Farming and the Fate of Wild Nature

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result, and the postimpact pair might then remain in resonance.

The tendency for oblique low-velocity collisions between similarly sized objects to produce substantial amounts of material in bound orbit suggests that the impact generation of satellites is a common outcome of late-stage accretion, with the Earth-Moon ($q = 0.01$ and $J = 0.115$) and Pluto-Charon offering examples of the potential range of q and J in systems produced by such events. Requiring $(v_{imp}/v_{esc}) < 1.3$ for forming large satellites based on the simulations here implies that binary systems produced through such singular impacts would have (from Eqs. 1 and 2) $J \lesssim 0.8$.

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19. The Roche limit, $a_R \equiv 2.456 R_p (\rho_p/\rho_s)^{1/3}$, is the closest distance a fluid strengthless body of density ρ_s can stably exist from a radius R_p and density ρ_p primary. At the end of each run, we classified particles as escaping (positive kinetic + potential energies), orbiting, or in the planet. A particle was considered to be orbiting if its total energy was negative, and the z component of its angular momentum exceeded that of a circular orbit at the surface of the planet. We defined an equivalent circular orbit as one having the same angular momentum as computed for a given particle but with $e = 0$. If $a_{equiv} > a_R$, the particle was considered to be on a Roche exterior orbit.
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Farming and the Fate of Wild Nature

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World food demand is expected to more than double by 2050. Decisions about how to meet this challenge will have profound effects on wild species and habitats. We show that farming is already the greatest extinction threat to birds (the best known taxon), and its adverse impacts look set to increase, especially in developing countries. Two competing solutions have been proposed: wildlife-friendly farming (which boosts densities of wild populations on farmland but may decrease agricultural yields) and land sparing (which minimizes demand for farmland by increasing yield). We present a model that identifies how to resolve the trade-off between these approaches. This shows that the best type of farming for species persistence depends on the demand for agricultural products and on how the population densities of different species on farmland change with agricultural yield. Empirical data on such density-yield functions are sparse, but evidence from a range of taxa in developing countries suggests that high-yield farming may allow more species to persist.

Clearance for cropland or permanent pasture has already reduced the extent of natural habitats on agriculturally usable land by more than 50% (*1–3*), and much of the rest has been altered by temporary grazing (*4*).

Intensive management to increase production—through irrigation and the application of fertilizers and pesticides—can further reduce the wildlife value of farmed land. Although growth in global food production outstripped population growth between 1961 and 1999, this was achieved through a 12% increase in the global area of cropland and a 10% rise in the area of permanent pasture (*2, 3*). Overall food crop yield per unit area (*3*) grew by 106%, but this was linked to a 97% rise in the area of land under irrigation, and 638%, 203%, and 854% increases, respectively, in the use of nitrogenous and phosphate fertilizers and the production of pesticides (*2, 5, 6*). These impacts look set to grow still further (*5*). With the human population predicted to rise to between 8 and 10 billion (*7, 8*) and with rapidly increasing per capita consumption (*9*), overall food demand is expected to increase two- to threefold by 2050 (*6, 10*). Here, we propose an agenda for the research needed to identify how this enormously increased demand can be met at the least cost to the other species with which we share our planet.

