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Concentrating vs. spreading our footprint: how to meet humanity's needs at least cost to nature

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Abstract

How to feed, house, clothe and power 11 billion of us without eliminating very many species and wrecking Earth's climate is perhaps this century's greatest challenge. We must obviously strive to curb growth in resource-intensive demand, but we also need to identify production systems that meet people's needs at least overall cost to nature. The land-sharing/sparing concept provides a quantitative framework for doing this, centred around the principle that generating meaningful insights requires comparing alternatives that are matched in terms of overall production. Applications of this framework to >2500 individually assessed species of vertebrates, plants and insects across five continents show that most species decline under farming, and that most would fare least badly under a land-sparing approach – with high-yield production meeting demand in a relatively small, farmed area, freeing-up space for conservation of intact habitats elsewhere in the landscape. However, important questions remain around how to deliver high yields sustainably, and how to ensure high-yield farming does indeed spare natural habitat. The framework is increasingly being applied in other domains too – including urban planning, recreation, forestry and fisheries – where it has the potential to shed light on long-running debates about whether nature would prefer us to concentrate our impact or spread it more lightly but widely. The realization that conservation cannot be delivered without simultaneously considering how humanity meets its needs in these and other sectors is of particular significance as policymakers meet to establish global environmental targets through to 2030 and beyond.

Introduction

We live on an increasingly crowded planet. Whether deliberately or inadvertently, humans unavoidably compete for limited space with most wild species. To date, our actions have roughly halved the biomass stored in terrestrial vegetation (Erb *et al.*, 2018) and altered over 70% of Earth's land surface (IPBES, 2019). More than 28% of all assessed species are now considered threatened with extinction (IUCN, 2021), and the size of monitored populations of vertebrates has fallen by an average of 68% since 1970 alone (WWF, 2020). While there are other important sources of anthropogenic threat, humanity's use of land and water for food, fibre, shelter, energy, minerals and recreation, and the resulting reductions in the extent and quality of natural habitats, are by some margin the greatest way we cause harm to other species (Vié *et al.*, 2009; Maxwell *et al.*, 2016; Tilman & Williams, ND).

As we become wealthier and more numerous, our demands for these goods will doubtless grow, in absolute scale, and – given our increasing appetites for animal-based protein,

biofuels and novel minerals – in breadth too. Consider agriculture and the food system, responsible for around one-third of all anthropogenic greenhouse gas emissions (Crippa *et al.*, 2021) and more of humanity's impact on biodiversity than any other sector (Green *et al.*, 2005; Tilman & Williams, ND). It seems likely that global demand for crops will roughly double over the first half of this century (Tilman *et al.*, 2011). Under current trajectories, meeting this demand will very substantially increase the level of threat faced by birds and mammals across most of Africa and Asia (Tilman *et al.*, 2017). One recent study estimates that under business-as-usual agricultural projections, vertebrate populations will halve once more by 2100 (Leclère *et al.*, 2020). Whether we are motivated to conserve wild species and functioning ecosystems for utilitarian or ethical reasons (Mace, 2014), there is an urgent need to identify ways of limiting humanity's escalating impacts on terrestrial and aquatic systems.

Demand-side measures are obviously essential (Godfray *et al.*, 2010; Foley *et al.*, 2011; Crist *et al.*, 2017; Poore & Nemecek, 2018; Springmann *et al.*, 2018a; Willett *et al.*,

2019; Williams *et al.*, 2021). Given that per capita wealth is forecast to rise more steeply than total population size (PwC, 2017; UNPD, 2019), tackling individual consumption is evidently key. Of course, there is a moral imperative to increase availability and affordability of nutritious food and other resources for billions living in poverty (Godfray *et al.*, 2010; Whitmee *et al.*, 2015). However, lowering excessive consumption by the already comfortably-off of meat, dairy and sugar-derived products (much of it stimulated by aggressive marketing and lobbying by major agribusiness – Gostin, 2016) offers the prospect of substantial health as well as environmental benefits (Tilman & Clark, 2014; Springmann *et al.*, 2016; Clark *et al.*, 2019; Willett *et al.*, 2019). There is also much progress to be made in increasing the efficiency with which resources are used (Jackson & Victor, 2019; Hickel & Kallis, 2020), most notably, perhaps, in cutting food waste, which currently accounts for at least one-third of all food produced in both developed and developing countries (Gustavsson *et al.*, 2011; Porter *et al.*, 2018). Reducing population growth is evidently essential too (Crist *et al.*, 2017), especially – given the vast disparities in individuals' per capita impacts – in wealthier countries, and also among the emerging middle classes in poorer ones; substantial evidence indicates that improving women's rights and in particular female access to education are critically important in lowering fertility rates (Crist *et al.*, 2017; Götmark & Andersson, 2020).

However, in parallel with these demand-side efforts it is also essential to ask how we might organize production to meet any given level of demand at least cost to nature. This supply-side question forms the focus of my review. Answers to it turn in large measure on the issue of how a place's yield of goods such as food or fibres (their rate of production per unit area) relates to its value for wild species or ecosystem services. Clearly, high-yielding practices can harm biodiversity. Early concerns about the impacts of agricultural intensification raised by Rachel Carson's pioneering work on the effects of pesticides (Carson, 1962) led in Europe and elsewhere to the widespread deployment of agri-environment subsidies (Pain & Pienkowski, 1997), encouraging alternative practices designed instead to recover on-farm wildlife. When carefully targeted, these have boosted populations of species of concern (Evans *et al.*, 2002), but the impact of more general, broad-scale agri-environment schemes appears far more limited (Kleijn *et al.*, 2001; Baker *et al.*, 2012). In addition, and importantly, assessments of these interventions rarely consider their effects on local yield, and hence, the potential consequences that displaced production might have on biodiversity elsewhere.

In some instances, measures that enhance wildlife on farms or other areas of production can be achieved without reducing yields and may sometimes even raise them (Rosenzweig, 2003; Kremen & Merenlender, 2018). Such practices represent win-settle or win-win solutions for meeting human needs while conserving nature, and should clearly be encouraged (Green *et al.*, 2005; Rasmussen *et al.*, 2018). However, a great deal of evidence – from continent-wide analyses of correlations between agricultural intensification and bird populations (e.g. Donald *et al.*, 2001; Pain & Pienkowski, 1997) to

the simple observation that farmers usually do not implement agri-environment measures unless compensated by subsidies – suggests that negative, trade-off relationships are much more typical (Green *et al.*, 2005; Phalan *et al.*, 2011a). This means increasing the conservation value of an area used to produce a good usually lowers its yield, so to meet the same demand, a greater area is needed under production, leaving less room for natural habitats. Conversely assigning more space primarily to nature necessitates (if demand is to be met) increasing yield on remaining production areas and hence reducing their value for conservation.

Whatever the relationship between the yield of an area and its biodiversity value, robust evaluations of contrasting approaches to meeting demand can only be made by comparing outcomes across alternatives that are matched in terms of total production. One might label this fundamental analytical tenet the MacKay Principle, after the author of *Sustainable energy – without the hot air* (MacKay, 2009), who proposed multiple low-carbon portfolios for meeting future energy needs but insisted they could only be meaningfully compared at the same level of output. Some frameworks developed for exploring interactions between biodiversity and farming, such as countryside biogeography (Daily *et al.*, 2001) and the concept of working landscapes (Kremen & Merenlender, 2018), can help identify ways of increasing biodiversity within areas under production. However, they rarely consider yields and do not compare outcomes matched for overall output. As a result, they are unable to provide information on system-wide impacts of different ways of meeting a specified level of demand. In contrast, the sharing/sparing paradigm has the MacKay Principle at its centre.

The sharing vs. sparing framework

The sharing/sparing framework is a device (developed by Green *et al.*, 2005, but independently proposed by van Noordwijk *et al.*, 1997) for assessing how in principle one might produce a given quantity of an area-demanding good such as food at least cost to biodiversity. It envisages sharing and sparing as two extremes which (in line with the MacKay Principle) achieve the same overall production (Fig. 1a). Sharing involves integrating practices which benefit biodiversity (such as retaining important microhabitat features like ponds and hedges, or reducing chemical inputs) within the area producing the good of interest. Under extreme sharing, this form of production occupies the entire landscape. Land sparing on the other hand builds on Norman Borlaug's observation (Borlaug, 1972) that high-yield production can reduce the area needed to meet a given level of demand. Sparing concentrates higher-yielding production – at its extreme into the smallest area necessary to meet demand – while simultaneously retaining or restoring other parts of the land- or seascape for conservation. The sharing/sparing framework also allows the exploration of a continuum of solutions involving yields and areas under nature which are intermediate between extreme sharing and extreme sparing (Fig. 1a).

