats, thus lowering connectivity by reducing their dispersal between habitat fragments, this effect is likely to be offset by two others. First, the distance between relatively intact patches of habitat can be considerably shorter under land sparing (compare distances between dark blocks in different panels of the same row in Figure 1), perhaps making movements between patches easier. Second, because under land sparing natural habitat patches are bigger and thus less impacted by edge effects, they may support higher densities with greater reproductive rates and hence higher production of dispersing individuals.

9. *Incorporating other societal objectives into the land-sharing/sparing debate.* Our analysis has focused on the trade-off between food production and species persistence, but conservation is also about safeguarding the provision of ecosystem services.⁵⁶ Much research remains to be done on this topic. In terms of climate regulation, retrospective global analyses suggest that yield growth since the 1960s has avoided substantial greenhouse gas emissions that would otherwise have occurred, with the effects of avoided land conversion more than outweighing those of increased emissions from soil and from fertilizer manufacture. However, the magnitude of the savings depends on how far historic yield growth lowered prices and hence fueled rising demand.⁵⁷ For cattle ranching, a regional modeling exercise and a landscape-level study again suggest that high-yield production and land sparing may help reduce emissions relative to lower-yield systems.⁵⁸

Andrew
Balmford,
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& Ben
Phalan

The consequences of alternative farming strategies for other ecosystem services (and disservices) have been less well explored but may again be quite complex. High-yield farming might reduce downstream water availability, but if it contributes to safeguarding wetlands and forests it may help regulate water flows. Likewise the practices needed to substantially increase farm yields would probably diminish people's enjoyment of farmland but might offer greater prospects of experiencing large and diverse natural habitats. In the context of the spread of zoonotic diseases, the intensification of animal production might increase transmission of pathogens among livestock but reduce transmission rates between livestock and humans.⁵⁹ Of course, other considerations are also crucial: the effects of different farming systems on people's livelihoods and values, how well they fit local institutions and cultural conditions, their consequences for equity and gender issues, and, above all, their impacts on food security. Clearly, analysis of density-yield curves gives no information on these other issues, but understanding them will be important for developing effective interventions that address multiple societal objectives.⁶⁰

The land-sharing/sparing debate remains controversial, with many important issues as of yet unresolved. However, we suggest that it has provided a valuable framework that forces us to be explicit about our objectives in evaluating alternative approaches to food production. The recognition that lowering the local environmental costs of production might reduce yields – with important knock-on effects elsewhere since more area is therefore required to meet demand – also has considerable relevance in other contexts:

- In the case of forestry, it is possible that the overall biodiversity value of produc-

tion landscapes is maximized by a system of intensive logging linked to complete protection of other areas that retain species dependent on old-growth forests, rather than by adopting lighter harvesting regimes across the landscape as a whole.⁶¹

- In the context of urban planning, increasing attention is focusing on whether compact growth – decreasing the size of gardens for instance, thus enabling larger greenspaces to be retained – reduces the impact of urbanization on biodiversity.⁶² A recent study from Brisbane suggests generalist and nonnative species fare better under urban sprawl, whereas specialists are more likely to persist if growth occurs via urban intensification.⁶³
- We suspect similar trade-offs might exist at sea.⁶⁴ For example, which would better promote biodiversity: a seascape that is fished entirely using relatively benign techniques, or one yielding the same catch, sustainably, but through large areas open to less-regulated fishing plus large, strictly enforced no-take zones? This might be an interesting line of inquiry in charting a sustainable future for capture fisheries.

For agriculture and conservation, our assessment is that the empirical evidence to date largely points to land sparing as having the greatest potential to limit the ecological cost of food production. Separating land for food and land for nature (while recognizing their interactions) may be better than managing land for both. But this is far from certain, and important gaps in knowledge remain: for many taxonomic groups and regions, for many ecosystem services, and in terms of how best to increase yields while minimizing negative externalities. Crucially, high-yield farming at present largely only provides the oppor-

tunity to spare land for wild species; it does not ensure that sparing occurs. Hence, a major challenge is how to make yield growth conditional on habitat conservation.

Our suggestion that high-yield farming could be linked to land sparing to enhance the conservation of biodiversity and perhaps some ecosystem services is somewhat counterintuitive, and is clearly an uncomfortable proposition for many. Nonetheless, we believe that the evidence to

date suggests there would be considerable benefits from conservationists working with agricultural technologists, policy-makers, development experts, and the food sector to identify ways of linking yield growth to habitat retention and restoration. We believe an equivalent approach may yield similarly unexpected but potentially useful insights in other contexts in which biodiversity and human interests compete for space.

Andrew
Balmford,
Rhys Green
& Ben
Phalan

ENDNOTES

* Contributor Biographies: ANDREW BALMFORD is Professor of Conservation Science in the Department of Zoology at the University of Cambridge. He is the author of *Wild Hope: On the Frontlines of Conservation Success* (2012) and has contributed articles to such journals as *Science*, *Nature*, and *Conservation Biology*.

RHYS GREEN is Honorary Professor of Conservation Science in the Department of Zoology at the University of Cambridge and Principal Research Biologist at the Royal Society for the Protection of Birds. He is the author of *Birds and Climate Change: Impacts and Conservation Responses* (with James W. Pearce-Higgins, 2014) and has contributed articles to such journals as *Science*, *Nature*, and *Journal of Applied Ecology*.

BEN PHALAN is the Zukerman Junior Research Fellow at King's College, Cambridge University. He has published articles in such journals as *Science*, *Philosophical Transactions of the Royal Society B*, and *Food Policy*.

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Andrew
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