Agricultural change: A tale of two worlds. From the perspectives of both development and conservation, globally averaged changes in agriculture mask important spatial variation, with more pronounced recent changes in the developing world, where most species reside. For instance, since 1961 the total area of cropland in the developing world has increased by over
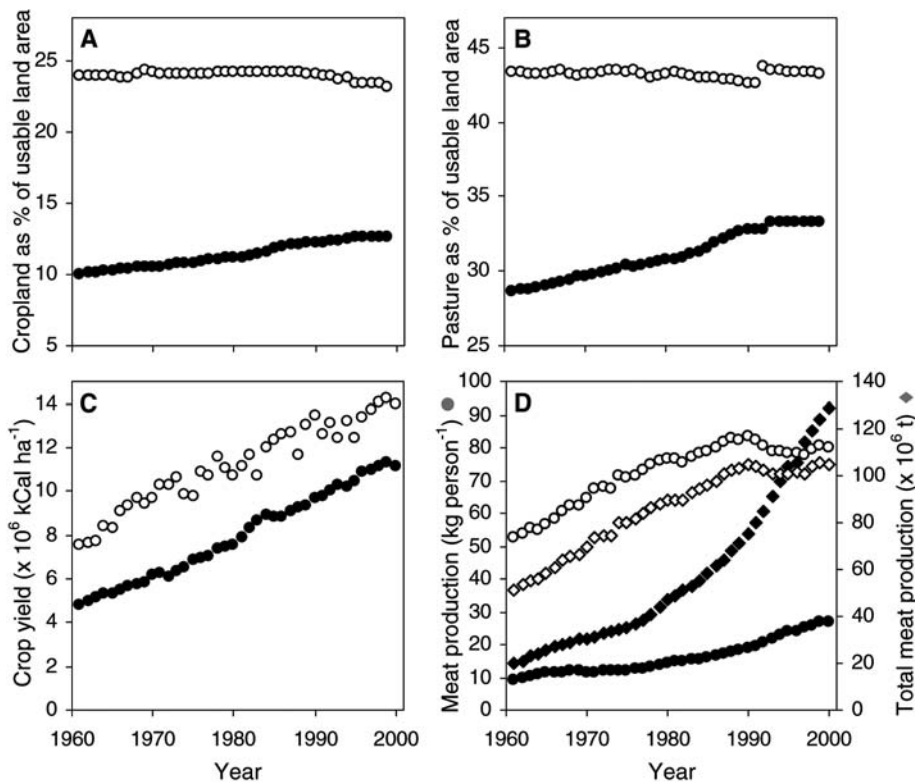
Fig. 1. Changes in agriculture in the developing and developed worlds (*3*), 1961 to 2000, showing annual changes in cropland (**A**), permanent pasture (**B**), mean crop yields for the 23 main food crops (*3*) (**C**), and per capita and total meat production (**D**). In (A) and (B), farmed areas are plotted as a percentage of usable land (*3*). Filled symbols are for developing world, open for developed. In (D), circles are for per capita meat production, diamonds for total meat production.

Fig. 2. The mean proportion of a species' listed threats that are attributable to agriculture plotted for threatened (**A**) and Near-Threatened (**B**) birds from the developed (white) and developing (black) world (*3*).

20%, whereas developed world cropland area has shrunk (Fig. 1A). A similar pattern emerges for permanent pasture (Fig. 1B). These differences in the rates of change of farmland area are not offset by lower yield growth in developing countries. Crop yields (*3*) have grown steadily in both the developing and developed world, with the former lagging the latter by an average of roughly 20 years (Fig. 1C). Annual growth in yield is now higher in the developing world. Further evidence that farming is changing faster in the developing world comes from trends in livestock production. Because of increasing domestic demand (*9*), per capita meat production is rising rapidly in the developing world, whereas elsewhere it is declining; more than half of global meat production now takes place in developing countries (Fig. 1D). How are these changes impacting wild habitats and species?

Differing impacts of farming on wild nature. Several kinds of data suggest that, although it is an important driver almost everywhere, the effect of agricultural change on wild nature is now greatest in developing countries. Coarse-scale evidence of changes in forest cover shows that recent net gains in temperate and boreal forest cover are more than offset by continued losses in tropical regions, largely by conversion to agriculture (*11*). Patchy data on changes in populations of temperate and tropical forest vertebrates confirm this pattern (*12, 13*). For a more detailed picture of the relative importance of threats to biodiversity posed by farming, we used BirdLife International's World Bird Database (*3*) to dissect the problems faced by all 1923 species of globally threatened and Near-Threatened birds; data for no other taxa permit such detailed and comprehensive analysis.