In terms of mechanism, as originally conceived by Borlaug and others, market-mediated factors alone (the effects of
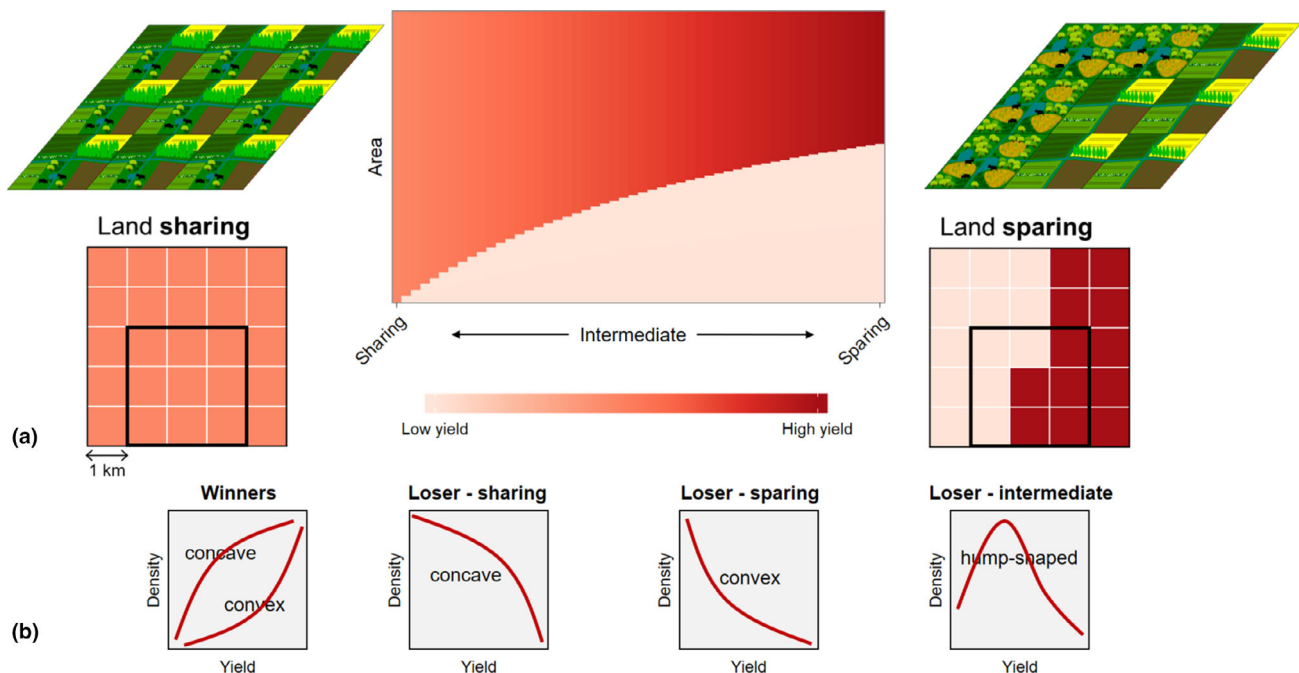
Figure 1 The sharing/sparing framework. (a) The sharing/sparing continuum, characterized for a hypothetical 5 km × 5 km landscape. Extreme sharing (far left) involves farming the entire landscape at the lowest yield (mid-pink) sufficient to meet the desired landscape-wide level of production. Extreme sparing (far right) involves farming at the highest sustainable yield (dark red) over the smallest area necessary to meet the same production, while retaining or restoring the rest of the landscape as zero-yielding natural habitat (light pink). Many intermediate solutions are possible. Cartoons illustrate portions of the landscape (inset rectangles). (b) Hypothetical density–yield curves, from left to right, for winner species whose population densities increase under farming, and for loser species whose landscape-wide populations are maximized under extreme sharing, extreme sparing and an intermediate approach. Images kindly drawn by Tom Finch [Colour figure can be viewed at zslpublica tions.onlinelibrary.wiley.com.]

higher-yield systems on prices, profits, capital or labour) might in principle increase the area available for natural habitat in direct proportion to any increase in yield (Ausubel, 1996; Waggoner & Ausubel, 2001). However, in practice such 'passive' sparing is unlikely to be this effective – higher yields can free-up capital or labour, and commonly stimulate increased demand (Byerlee et al., 2014; Villoria et al., 2014; Paul et al., 2019). Hence, more active coupling of high-yield production and habitat conservation will be needed if most of the potential gains from sparing are to be realized (see *Land-use realities* below).

One last key attribute is scale (Ekroos et al., 2016). The framework conceptualizes sharing or sparing of patches that are sufficiently large (in practice at least 1–10 km²) to be relevant to decision-makers and to meet the needs of individuals of a wide range of species (Green et al., 2005; Phalan, 2018). In some contexts – where landscapes are relatively homogenous, or land holdings very large – appropriate patch sizes might be substantially larger. However, the notion of extremely large-scale sparing (of blocks >10⁴–10⁵ km² in size) will typically be impractical, as it raises major concerns around the fairness and political feasibility of removing very large areas from production, and around the fate of species occurring only in more productive regions (Egli et al., 2018).

Parameterizing the continuum of possible approaches to meeting demand requires estimating the conservation value of entire land- or seascapes managed in contrasting ways to achieve a specified level of output. The first step is to quantify conservation outcomes and yield across a wide range of production systems, and crucially in zero-yielding natural habitats (for details, see Green et al., 2005; Phalan et al., 2011b). Measurements need to be made across the full cycle of production (so across age classes, in the case of perennial crops). Survey sites should be matched as far as possible except in terms of management practice and sufficiently large that the organisms recorded are likely to be sustained locally. Given conservation is above all concerned with limiting extinctions, conservation metrics might focus predominantly on indicators of the likelihood of species persistence, estimated individually for large numbers of wild species. Effort should be made to survey all species, where possible across several taxa, while acknowledging that no species groups are perfect surrogates for biodiversity as a whole, and that some particularly rare species (likely to be restricted to natural habitats) will escape detection. Surveying only those species of direct value to the production system, such as crop pollinators, is probably less helpful, as management practices that sustain these may well not support other species (Kleijn et al., 2015); a site's value for species

that enhance productivity is probably better captured through its effect on yield (Phalan, 2018). In terms of which metric of biodiversity is estimated, Green *et al.* (2005) propose that quantifying individual species' population densities represents a sensible compromise between tractability and robustness; other measures of relative abundance can also be used. More detailed indicators of long-term persistence may be impractical to obtain, while simpler pooled metrics such as species richness are insensitive to population declines of still-extant species, and may not register the replacement of localized specialists with widespread generalists (Dornelas *et al.*, 2014; Blowes *et al.*, 2019). Yields might be measured in calories, profit or other currencies, all expressed per unit area and time. Putative correlates of yield (such as measures of input intensity) preclude estimation of production and so are less useful (Phalan *et al.*, 2011*a*).

Information on how the population density of each species varies with yield can then be summarized in so-called density–yield curves (Fig. 1b; Green *et al.*, 2005). These curves provide clear tests of how far there are indeed trade-offs between production and conservation outcomes. So-called 'winner' species, that benefit from farming, have positive population density–yield curves. Conservation attention should probably focus instead on loser species, with negative-trending curves. The shape of density–yield curves (above the minimum yield necessary to meet demand) also anticipates which approach to production would maximize a species' abundance (Green *et al.*, 2005). Populations of species exhibiting concave curves are maximized under extreme land sharing, those with convex curves are maximized under extreme sparing, and those with hump-shaped curves are usually favoured by intermediate strategies (see Green *et al.*, 2005 for derivation). Density–yield curves can in turn be used to estimate each species' aggregate population size across simulated land- or seascapes which achieve the same overall level of production in different ways. The results can be expressed relative to a baseline (most commonly the population size estimated in the absence of production – Green *et al.*, 2005) and then summarized across all species. Last and importantly, these calculations can be re-run to consider other levels of output: the framework can thus be used to compare production approaches even if (for example) demand was to fall.

Some prominent criticisms of the sharing/sparing framework – that it assumes rather than tests for trade-offs between yield and biodiversity values, that it ignores intermediate-yield solutions, that it is unclear about the scale at which sparing might occur, and that it assumes food demand will increase (Perfecto & Vandermeer, 2008; Fischer *et al.*, 2014*a*; Fischer *et al.*, 2017) – have been addressed in detail elsewhere (Phalan *et al.*, 2014; Balmford *et al.*, 2015*b*). More significant, in my view, is the argument that by ignoring socio-economic issues such as food security, rural livelihoods and social equity, the sharing/sparing framework is too simple to be useful (Perfecto & Vandermeer, 2008; Fischer *et al.*, 2014*a*; Kremen, 2015; Fischer *et al.*, 2017). However, the framework was never designed to address these important outcomes, which are unlikely to vary with yield in any simple fashion, and may thus be best addressed through different, complementary approaches (see

Phalan, 2018 for a careful commentary). In its favour, despite its restricted focus the framework does succeed in clarifying the sorts of quantitative measurement needed to understand how decisions about the way we produce food and other goods impact biodiversity. Moreover, many additional considerations can be incorporated (see Elaborations and limitations below): other conservation metrics beyond relative population size can be used (including measures of ecosystem service delivery); adjustments can be made to account for population–landscape interactions such as edge effects; and mixed solutions (involving three or more levels of production in different areas) can be explored.

Structure of rest of review

Farming provided the context for the original formulation of land sparing, and for most applications of the sharing/sparing framework that have followed. This review therefore focuses next on agriculture, and particularly, the results of quantitative, field-based studies that have parameterized density–yield curves to identify which approaches to meeting food demand might have least impact on biodiversity. The paper then considers limitations of these analyses and the results of empirical studies which have attempted to address them through elaborations to the framework. I close this section on farming by examining two major, still-unresolved concerns about land sparing – the importance of rebound effects; and the sustainability and potentially negative impacts of high-yield food production. Given that the sharing/sparing paradigm is attracting increasing attention in other sectors where producing goods potentially reduces an area's value for conservation, I next move on to examine initial applications of the framework in four more domains – nature-based recreation, urban planning, forestry and seafood production. The review then closes by considering the insights which sharing/sparing studies might provide for conservationists, producers and current policy efforts to secure ambitious conservation targets in an era of apparently diminishing appetites for government intervention and international collaboration.