These data show that farming (including conversion to farmland and its intensifying use) is the single biggest source of threat to bird species listed as threatened (accounting for 37% of threats) and is already substantially more important for species in developing countries than those in developed countries (40% and 24% of threats, respectively; Fig. 2A). For developing and developed countries alike, the scale of the threat
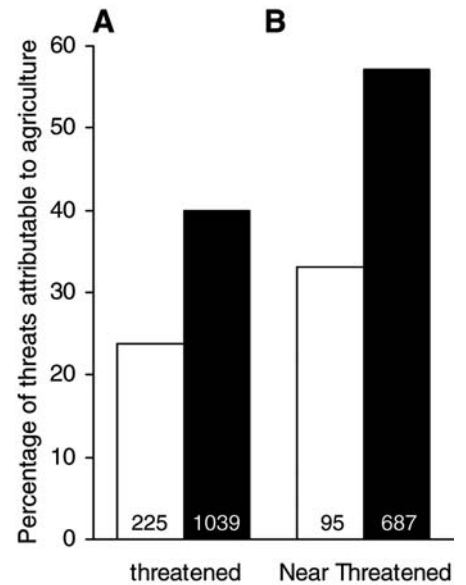
posed by agriculture is even greater for Near-Threatened species (57% and 33% of threats, respectively; Fig. 2B). Because these species are likely to become threatened in the near future (*14*), this implies that agriculture is a growing threat to bird species. There are also larger absolute numbers of threatened and Near-Threatened species in developing countries than in developed countries (threatened, 1039 versus 225 species; Near Threatened, 687 versus 95). Taken together, these data indicate that agriculture is the major current and likely future threat to bird species, especially in developing countries. Given the growing scale and impacts of agriculture, how should we best resolve the need for increased food production with the desire to minimize its impact on what remains of wild nature? Two sorts of suggestions predominate.

Wildlife-friendly farming. Many conservation biologists argue that the global application of wildlife-friendly farming methods would reduce the impact of agriculture on biodiversity. Approaches include the retention of patches of natural habitat and extensively farmed seminatural habitats within the countryside and farming in ways that minimize the negative effects of fertilizers and pesticides on nontarget organisms (*15–20*). Such wildlife-friendly farming receives particularly strong support in Europe, where evidence of declines in the previously high biological value of long-established agroecosystems (*17, 21, 22*) is used to justify agri-environment payments worth over $2.7 billion each year to European Union farmers (*23*). There are far fewer data on farmland biodiversity in less

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developed regions, but evidence that about half of Costa Rica's native forest species of birds, mammals, butterflies, and moths also occur in agricultural areas (table S1) has been used to argue that maintaining low-intensity agriculture will benefit biodiversity in developing countries as well (*18–20*) (table S1).

It is clear that adopting farming methods that enhance population densities of wild plant and animal species on farmland is beneficial to biodiversity, provided that the change to wildlife-friendly farming does not require a reduction in crop yield (*19, 24*). However, it is frequently observed that the biodiversity value of farmland declines with increasing yield (*17, 21, 22*), which suggests that maintaining high wild-

life interest on farmland often requires foregoing opportunities for high crop yields. Existing agri-environment schemes depend on farmers receiving large amounts of financial compensation for lost production, demonstrating that such yield penalties are perceived as real. Their existence underlies a very different school of thought on how best to simultaneously deliver food production needs and meet conservation goals.

Land sparing. This second approach hinges on moving beyond thinking solely about the farmed landscape to considering the consequences of yield penalties for the total area of farmed versus nonfarmed land. Although wildlife-friendly farming is beneficial on farmland, if it reduces yield then

a larger area must be farmed to meet any given production target. Both the Costa Rican and other results (table S1) show that even under benign agriculture, farmland usually hosts far fewer species—especially those of conservation concern—than do the relatively intact habitats from which it was derived. Hence, if yield penalties from wildlife-friendly farming are sufficiently large, the best route to meeting both food production and conservation goals may be to increase yields on already converted land, thereby reducing the need to convert remaining intact habitats, and potentially freeing up former farmland for restoration to a more natural state.

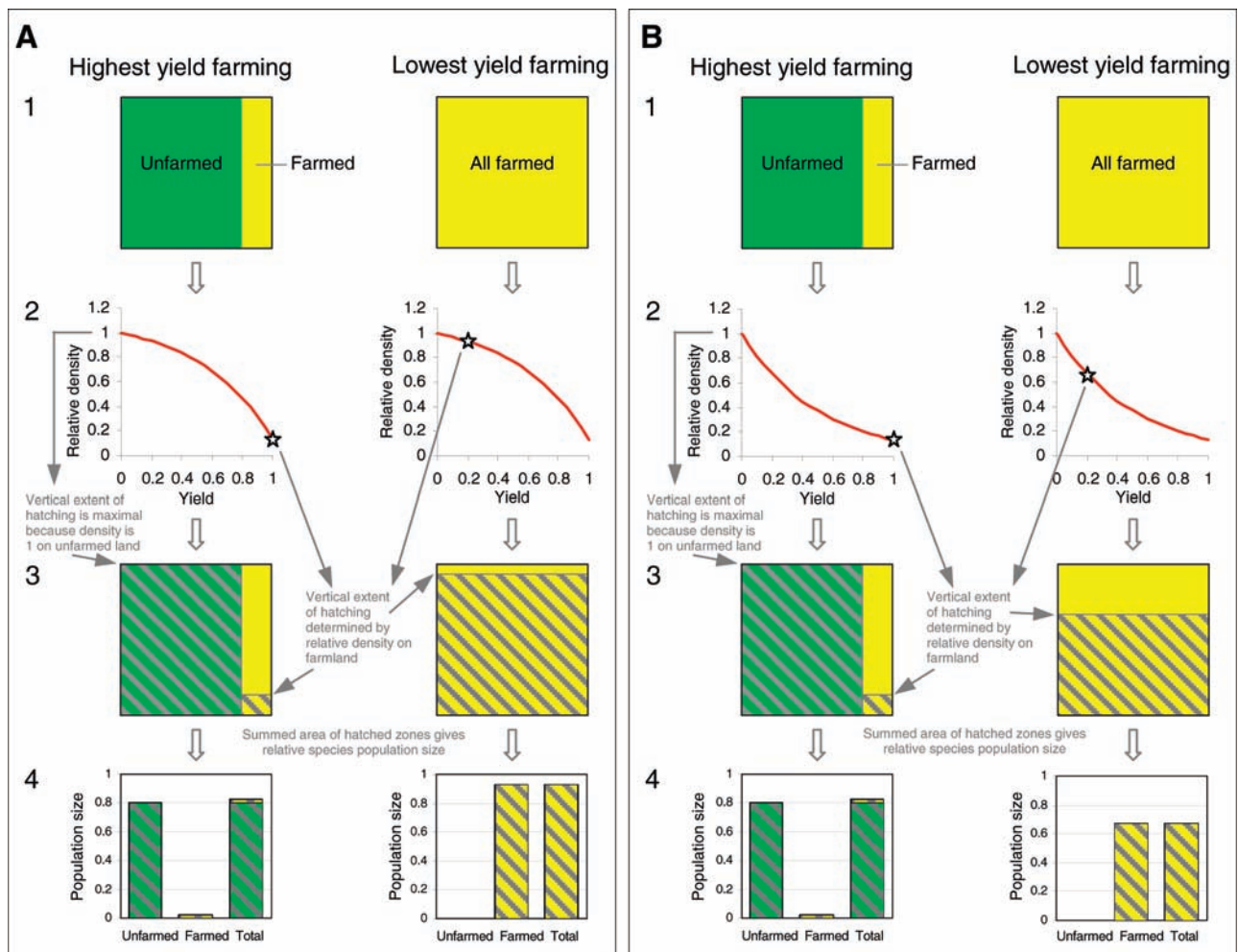This land-sparing argument is rarely made by conservationists (*25, 26*), but is