Sharing and sparing in agriculture

Results from basic sparing–sharing studies

The first paper to apply Green *et al.*'s framework presented the results of surveys counting birds and trees and quantifying yields across diverse farming systems in southwest Ghana and northern India (Phalan *et al.*, 2011*b*). Individual density–yield curves were constructed for 167 and 174 bird species (in Ghana and India, respectively) and 220 and 40 tree species. These revealed that most species in both taxa and regions are losers from agriculture, with most loser species in each group having convex density–yield curves: for these taxa and locations, trade-offs between biodiversity and yield thus appear to be the norm. Using the curves to estimate landscape-wide populations under contrasting land-use approaches (each set to meet production projected for 2050) suggested most species will decline from their 2007 levels, but those declines would

be substantially less severe under extreme land sparing than under land-sharing or any intermediate approach (Fig. 2a). The preponderance of loser species whose populations would decline least under extreme sparing is greater for birds and trees with narrow geographical ranges (which are often of greater conservation concern), and in simulations assuming higher levels of food production (Fig. 2b). However, the overall result – that most species would fare least badly under land sparing – also holds in scenarios assuming food production drops below current levels, indicating that high-yield farming combined with sparing natural habitat would outperform sharing and all intermediate approaches even if food demand was somehow to fall.

Similar field campaigns and analyses have since been conducted in Uganda, Kazakhstan, the Brazilian and Uruguayan pampas and Mexico's Yucatán Peninsula (Dotta, 2013; Hulme *et al.*, 2013; Kamp *et al.*, 2015; Dotta *et al.*, 2016; Williams *et al.*, 2017; Alvarado *et al.*, 2018*a*). Together with unpublished data on Indian insects (Onial, 2010), these studies generated individual density–yield profiles for 990 further species of birds, butterflies, dung beetles, trees, grasses and daisies. Although there is variation (particularly across taxa), the broad findings are remarkably consistent with those from Ghana and India (Fig. 3a): in every taxon in each region, most species surveyed are losers under farming, with most losers exhibiting negative-convex responses to increasing yield and thus

projected to fare least badly under extreme land sparing. In each case, this conclusion was again more marked for species with smaller geographic distributions, and as region-wide food production increased, but held even at lower than current production levels. Importantly, between them these studies span a very wide range of biomes (from forest to steppe), latitudes and farming systems. Thus, while some modelling work on hypothetical species and environments (Law & Wilson, 2015; Butsic *et al.*, 2020) suggests that optimum solutions might shift away from extreme sparing in certain contexts, the evidence from these field-based sharing/sparing studies indicates such situations may be quite rare.

In contrast to these consistent empirical results, other studies have reached mixed conclusions – variously finding in favour of land sharing, land sparing or more complex solutions (Dorrough *et al.*, 2007; Gordon *et al.*, 2007; Steffan-Dewenter *et al.*, 2007; Ranganathan *et al.*, 2008; Clough *et al.*, 2011; Egan & Mortensen, 2012; Lentini *et al.*, 2012; Mastrangelo & Gavin, 2012; Quinn *et al.*, 2012; Wright *et al.*, 2012; Blanco & Waltert, 2013; Teuscher *et al.*, 2015). However, all of these studies lack one or more key features of the basic sharing/sparing framework: they omit zero-yielding natural habitats (or in some cases high-yielding farm systems); they do not report farm yields; they consider very few species; or they use easier-to-derive but less informative biodiversity metrics such as species richness (Phalan *et al.*, 2011*b*; Balmford *et al.*, 2015*b*;
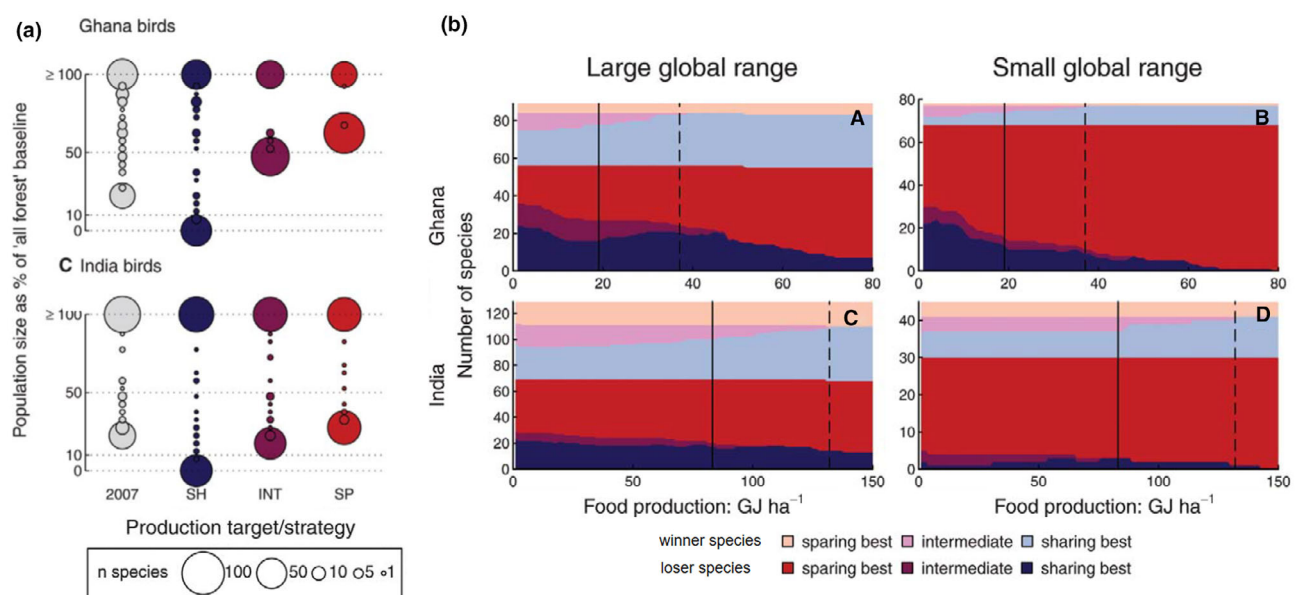

Figure 2 Results from applying the basic sharing/sparing framework for birds in agricultural landscapes in southwest Ghana and northern India, first published in Phalan *et al.* (2011*b*). (a) The distribution of expected population sizes (relative to an all-natural habitat baseline) in 2007 and under three contrasting approaches to meeting estimated 2050 production levels – extreme sharing (SH, blue), an intermediate approach (INT, purple) and extreme sparing (SP, red). Circle sizes denote the number of species with that relative population size. (b) Numbers of species which are winners (light colours) or losers (dark colours) under agriculture, and whose populations are expected to be greatest under extreme land sparing (red), an intermediate strategy (purple) or extreme sharing (blue), in the relation to total landscape-wide food production. Species are split into those with large (left) and small (right) global ranges. Vertical lines show food production recorded in 2007 (solid) and estimated for 2050 (dashed). Results in both (a) and (b) were broadly consistent when yields were measured in terms of profit rather than calories [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]
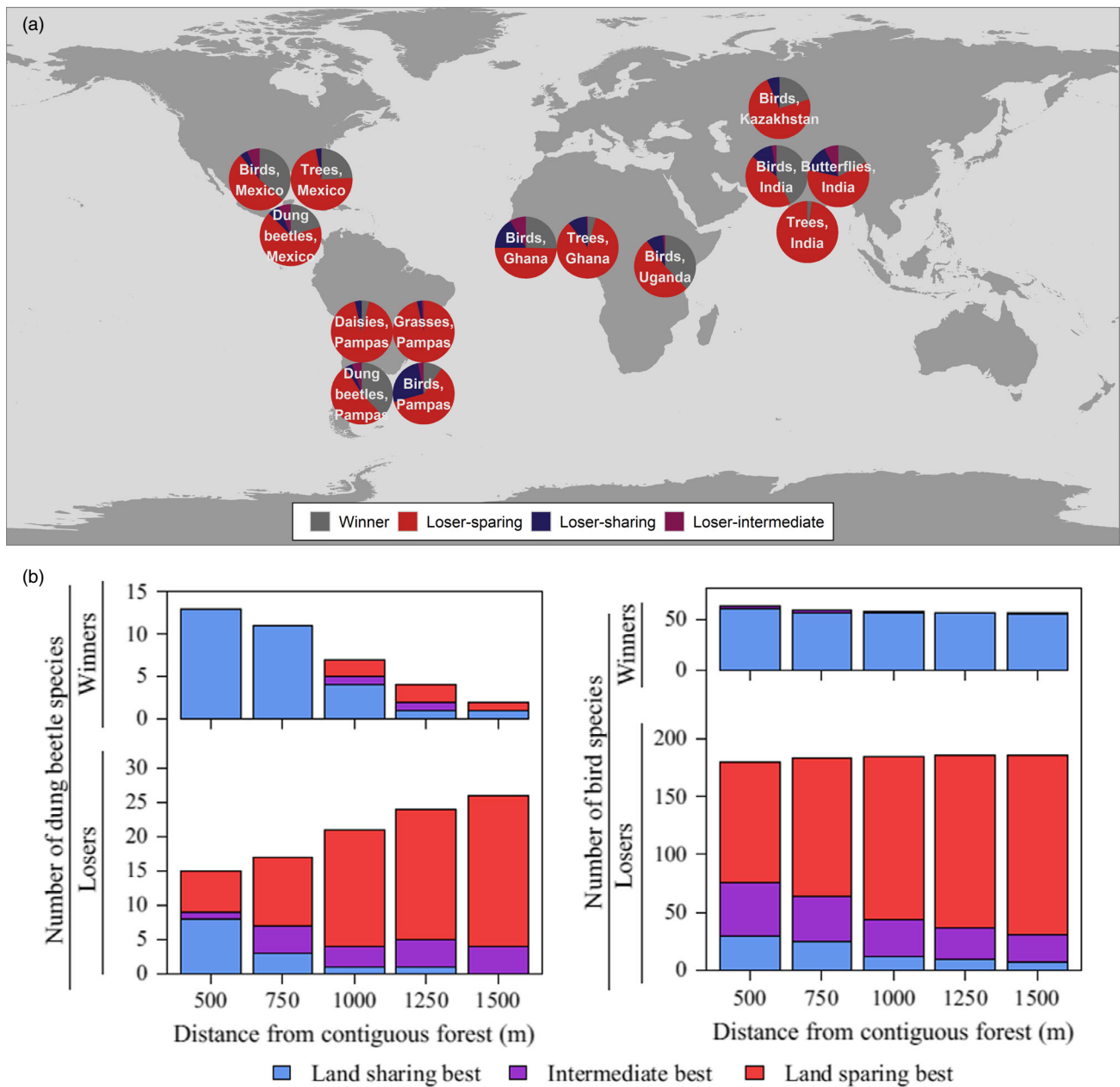
Figure 3 (a) Summary of results from all basic sharing/sparing studies using the Green *et al.* (2005) framework. Pie charts show proportions of winner species (grey) and loser species whose landscape-wide populations would be greatest under extreme land sparing (red), extreme sharing (blue) or any intermediate (purple). Data are plotted for a total of 1591 individually assessed species; 77% are loser species, of which 84% would fare best under extreme sparing. Calculations assume present-day production levels. Image produced by Tom Finch. (b) Data from occupancy modelling for 346 species of dung beetles (left) and birds (right) in the Colombian Chocó-Andes, showing how many are winners (top rows) or losers (bottom rows) from cattle pastures, and would have their largest populations under extreme sharing (blue), an intermediate strategy (purple) or extreme sparing (red). Different bars show results for contrasting scenarios of where sharing occurs, relative to contiguous forest. Results are for the lowest production level modelled. Figure first published in Gilroy *et al.* (2014*a*) [Colour figure can be viewed at zslpublications. onlinelibrary.wiley.com.]