Fig. 3. Essential features of the model relating species population size to agricultural yield, shown by two examples. In the first (**A**), a province, shown as a map (1), is composed of farmed (yellow) and nonfarmed (green) land. The target agricultural production is $\alpha = 0.2$, which could be achieved by highest yield farming on 20% of the land area ($x = 1$, left panels) or by farming all the land at lowest possible yield ($x = 0.2$, right panels). The organism exhibits a concave density-yield function (red curve in 2), with its highest population density on nonfarmed land (where it is set to 1) and far lower density under highest yield farming than under lowest yield farming (compare stars on left and right panels in 2). The total population size of the whole province can be visualized by shading the maps (3), so that for each habitat, the vertical extent of hatching is proportional to relative population density. The summed area of the hatched zones, relative to that of the whole province, then gives the total population size relative to the population size that would occur if the whole province were unfarmed. These relative population sizes, for nonfarmed and farmed areas and the province as a whole, are shown in the histograms (4). In this case, the total population is higher with lowest yield farming. In the second example (**B**), the situation is the same, except that the density-yield relationship is convex. In this example, the steep drop in density even at low yields means that land sparing is worthwhile and the total population is higher with highest yield farming.

widely advocated in the agriculture and development literature (27–33). Retrospective calculations for the United States, China, and India suggest that, without the marked increases in yields seen over recent decades, producing the amounts of food currently grown there would require 2 to 4 times more land under crops than at present (28, 33–35). Moreover, comparisons among Latin American countries provide empirical evidence that, taking other factors into account, land sparing has occurred: In the 1980s, countries with higher agricultural yield had lower deforestation rates (30), and those with higher yield increases had lower rates of increase in farmland area (27). Finally, prospective calculations show that without yield increases, even maintaining current per capita food consumption would necessitate a near doubling of the world's cropland area by 2050; by comparison, raising global average yields to those currently achieved in North America could result in very considerable land sparing (28).

Hence, although wildlife-friendly farming offers scope to increase the biodiversity value of farmed land on a per unit area basis, this may not result in a net benefit to biodiversity if it reduces crop yield. On the other hand, increasing yield could reduce the requirement for farmland and the rate of conversion of currently nonfarmed land. We may therefore face a choice between having a greater area of low-yielding wildlife-friendly farmland and less intact habitat or having a smaller area of high-yielding, less

wildlife-friendly farmland and more area available for wild nature elsewhere. Identifying the key parameters that can resolve this trade-off requires a model.

Modeling the trade-off. Our model relates the population size of individual species within a large area ("province") to the yield per unit area of farmed land and the target agricultural production required. We focus on one species at a time to allow for evident differences between species in how they respond to changing agricultural activity. Results can later be combined across species and used to optimize province-wide metrics such as the proportion of species committed to extinction. The model province consists of a farmed part (which can include patches of natural habitat) and a nonfarmed part, and it is uniform in its potential suitability for both farming and the species of interest. We ignore any negative external effects of farming on wildlife in nonfarming areas. Crop yield x of the farmed land is scaled relative to the maximum attainable over a large area, and the target level of production of agricultural goods α is assumed to be fixed and is scaled in terms of the proportion of the province needed to grow it if yield were at the maximum (i.e., at $x = 1$). The minimum yield that can still produce the production target is $x = \alpha$ (because the whole of the province must be farmed to grow the target at this yield), and the permissible yield lies in the range $\alpha \le x \le 1$. For a given yield x' within this range, we assume that the production target is just

met, so that the proportion of the province that is farmed is α/x' and the proportion that is nonfarmed is $1 - (\alpha/x')$.

To see how yield then affects the population of a given species, consider a species-specific density-yield function, whereby population density is some function $f(x)$ of yield, and is scaled to 1 on nonfarmed land ($f(0) = 1$). The overall population of a species across the whole province is then the sum of its population on nonfarmed land $1 - (\alpha/x')$ and its population on farmed land $f(x')$ (α/x'), which is $1 + (\alpha/x')$ $(f(x') - 1)$. Considering first a concave density-yield function (Fig. 3A, red curve), highest yield farming (at $x = 1$, summarized in the left panels) is associated with very low relative population density on farmed land (star in step 2), but with a large area of nonfarmed land with relative population density of 1 (step 3), containing most of the total population (step 4). In contrast, farming at the lowest permissible yield ($x = \alpha$, right panels) results in a far higher density on farmed land than with high-yield farming (star in step 2), which in this case more than offsets the loss of population associated with having no nonfarmed land. For this density-yield function, the total population size of this species is thus higher with lowest yield than with highest yield farming. Working through the same logic with a convex density-yield function (Fig. 3B), it can be seen that the population density on lowest yield farmed land is now considerably lower than with the concave function, and the total population is higher with highest yield farming (the sum of few individuals on farmed land plus many on the nonfarmed land spared from conversion). Comparison of these two examples therefore shows that the shape of a species' density-yield function affects which farming regime maximizes its overall population.

To explore the effects of different density-yield functions more systematically, consider a graphical version of the model (Fig. 4A). This includes both a density-yield function (red curve) and a vertical threshold line (in black) at $x = \alpha$, representing the minimum yield that can meet the production target. For any given yield x' in the permissible range ($\alpha \le x' \le 1$), it can be shown that the y value at which a chord drawn from $x = 0$, $y = 1$ to the red curve [at $x', f(x')$] intersects the vertical threshold line gives the total population size of the organism at x', summed across the entire province and scaled relative to the population that would result if the entire province were nonfarmed [relative population size = $1 + (\alpha/x')$ $(f(x') - 1)$]. By considering where all such permissible chords intersect the vertical threshold, one can identify the yield at which total population size is maximized.

Thus, in Fig. 4A (corresponding to Fig. 3A), the chord for lowest permissible yield

Fig. 4. A graphical version of the model. (**A**) A concave density-yield function $y = f(x)$ (red curve; same as 2 in Fig. 3A). The vertical threshold line (black) shows the minimum yield that can meet the target agricultural production ($\alpha = 0.2$). A chord drawn from $x = 0$, $y = 1$ to the red curve at x', $f(x')$ at any point in the permitted range $\alpha \le x' \le 1$, intersects this vertical threshold at $1 + (\alpha/x')$ $(f(x') - 1)$, which is the total population size of the organism in the entire province scaled relative to the population size that would occur if the entire province were nonfarmed. The blue line (termed the critical chord) joins the points on the red curve for $x = 0$ and $x = 1$; its intersection with the vertical threshold (blue square) gives relative population size under maximum yield farming. The green line runs from $x = 0$, $y = 1$ to the red curve at 0.2, $f(0.2)$, and so its intersection with the vertical threshold (green square) gives the relative population size at lowest possible yield; this is greater than that under highest yield farming, and indeed that of any other chords in the permitted yield range, indicating that the total population size is maximized under lowest yield farming. These results are the same as those obtained in steps 1 to 4 of Fig. 3A. (**B**) Same as (A), except that the convex function from step 2 of Fig. 3B is used (with the same results as steps 1 to 4). This time the critical chord cuts the vertical threshold above the green chord and any other permissible chords, so the total population is highest when yield is highest.
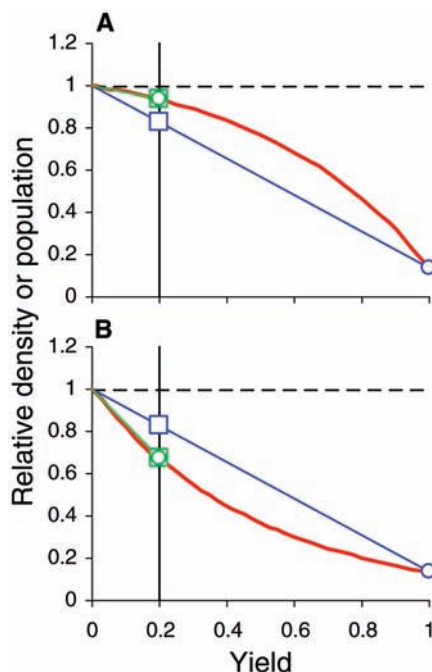
(in green) intersects the vertical threshold above the line for maximum yield (in blue, termed the critical chord) and all other chords. Indeed, whenever the $f(x)$ curve is concave between $x = 0$ and $x = 1$, then the chord for lowest permissible yield always cuts the vertical threshold at the highest point of any yield in the permissible range: Thus, the total population of the species is highest at lowest possible yield. On the other hand, if as in Fig. 4B (corresponding to Fig. 3B), the $f(x)$ curve is convex between $x = 0$ and $x = 1$, the critical chord always cuts the vertical threshold above all other permissible chords, and farming at the maximum yield results in the highest population of the species. This rule also applies for species whose density increases with increasing yield (fig. S1). Results for more complex density-yield functions include dependence of the optimum on α, and an optimum at yields intermediate between the minimum and maximum [supporting online material (SOM) text].