Luskin *et al*., 2018). This means they are unable to estimate the effects on the abundances of large numbers of species of alternative approaches to meeting a given level of agricultural production (Phalan, 2018). As a result, they cannot, I believe, generate reliable inferences about the merits of sharing and sparing. The use of species richness scores can be especially uninformative (Dornelas *et al*., 2014): indeed, when abundance data for birds in Ghana and birds, dung beetles and trees in Mexico are degraded to simple richness counts, they appear to provide support for land sharing, even though this would see the extinction of localized specialists and their replacement by widespread generalists (Balmford *et al*., 2015*b*; Williams *et al*., 2017). Beyond these studies, one abundance-based analysis (lacking yield data) has concluded sparing probably outperforms sharing for birds in a Bornean forest/oil palm landscape (Edwards *et al*., 2010). Two more recent studies that have used density measures have highlighted the value, within agricultural landscapes, of retaining forest blocks (Karp *et al*., 2019) or woodlands (Macchi *et al*., 2020), but do not consider the consequences (if these are to be safeguarded while production is to be sustained) of maintaining high yields elsewhere.

The apparently consistent observation from abundance-based studies that a large portion of all wild species would fare better under land sparing than sharing or any simple intermediate makes biological sense. As field ecologists know, a very high proportion of all species are specialized to particular environmental conditions (Forister *et al*., 2015). Even modest disruptions to these are likely to reduce those species' populations. This explains why so many species decline under farming, and why most of these losers have negative-convex density–yield curves. This argument receives support even from presence–absence sharing/sparing studies, where in most cases, a large fraction (often half or more) of all recorded species are entirely restricted to natural habitats (Aratrakorn *et al*., 2006; Komar, 2006; Steffan-Dewenter *et al*., 2007; Anand *et al*., 2010; Clough *et al*., 2011; Mahood *et al*., 2012; Chandler *et al*., 2013). The long-term persistence of such specialists (which may make up the bulk of all global biodiversity) would seem to depend on sparing natural habitats from the advance of farmland (see also Socolar *et al*., 2019).

Elaborations and limitations

Several field studies have applied the basic sharing/sparing framework in slightly different ways, or developed elaborations to address some of its limitations. An important series of papers based on intensive surveys of 318 bird and 28 dung beetle species across a forest/pasture landscape in the Colombian Chocó-Andes has used occupancy modelling to estimate population-level impacts of contrasting land-use configurations. These have concluded that land sparing would again outperform sharing, except if sharing occurs immediately adjacent to contiguous forest (Fig. 3b; Gilroy *et al*., 2014*a*). These findings are reiterated if biodiversity is assessed instead using metrics reflecting phylogenetic or functional diversity (Edwards *et al*., 2015; Cannon *et al*., 2019; see also Alvarado *et al*., 2018*b*), and even when sparing is constrained to allow the

retention only of secondary habitats (Edwards *et al*., 2021). Other abundance-based studies have explored the effects of different assumptions about the pre-agricultural mix of baseline habitats (Macchi *et al*., 2016) and have adjusted estimates of population sizes to account for the possibility of spared habitats potentially being highly fragmented, subject to marked edge effects, or substantially lower quality than the natural habitats surveyed in fieldwork (Lamb *et al*., 2016; Balmford *et al*., 2019). In all these studies, sparing still outperforms sharing except under unusual circumstances.

Some other concerns about biodiversity metrics, landscape dynamics and yield measurement have yet to be addressed empirically. Instantaneous measures of abundance, for instance, may overestimate the persistence of populations maintained only by dispersal from elsewhere (Kremen, 2015; Kremen & Merenlender, 2018). Though hard to tackle in short-term studies, this bias is presumably more likely for agricultural areas and fragmented natural habitats than for large blocks of natural habitat, so would tend to overestimate the benefits of land sharing. A related issue is the overall lack of information on dispersal. One suggestion is that for species exhibiting source–sink dynamics where individuals in low-yield farmland originate in forest, concave density–yield profiles suggesting land sharing is optimal might conceal negative population growth – with persistence actually being more likely under land sparing (Gilroy & Edwards, 2017). More generally, although high-yield farming practices may make the matrix between habitat patches more hostile to dispersing organisms, by incorporating larger habitat blocks covering more of the landscape, sparing could enhance both inter- and intra-patch dispersal (Balmford *et al*., 2015*b*; Phalan, 2018). Another area for improvement might be in obtaining more robust estimates of yields – ideally over many harvests (D. Edwards, pers. comm.), incorporating not just mean yields but yield resilience (Redhead *et al*., 2020), and reflecting nutritional value rather than simple caloric or protein content (Cassidy *et al*., 2013; DeFries *et al*., 2015; but see Springmann *et al*., 2018*b*). However, the challenges in obtaining such data in small-scale field campaigns should not be underestimated.

One significant elaboration in recent studies has been the exploration of mixed solutions, in which rather than yields being uniform across all farmed land in a simulated landscape, different areas under production are farmed at different yields (Butsic & Kuemmerle, 2015; Fig. 4a). Mixed approaches might be most promising where a significant portion of species exhibit hump-shaped density–yield curves, peaking at yield levels below those capable of meeting region-wide food demand. Such species might be expected to be particularly prevalent in regions where people have largely eliminated major natural disturbances (such as large-scale fires, flooding or megaherbivore foraging – Müller *et al*., 2013; Navarro *et al*., 2015). In these areas, low-yield farming methods (termed High Nature Value farming in Europe; EEA, 2004) may nowadays substitute for lost natural disturbances, absent even from large areas of natural habitat, and hence be key to retaining species on the landscape. New studies from Europe seem to support this notion. Thus, abundance data for a suite of
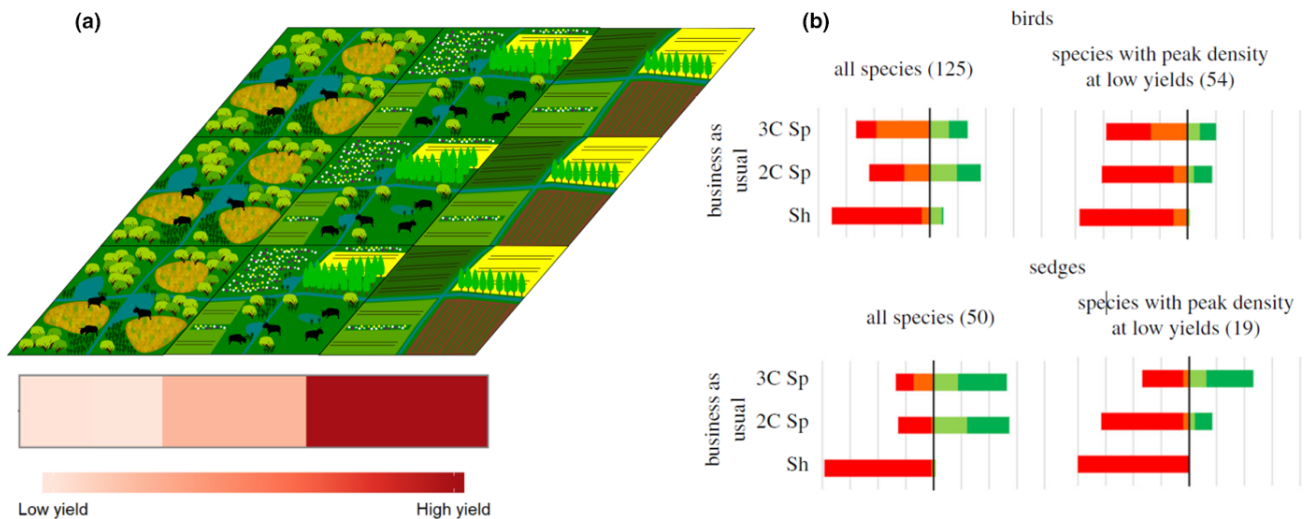
Figure 4 Three-compartment sparing in farmland. (a) A cartoon landscape with zero-yielding (left), intermediate-yielding (centre) and high-yielding (right) compartments. Bars indicate yields. Drawn by Tom Finch. (b) In eastern Poland, two-compartment sparing solutions (2C Sp) would lead to slightly fewer bird and sedge species experiencing major declines (red) or declines (orange) combined than would three-compartment sparing (3C Sp; left-hand plots), but three-compartment sparing would be better for those species with hump-shaped density–yield curves (right-hand plots); land sharing (Sh) consistently performs worst across all species groups. Estimates assume projected 2050 production levels. Figure first published in Feniuk *et al.* (2019) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