Extension from individual species to province-wide biodiversity. Our model offers a quantitative comparison of the benefits to biodiversity of wildlife-friendly farming and land sparing, and it highlights the fundamental importance of the shape of density-yield functions. It can be extended from the single species case by considering density-yield functions for all species, or a representative sample, to estimate a province-wide metric such as the proportion of species committed to extinction under a particular farming regime. Those species with density-yield functions that exceed 1 at the selected yield value would be assumed not to be at risk of extinction, because they would have higher total populations under that regime than before agricultural modification of the landscape. For species with total populations that are lower than they would be if the whole province were nonfarmed (because their density is lower on land farmed at the chosen yield than on nonfarmed land), extinction risk might be calculated with methods derived from the species-area relationship (*36*). One could then calculate an optimal farming regime, which minimizes the proportion of species committed to extinction (but which would nevertheless be less favorable for some species than for others).

Limitations. Despite these potentially valuable applications, the model can be criticized for being much simpler than the real world, in various ways. First, our model assumes that farming does not affect the population density of species in nonfarmed areas. High-yield farming often leads to external effects such as pollution from pesticides and fertilizers and abstraction of water for irrigation (*5*, *6*). However, such adverse effects can be reduced, through a combination of techni-

cal development and regulation (*6*, *24*, *32*, *37*). Furthermore, low-yield farming may also affect nonfarmed habitats and, although the effect per unit of farmed area may be less severe, the total impact might be greater than for high-yield farming if larger areas of farmland are needed to meet a production target.

Second, the model supposes that agricultural production is at a fixed level for a given scenario, so that an increase in yield results in a proportionately reduced area required for farming. In practice, both empirical and theoretical evidence suggest that land sparing can sometimes be imperfect. If product demand or labor supply are elastic, or if technological changes free up rather than use up labor, increasing yields can in effect increase production targets, thereby adding to the requirement for agricultural land (*24*, *31*, *38*). The model also assumes that nonfarmed land spared from agricultural use will not be converted to some other human use unfavorable for biodiversity. Offsetting these points about likely imperfections in the operation of land sparing, it is also worth noting that there are imperfections in the real world in the delivery of biodiversity benefits by wildlife-friendly farming techniques (*39*).

Last, the model assumes that population size is given simply by the product of density and area. The size and distribution of patches of farmed and nonfarmed land are ignored, but fragmentation of preferred habitat would be expected to influence population density and viability. We also ignore dispersal between farmed and nonfarmed land, yet because of the effects of habitat quality on demographic rates, the population in one compartment might only persist because of net immigration from the other (*40*).

Although the model could be elaborated to incorporate externalities, imperfect land sparing, the spatial configuration of different land-use patches, and source-sink dynamics, we consider that our main conclusion would hold: The best way to reconcile farming and conservation depends on actual production targets and, crucially, on the relative frequency of species with different density-yield functions.

Prospects for wildlife-friendly farming versus land sparing. At present, we know little about how population densities of species on farmed land change with yield, although some forms of the density-yield function seem unlikely to be frequent (SOM text). Few studies have measured density comparably across a range of production regimes, and fewer still have simultaneously measured agricultural yields. Nevertheless, the growing number of studies indicating that half or more of all species of unmodified habitats are absent even from low-intensity farmland (table S1) suggests that many spe-

cies are likely to exhibit negative-trending convex density-yield functions (Fig. 4B). These species will fare best under maximum-yield agriculture combined with land sparing. Such beneficial land sparing is perhaps easiest to envisage in developing countries with limited histories of farming and large numbers of agriculturally naïve species, where increasing yields may reduce the pressure to clear intact habitat. However, insofar as valuable wildlife habitat can be restored or recreated on abandoned farmland, and agriculturally sensitive species still exist, land sparing through yield increases may also be important in regions with long histories of agriculture; indeed, coupling appropriately managed intensification with abandonment and restoration elsewhere may be a principal route to achieving new and ambitious programs of large-scale habitat recovery in Europe and elsewhere (*41–43*).