common grassland arthropods in Germany suggest mixed solutions involving different yields across different meadows may be optimal (Simons & Weisser, 2017). Working in eastern Poland with entire assemblages of birds, sedges and trees, Feniuk (2015) and Feniuk *et al.* (2019) found that a three-compartment approach (comprising natural habitat, high-yield and very low-yield farmland) buffered more intermediate yield-preferring species from the effects of rising food production than either sharing or basic two-compartment sparing (Fig. 4b). Most recently, analyses of abundance data for all birds in two UK landscapes, exploring thousands of combinations of yield and area for both high- and low-yield farm compartments, suggest that three-compartment strategies might again provide near-optimal solutions to conserving species assemblages in regions where natural disturbance regimes have been substantially dampened (Finch *et al.*, 2019, 2020).

A second major extension of the original sharing/sparing framework has been to consider additional outcomes of conservation concern besides biodiversity. For example, analysis of data on above-ground carbon in the Chocó-Andes study system reveals that landscape-wide carbon retention there would be greater under land sparing than sharing (Gilroy *et al.*, 2014b). Similar results have emerged from Ghana, Mexico and Poland (Williams *et al.*, 2018; Figure 5a): in these cases, carbon density–yield associations are consistently negative convex, with carbon storage as a result projected to be higher under sparing than sharing or any intermediate approach. A land-sparing landscape would also secure greater soil organic carbon than a sharing or mixed landscape in an Austrian case study (Jost *et al.*, 2021), while a US biofuels study concluded that climate mitigation gains would be greater if biofuel crops were produced at high yields alongside sparing as much area as

possible under natural vegetation (Anderson-Teixeira *et al.*, 2012). Other empirical work has estimated the consequences of contrasting farming approaches for dung removal by beetles in Mexico (Alvarado *et al.*, 2018c); and for outdoor recreation, nitrogen and phosphorus pollution, greenhouse gas emissions and biodiversity in two regions of the UK (Finch *et al.*, 2021). In both cases, sparing again outperformed sharing, although in one UK region, mean outcomes were marginally greater under a three-compartment, mixed approach with substantially more land spared from production than at present (Figure 5b). Mixed and simple two-compartment sparing also markedly outperformed land sharing in an analysis of biodiversity, carbon, timber and agricultural outcomes in central Kalimantan (Law *et al.*, 2017).

Thus, in terms of biophysical outcomes, it seems that across diverse farming systems, regions and taxa, empirical studies point consistently in favour of increasing farm yields and sparing other land as natural habitat, and in some instances as lower-yield farmland too. This appears to hold for the bulk of the >2500 species whose abundance has now been quantified across the full yield spectrum; for climate change mitigation; and for other assessed land-use outcomes. Nevertheless, important limitations remain. There are questions around yield measurement and population persistence, and many biophysical outcomes have yet to be considered. More challenging, there is a clear need to identify pathways to delivering land sparing in ways that improve socio-economic outcomes. These considerations are especially important wherever poor rural communities shoulder disproportionate conservation costs (Balmford & Whitten, 2003; Mohai *et al.*, 2009). In such situations, local communities should be partners and protagonists in conservation initiatives, with any promising approach to limiting the
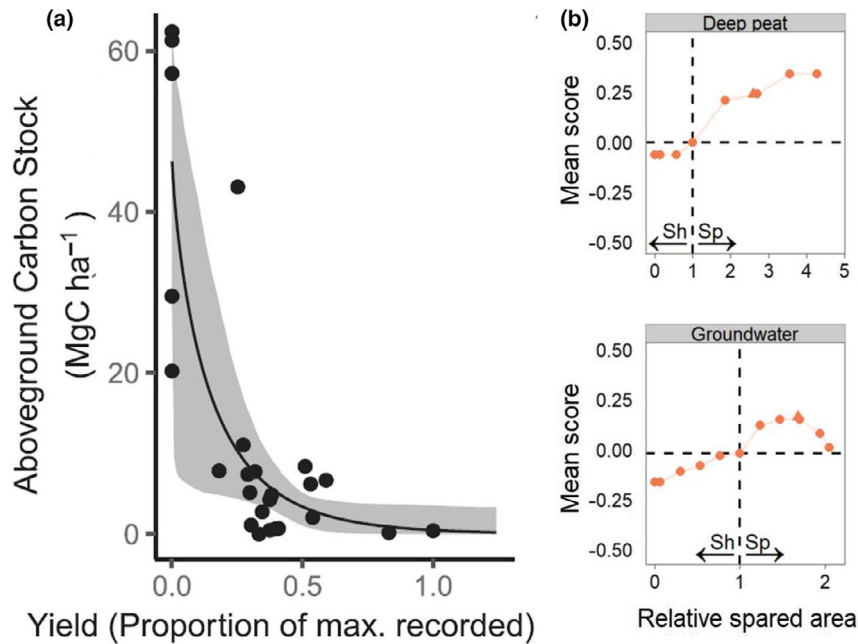
Figure 5 Other outcomes of conservation concern assessed through the sharing/sparing framework. (a) Relationship between above-ground carbon density and farm yield in Yucatán, Mexico is strongly negative convex, indicating extreme land sparing has greater greenhouse gas mitigation potential than extreme sharing or any intermediate approach. The data were first published in Williams *et al.* (2018). (b) Mean of five environmental outcomes from simple sharing (Sh) and sparing (Sp) scenarios (plotted as circles) and from three-compartment sparing (triangles), for two regions of the UK: The Fens (top, with spared land selected to maximize retention of peat), and Salisbury Plain (bottom, with spared land chosen to maximize groundwater quality). Horizontal dashed line: current mean outcome score; vertical dashed line: current area spared. Calculations assume present-day production levels. Figure first published in Finch *et al.* (2021) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

environmental impact of food production scrutinized for its likely social consequences. However, it is also important to note that sparing is not about endorsing industrial production, and that high yields can be achieved in many different ways (see below) – including land tenure reform and targeted agronomic and financial support for smallholders (Sankaran & Madhusudan, 2010; Khan *et al.*, 2014; Stabile *et al.*, 2020; Wren-Lewis *et al.*, 2020). By prioritizing retention of natural habitats, sparing can also help support the livelihoods of indigenous communities who depend on them; the conservation values of such areas can provide additional arguments for communities asserting their territorial rights (Phalan, 2018). Hence, efforts geared towards sparing land have the potential – which of course needs to be tested rather than assumed – to simultaneously enhance local people's wellbeing.

In the next two sections, I consider two other major challenges to the real-world delivery of land sparing via increased farm yields: translating yield growth into habitat sparing; and achieving high yields sustainably. Both have been the subject of substantial empirical work, though in both cases, much remains to be done.

Land-use realities

Despite the evidence from many different contexts that conservation might be best reconciled with food production through land sparing, high yields by themselves are obviously insufficient: area-saving agriculture can only be of environmental benefit if it results in habitats actually being spared. Early formulations of land sparing (Ausubel, 1996; Waggoner & Ausubel, 2001) and indeed the scenarios assessed in most sharing/sparing analyses assume that sparing is perfect – that is, that total region-wide production remains constant, and thus that the area under production decreases in direct proportion to any increases in yield (Fig. 6a; note log-transformed axes). In principle, this might occur though 'passive' sparing (Phalan *et al.*, 2016), with practices that boost yields lowering prices, absorbing labour or capital, or in other ways disincentivizing land clearance. In reality however, without active sparing mechanisms to limit them (see below), rebound effects are likely, through lower prices stimulating increased consumption locally or in distant markets, or higher-yielding techniques increasing capital or freeing-up labour that might accelerate clearance (Byerlee *et al.*, 2014; Villoria *et al.*, 2014; Paul *et al.*, 2019). Rebound effects make sparing imperfect, with area reductions less than proportionate to yield increases. At the extreme, yield increases might even (by encouraging novel uses of crops, for example) lead to a backfire or Jevons effect – as observed when 19th century gains in engine efficiency paradoxically stimulated a rise in coal consumption (Alcott, 2005). Rebound is then so marked that yield increases drive an expansion in farmland area.

The empirical data suggest that passive sparing is usually imperfect, but that backfire effects are also rare. A major
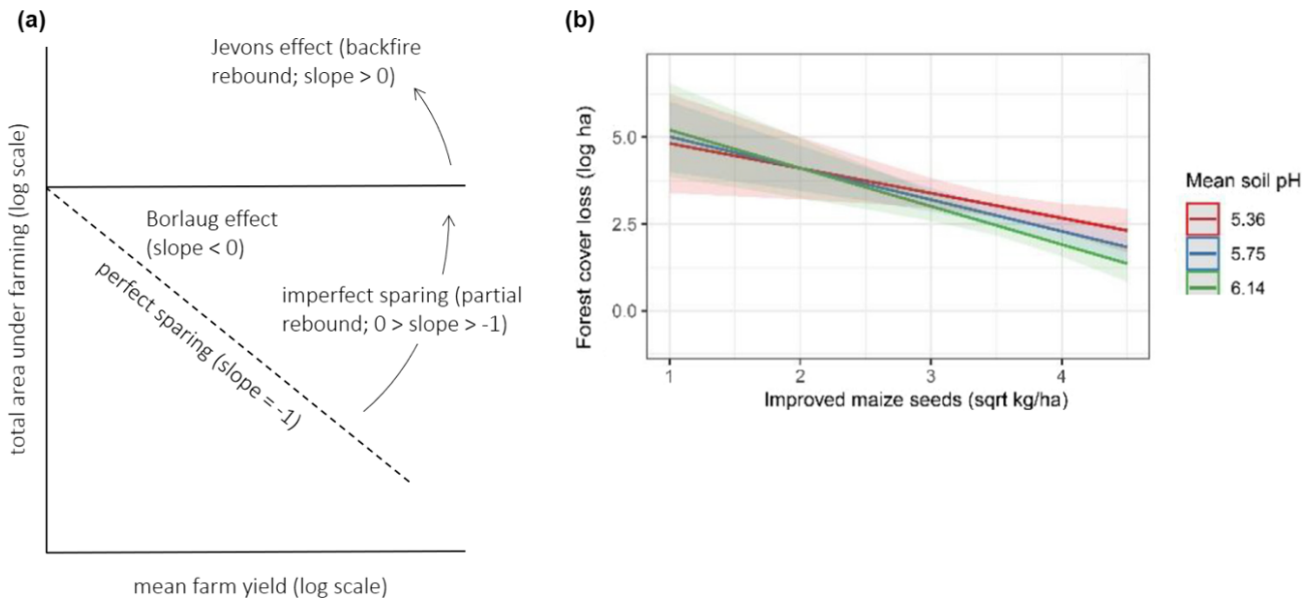
Figure 6 Land sparing occurs when the total area of land under production decreases as average yields increases. (a) Perfect sparing involves farmland area decreasing in direct proportion to increases in yield (and so is described by a slope of −1 on a log-transformed area-yield plot). Rebound effects reduce sparing, leading to imperfect sparing (described by negative slopes >−1). At the extreme, backfire rebound (also known as the Jevons effect) is seen, with yield increases leading to farmland expansion. (b) Habitat sparing observed across Zambia as a result of providing smallholder farmers with improved maize seed. Note that approximately 2/3 of the country has soils with pH > 5.5. Figure first published in Pelletier *et al.* (2020) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

compilation of case studies (Angelsen & Kaimowitz, 2001) found that whether yield increases slow deforestation is highly context-dependent. In the Peruvian Amazon, for instance, introducing fertility-enhancing kudzu as a fallow crop did slow primary forest loss but because it also reduced the labour needed for subsequent clearing, it increased conversion of secondary forests (Yanggen & Reardon, 2001). In contrast irrigation schemes for lowland rice production on the Philippine island of Palawan increased local demand for labour, attracting villagers from elsewhere and slowing upland deforestation (Shively, 2001; Shively & Pagiola, 2004). There is some encouraging evidence from African subsistence systems, where it is feared that without dramatic yield improvements, rapidly rising food demand will have severe consequences for biodiversity (Tilman *et al.*, 2017). In Malawi, providing smallholders with fertilizer and improved maize seeds boosted yields and significantly slowed forest clearance (Chibwana *et al.*, 2013), while in Zambia, providing improved seeds reduced deforestation on less acidic soils by roughly one-half (Pelletier *et al.*, 2020; Fig. 6b).

This complexity in case study outcomes is reiterated in large-scale analyses using panel regressions or equilibrium models to investigate how past yield changes relate to trends in farmland or forest area (Barbier & Burgess, 1997; Ewers *et al.*, 2009; Rudel *et al.*, 2009; Stevenson *et al.*, 2013; Ceddia *et al.*, 2014; Hertel *et al.*, 2014; Pellegrini & Fernandez, 2018; Gollin *et al.*, 2019; Villoria, 2019; García *et al.*, 2020). While a few studies find that sparing has been very limited (e.g. Rudel *et al.*, 2009) or very strong (Gollin *et al.*, 2019), most

conclude that sparing occurs but is patchy and vulnerable to substantial rebound. The variation in findings arises in part from methodological differences – studies differ in whether they adjust for population growth, for example, and whether they look at yield overall or decompose it into effects of increasing inputs and increasing efficiency of input use (Total Factor Productivity or TFP; Villoria, 2019; García *et al.*, 2020). However, underlying patterns also emerge. In line with case studies and theory (Angelsen & Kaimowitz, 2001), rebound is stronger when demand for products is price-elastic (so is much greater for meat, rubber and oil palm than for staples — Ewers *et al.*, 2009; García *et al.*, 2020); where yield-enhancing technologies are labour- or capital-saving; and where yield gains are achieved through increases in TFP (Villoria, 2019; García *et al.*, 2020). Sparing also appears less pronounced where environmental regulations are weak but conventional governance is relatively strong (Ceddia *et al.*, 2014); where there are marked land or wealth inequalities (Ceddia, 2019); and in regions which are well connected to global markets, so that increases in efficiency stimulate exports (Villoria, 2019). Unpacking this last observation provides one other significant insight: increased Total Factor Productivity can stimulate local conversion to supply distant markets, but provided demand is relatively inelastic it will in turn reduce production and cropland area in importing regions. Hence, despite local rebounds, when analysed at global scale, TFP growth appears to be strongly land sparing (Villoria, 2019).

The market-mediated, passive effects of yield increases thus do generally appear to result in land sparing – probably

sufficient, despite being imperfect, to outperform land sharing by a substantial margin (Balmford *et al*., 2019). Nevertheless, to realize more of the potential benefit of high-yield farming and limit risks of backfire, active land-sparing interventions – intentionally designed to safeguard or restore natural habitats alongside improving farm yields – would clearly be preferable to a reliance on passive effects alone. An initial exploration of how active sparing might operate identified four broad intervention types (Phalan *et al*., 2016). Prospects for coupled yield growth and habitat protection might be enhanced by zoning of agricultural lands and areas for conservation; by initiating subsidies, taxes and payments which incentivize yield increases and reward habitat retention; via strategic targeting of infrastructure, training and advice to largely converted regions with significant yield gaps (Laurance *et al*., 2014); and by making access to markets or credit conditional on retention (or restoration) of sizeable patches of habitat.

Phalan *et al*. (2016) gave real-world illustrations of each approach. The recent literature provides more (Table 1). For instance in Benin, analysis of a randomized rollout programme shows that formalizing land rights (a fine-scale version of zoning) cut deforestation by one-fifth, by stimulating greater smallholder investment and cross-household cooperation (Wren-Lewis *et al*., 2020). Around Bandipur in southern India, conservation funding enabled farmers to install solar-powered electric fences which greatly reduced crop-raiding by wildlife and encouraged smallholders to invest in wells and hence achieve three harvests (rather than one) per year (Sankaran & Madhusudan, 2010); as a result, farmers no longer needed (or had time) to graze their cattle in the National Park. In eastern Amazonia, technical support doubled smallholder incomes while reducing forest clearance by nearly 80% (IPAM, 2017 cited in Stabile *et al*., 2020). Targeted training combined with access to high-value markets increased yields and reduced deforestation by one-third in the buffer zone around Sierra Leone's Gola Forest (Malan *et al*., 2021), and tripled incomes while helping to recover wildlife populations in Luangwa, Zambia (Lewis *et al*., 2011; Lewis, 2014). As in these last two examples, interventions will commonly operate through several different mechanisms – exemplified by the complex of interventions successfully deployed to reduce forest conversion and boost stocking rates on cattle pasture in the Brazilian Amazon (Table 1). The evidence from all these examples of simultaneous improvements in farm yields (and/or livelihoods) and positive outcomes for natural habitats suggests active mechanisms will be key to delivering land sparing in practice, especially in areas supplying external markets with products for which there is high demand elasticity.