An agenda for empirical research. What kinds of farming give the best prospect of minimizing losses of wild nature to habitat removal and change while providing food for a growing and more demanding human population? This paper does not provide an answer to that question. However, it does make explicit the nature of the quandary about whether high-yield or low-yield farming, or something in between, is best for biodiversity. Above all, our analysis highlights the need to know more about density-yield functions of real species in the real world, about how they might be modified by changes in agricultural and conservation methods, and about how far different kinds of farming influence the wildlife of nonfarmed areas. We also need to know much more about the extent and limits to which land is spared from agricultural use because of increased yields. Rapidly acquiring the data to address these issues is essential if we are to make wise and informed choices about how and where we farm. Few other decisions will have as great an influence on the fate of wild nature.

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REPORTS

Ammonia Synthesis from First-Principles Calculations

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The rate of ammonia synthesis over a nanoparticle ruthenium catalyst can be calculated directly on the basis of a quantum chemical treatment of the problem using density functional theory. We compared the results to measured rates over a ruthenium catalyst supported on magnesium aluminum spinel. When the size distribution of ruthenium particles measured by transmission electron microscopy was used as the link between the catalyst material and the theoretical treatment, the calculated rate was within a factor of 3 to 20 of the experimental rate. This offers hope for computer-based methods in the search for catalysts.

Detailed theoretical descriptions of the way in which solid surfaces act as catalysts for chemical reactions are now being obtained from density functional theory (DFT) calculations, which can be used to obtain the relevant activation energies. For example, Linic and Barteau have shown that a mean-field kinetic model of the selective oxidation of ethylene on an Ag catalyst, developed on the

basis of DFT calculations, can describe experimental data (*1*). However, the mean-field description implicitly neglects the complexity associated with interactions between adsorbed surface species and the resulting existence of many different possible reaction paths. This problem was overcome recently by Reuter *et al.*, in a DFT-based kinetic Monte Carlo description of the oxidation of carbon monoxide over a $RuO_2(110)$ surface (*2*).

Here we take the further step of developing a kinetic description that includes the full complexity of interactions and reaction paths for a complete catalytic reaction under industrial conditions over a packed bed of a high-surface-area nanoparticle catalyst. Using the

ammonia (NH_3) synthesis as the example, we show that DFT calculations can be used to directly predict a reaction rate for a supported nanoparticle Ru catalyst that is in good agreement with rate measurements performed over a wide range of industrially relevant synthesis conditions. The only experimental input included was the particle size distribution for the Ru catalyst, which was determined from transmission electron microscopy (TEM).

The synthesis of NH_3 is probably the most studied reaction in heterogeneous catalysis, and it acts as the prototype reaction that has been used to develop many key concepts in the field (*3*). The best elementary metal catalysts (Ru and Fe) were discovered in large-scale screening experiments almost 100 years ago (*4–6*), and the nature of the rate-determining step for Fe-based catalysts, N_2 dissociation, was pinpointed as early as 1934 (*7*, *8*). About 25 years ago, surface science studies became possible and revealed a detailed picture of the N_2 dissociation process (*9–13*). It has been shown experimentally (*14–16*) and theoretically (*17–19*) that there is a direct link between the results of the ultra-low-pressure surface science results and NH_3 synthesis data at elevated pressure and temperature. Most recently, DFT calculations were used to quantitatively outline the complete reaction mechanism with all elementary steps on Ru (*20*). It has also been shown that it is possible to predict and understand the trends in reactivity when DFT calculations of

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