One other consideration about how in practice to spare land comes from examining how land-use zoning might boost yields. As argued by Danish economist Ester Boserup, land scarcity (which can arise as a result of slowing habitat conversion) places a premium on land; if combined with strong land tenure, this can incentivize investments in its more efficient use (Boserup, 1965). There is growing evidence – from simulations, cross-country analyses and case studies – that such induced intensification does indeed occur (Eitelberg *et al*., 2016; García *et al*., 2020; Wren-Lewis *et al*., 2020). In Brazil

Table 1 Examples of four mechanisms of active land sparing

Study region and source	Mechanism for delivering both increased yields and habitat conservation:				Evidence of:	
	Land-use zoning	Economic incentives	Strategic deployment of technology, infrastructure or knowledge	Standards and certification		
Benin Wren-Lewis *et al*. (2020)	Formalizing land tenure				Habitat conservation; 20% decrease in tree cover loss	Increased yields
Bandipur, India Sankaran & Madhusudan (2010)		Funding for electrified fencing			Reduced grazing in National Park	3 crops/year *cf* 1; Increased yield
Eastern Amazonia, Brazil IPAM, 2017 in Stabile *et al*. (2020)			Targeted agronomic advice; infrastructure improvement		79% decrease in deforestation	Incomes > doubled
Gola forest, Sierra Leone Malan *et al*. (2021)			Targeted agronomic training	Access to high-value market	30% decrease in deforestation	Increased yield
Luangwa, Zambia Lewis *et al*. (2011), Lewis (2014)			Targeted technical advice	Access to high-value market	Wildlife populations stabilized or recovering	300% increase in farmer incomes
Brazilian Amazon Koch *et al*. (2019) Moffette *et al*. (2021)	Enforcement of deforestation restrictions	Financial support for ranchers		Access to slaughterhouses committed to zero deforestation	Reduced deforestation	Increased cattle stocking rates

for instance, recent work indicates that both enforcement of fines and reduced access to slaughterhouses for Amazon ranches that continue to deforest have driven increased investments and productivity, and reduced deforestation (Gibbs *et al*., 2016; Moffette *et al*., 2021). But if farmers lack technology, labour or capital to boost yields, there is a risk that zoning may simply lower production – damaging livelihoods, and weakening conservation gains by displacing production into conservation areas (or indeed other regions). The case could therefore be made that, in seeking ambitious conservation targets (e.g. Locke, 2013; Wilson, 2016; Dinerstein *et al*., 2017, 2019), conservationists should simultaneously call for financial, technical and regulatory support to encourage yield growth within farmed areas. This shift – which I return to towards the end of this review – would involve seeing farmers who increase their yields as key agents making space for nature, and as critical partners in delivering equitable conservation solutions.

Increasing farm yields sustainably

One final important area of residual concern about land sparing in agriculture is around how yields are increased, and whether these shifts in farm practices are sustainable. While some critics assume sparing is necessarily dependent on industrial intensification, as the examples in Table 1 show this need not be the case. Those proposing land sparing as part of the solution to reconciling food needs with conservation have instead argued that any promising approach to delivering high yield should be considered (Phalan *et al*., 2011*b*; Balmford *et al*., 2015*b*). As David MacKay argued for alternative low-carbon energy options (MacKay, 2009), conservationists should be agnostic, and evaluate options based on objective criteria – among them long-run yield, and possible negative environmental impacts (Balmford *et al*., 2015*b*; Phalan, 2018).

Despite slowdowns in yield growth for key staple crops in several regions (Grassini *et al*., 2013), there are many technologies in development with the potential to substantially boost yield ceilings (see reviews by The Royal Society, 2009; Fischer *et al*., 2014*b*). At the more radical end, key targets include efforts to dramatically increase photosynthetic efficiency by transferring C4 metabolism into C3 plants (particularly rice), and to greatly lower farm inputs by perennializing currently annual crops and incorporating nitrogen-fixing capacity into non-legumes (von Caemmerer *et al*., 2012; Bailey-Serres *et al*., 2019). More immediately, whole-genome sequencing, marker-assisted breeding and a raft of gene-editing techniques offer prospects of improving yields through better feed conversion ratios in livestock; improved photosynthetic and water-use efficiency, mineral acquisition, and flood, drought, salinity and thermal tolerance in plants; and enhanced crop and livestock protection against pests and diseases (for examples see Jaggard *et al*., 2010; Reynolds *et al*., 2012; Basarab *et al*., 2013; Hayes *et al*., 2013; Sitzenstock *et al*., 2013; Bailey-Serres *et al*., 2019).

Consideration of existing yield gaps (Mueller *et al*., 2012) makes plain that there is also scope for dramatic improvements in yield through greater adoption of existing practices tailored to the needs of smallholder producers. Yield gaps are especially pronounced across much of sub-Saharan Africa, where adoption of approaches that are widespread elsewhere – such as the use of improved seed varieties, application of even modest quantities of inorganic fertilizer and the use of mulching and plant spacing to enhance soil retention and structure – can double yields in just a few seasons (e.g. Twomlow *et al*., 2010; Gockowski & Sonwa, 2011; Chibwana *et al*., 2013; Jayne *et al*., 2019; Pelletier *et al*., 2020). Existing technologies can also boost yields while simultaneously improving sustainability. Across China, for instance, the uptake by a staggering 21M farmers of an experimental system for carefully matching cropping and resource inputs to local conditions has achieved an 11% increase in maize, rice and wheat yields while simultaneously cutting nitrogen inputs by almost one-sixth (Cui *et al*., 2018).

Evidence is accumulating that many other systems – including silvopasture, co-culture methods, integrated pest management, so-called 'push-pull' approaches for crop protection, and drip irrigation – can often deliver sustained yield increases while reducing the use of environmentally damaging inputs (Burney *et al*., 2010; Broom *et al*., 2013; Khan *et al*., 2014; Hu *et al*., 2016; Midega *et al*., 2018). Agroecological techniques such as promoting pollination and pest control by native species could also contribute to land sparing, provided there are net increases in yield after accounting for any crop area removed from production to support beneficial species (Pywell *et al*., 2015). Organic techniques may offer promise in certain contexts (Seufert & Ramankutty, 2017), although once land needed for green manures and fallows is taken into consideration it seems they may typically achieve poorer yields and create greater greenhouse gas emissions than conventional practices (de Ponti *et al*., 2012; Bergström & Kirchmann, 2016; Clark & Tilman, 2017; Meemken & Qaim, 2018; Smith *et al*., 2019). Combinations of conservation agriculture methods can boost yields in drier climates (Pittelkow *et al*., 2015), though results are patchy. A meta-analysis of south Asian studies suggests that zero tillage coupled with using crop residues as mulch can lift yields by almost 6% while increasing water-use efficiency (Jat *et al*., 2020). However, a similar assessment for sub-Saharan Africa concluded yield increases are minor and the increased need for manual weeding and the diversion of crop residues away from livestock means conservation agriculture may do little to enhance African food security (Corbeels *et al*., 2020; Descheemaeker, 2020).

The suitability of any novel system for contributing to sustainable food production needs to be evaluated in several ways. Whether innovations contribute to food security, rural livelihoods and other aspects of social wellbeing is key. Yields need to be estimated over long periods: land sparing will not be achieved by systems that degrade soils or that lack resilience to climatic change (Phalan, 2018). Consideration needs to be given to barriers to the uptake of innovations – in terms of capital, and technical capacity, but also cultural sensitivities, farmers' aversion to risk, and so on (see zu Ermgassen *et al*., 2018 for one worked example). And critically, possible negative externalities – such as greenhouse gas emissions, water

use, soil loss, and pollution through fertilizer and pesticide escape – need to be quantified and compared across contrasting systems. One potentially useful device for examining these biophysical outcomes is to express them (in line with the MacKay Principle) per unit production, and then to plot different dimensions of cost against one another, across alternative systems (Figure 7a; Balmford *et al.*, 2018). If, as perhaps sometimes perceived, high-yield (i.e. low land cost) systems generate disproportionate environmental costs, one would expect externality costs to co-vary negatively with land costs.

In practice, data for exploring these putative trade-offs are surprisingly limited: few studies have reported both yield and externality measurements for contrasting systems evaluated in the same (or comparable) environments. However, an exploration of the available evidence suggests that while there are some trade-offs between yields and externalities, these are far from ubiquitous (Balmford *et al.*, 2018; Figure 7b). For example, data from Chinese field trials estimating the water use and yields of different paddy rice systems suggest no clear association between water cost per tonne of production and land cost (the inverse of yield). Results from a process-based model of UK dairy production indicate phosphorus escape is substantially greater for high land cost (in this case organic) systems, while a compilation of life-cycle analyses for Latin American beef systems shows greenhouse gas costs also co-vary positively with land cost. Other cost–cost comparisons give a similarly mixed picture – although for every sector assessed, when greenhouse gas costs are adjusted for forgone sequestration on farmed land (Searchinger *et al.*, 2018) they are consistently positively associated with land costs (Balmford *et al.*, 2018).
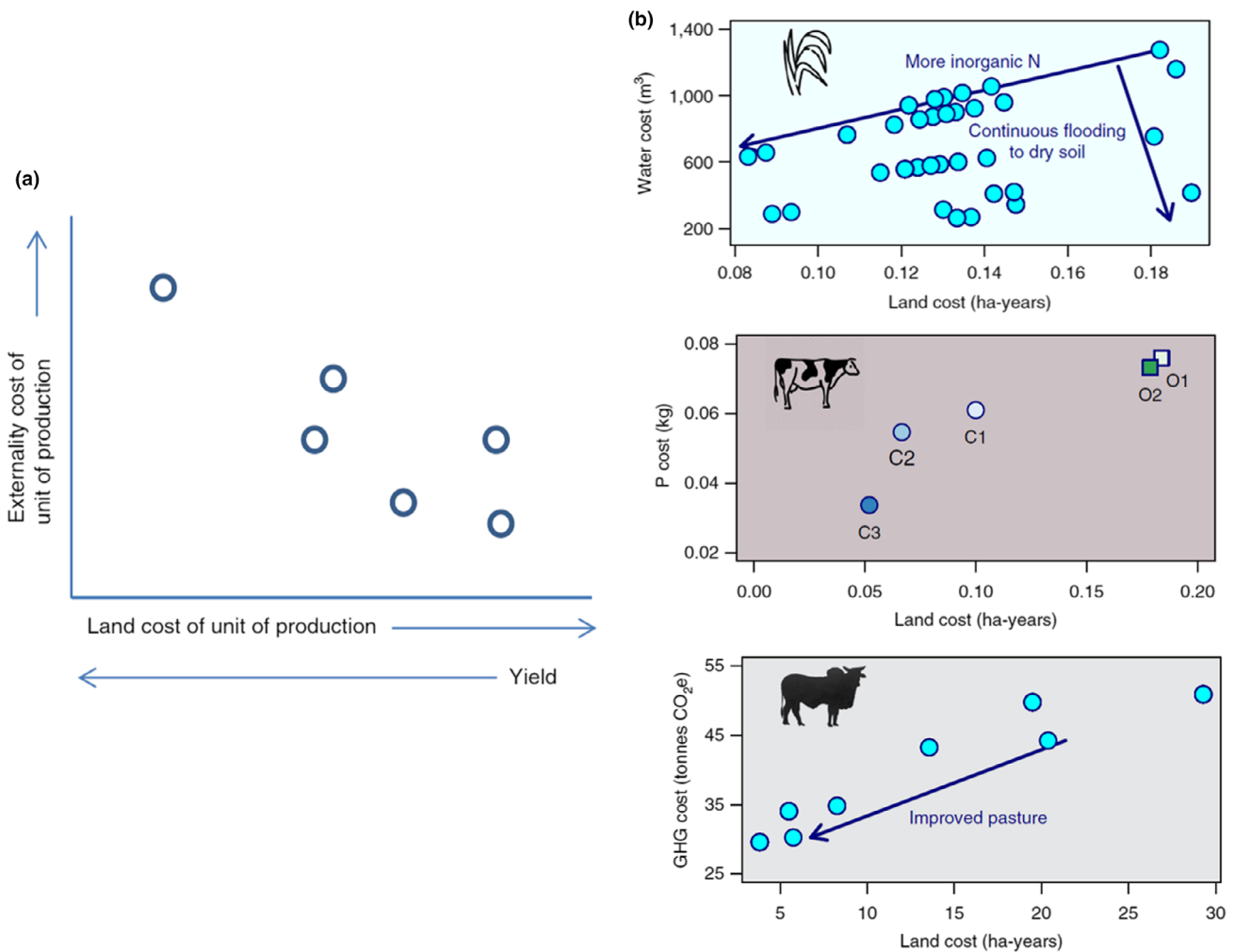

Figure 7 (a) Hypothetical cost–cost plot illustrating how the external cost of generating a given amount of product might vary with the area of land needed (i.e. the inverse of yield) across contrasting production systems, all measured under the same environmental conditions. This example illustrates a trade-off relationship. (b) Three real-world cost–cost plots – from top to bottom the water costs of contrasting systems for producing paddy rice; the phosphorus escape associated with contrasting UK dairy systems; and the life-cycle greenhouse gas emissions created in contrasting Latin American beef systems. Each plot shows costs estimated for matching climatic and edaphic conditions. Arrows show management practices with statistically significant effects. Symbols in the middle panel denote three conventional and two organic systems. Figure first published in Balmford *et al.* (2020) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

These early findings are obviously insufficient to support general conclusions – for most outcomes, data are too sparse. For some locally concentrated impacts (such as groundwater abstraction), deploying a threshold approach – excluding from further consideration any practices which exceed tolerance limits – may be more appropriate than testing for trade-offs (T. Finch, pers. comm.). Extending cost-cost analyses to consider other concerns about high-yield systems such as pesticide pollution, antimicrobial use and animal welfare is challenging because robust measurements across multiple systems are rarely reported in tandem with yield data. As further data accumulate, we might anticipate other impacts (besides greenhouse gas fluxes) for which high-yielding systems appear to best limit negative externalities. But we might also usefully be able to single out those costs where achieving high yields incurs disproportionate environmental or other negative impacts, indicating where difficult societal decisions may have to be made.

One particularly pressing need is for data to develop robust assessments of how the risks of Emerging Infectious Disease (EID) spillover and takeoff might vary across contrasting livestock systems (Jones *et al.*, 2013; Liverani *et al.*, 2013). Because some novel zoonoses have been linked to relatively intensive production (e.g. Pulliam *et al.*, 2012), there have been calls in the media for a shift towards more extensive livestock systems. But to the extent these are characterized by smaller, more fragmented patches of natural habitat scattered through farmed landscapes, such systems might plausibly lead (for a given level of production) to an enhanced risk of EID emergence (Di Marco *et al.*, 2020). However, links between natural habitat extent, biodiversity and zoonotic disease risks remain contested (Hosseini *et al.*, 2017; Wood *et al.*, 2017). System-wide comparisons and better data are badly needed.

Sharing and sparing in other sectors

Although the sharing/sparing concept has been most fully explored for crop and livestock production, it may be useful in any sector where meeting human needs imposes area-based, yield-linked costs on nature. In each case, limiting demand will obviously be important, but the sharing/sparing framework might provide a helpful lens for exploring the least damaging approach to meeting whatever demand exists (Phalan, 2018; Renwick *et al.*, 2020). Relevant yet so far unexplored sectors include energy production, which is now becoming the USA's biggest driver of land-use change (Trainor *et al.*, 2016); and transport, where early work has concluded that bundling of roads may reduce their impacts on biodiversity (Jaeger *et al.*, 2007) and that restricting shipping lanes could help limit collisions with whales (Roman *et al.*, 2013). The rest of this section describes what we have learnt from analogues of the agricultural sharing/sparing debate in four other domains.

Nature-based recreation

The world's terrestrial protected areas collectively host an estimated 8 billion visits annually (Balmford *et al.*, 2015*a*).

Recreation ecologists have been quantifying and examining how best to limit the resulting environmental impacts for several decades (Monz *et al.*, 2013). Negative effects include widely documented behaviour changes in resident animals, increased spread of non-native species, and declines in species richness and abundance of native vertebrates (Zhou *et al.*, 2013; Anderson *et al.*, 2015; Larson *et al.*, 2016, 2019; Wolf *et al.*, 2019). Evidence that these and other impacts are manifest even at low levels of exposure (e.g. Reed & Merenlender, 2008) has led a view that 'use-impact' responses are typically curvilinear (analogous to density–yield curves being negative convex), and that the effects of recreation are thus best managed by concentrating visitor access into small portions of wild landscapes (i.e. by sparing; Zhou *et al.*, 2013; Larson *et al.*, 2016, 2019). However, other response curves have been reported, suggesting alternative solutions (Monz *et al.*, 2013). Developing a consistently designed set of studies which quantify common metrics of visitor use and population response across diverse ecological and tourism contexts may be helpful to making further progress.

Urban planning

Over 55% of people now live in urban areas, with that figure projected to rise to 68% by 2050 (United Nations, 2019). Concerns about this dramatic growth have spawned a series of studies using the sharing/sparing framework to examine how the provision of housing and associated infrastructure might be increased at least cost to biodiversity and ecosystem services. Land sharing in this context refers to relatively low-density construction, with houses perhaps having individual gardens, while sparing consists of multi-storey dwellings along with large patches of public greenspace (Lin & Fuller, 2013; Fig. 8a). Early abundance-based tests comparing sharing/sparing landscapes matched for overall housing provision suggested that for birds in Brisbane (Sushinsky *et al.*, 2013), ground-beetles and butterflies in Tokyo (Soga *et al.*, 2014) and bats in Melbourne (Caryl *et al.*, 2016), urban sparing consistently outperforms sharing, particularly for native species and specialists, and at medium to high levels of housing provision. A more recent optimization exercise exploring large numbers of mixed (rather than simple one- or two-compartment) approaches found that for Melbourne's birds, the best solutions for maximizing their mean abundance converged on extreme land sparing (Geschke *et al.*, 2018; Fig. 8b).

A few studies have considered additional outcomes of concern, concluding that high-density housing combined with provision of parks would also be better than sprawling urban growth for reducing car use, traffic congestion and noise levels (Geurs & van Wee, 2006); for increasing people's access to greenspace (Sushinsky *et al.*, 2013); for carbon storage (Collas *et al.*, 2017); and for several other ecosystem services (Stott *et al.*, 2015). Importantly, those ecosystem services favoured by sparing appear to be delivered poorly by sharing cityscapes, but the smaller number favoured by sharing seem to be delivered reasonably well by urban sparing (Stott *et al.*, 2015).
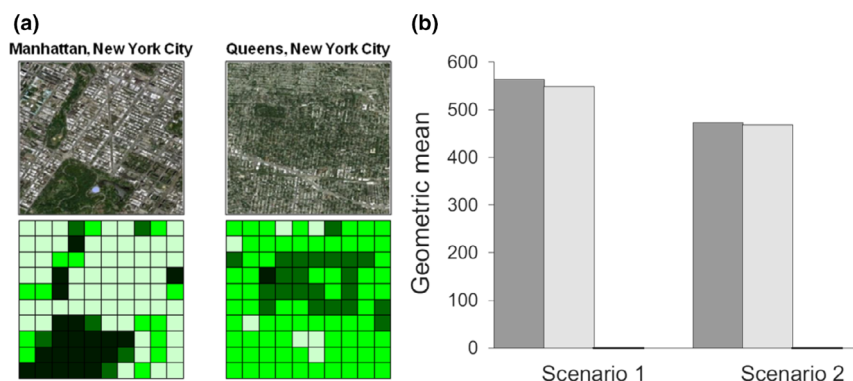
Figure 8 Sharing/sparing in urban planning. (a) Patterns corresponding to urban land sparing (left) and sharing (right); darker green denotes greater tree cover. From Lin & Fuller (2013). (b) Geometric mean abundance of native bird species in hypothetical Melbourne landscapes capable of housing its current human population (Scenario 1) and its medium-projection population in 2050 (Scenario 2). Dark grey bars show the optimum mixed solution; light grey the result for extreme sparing; black the result from land sharing. Figure first published in Geschke *et al.* (2018) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Forestry

Contrasting approaches to meeting given levels of production at least cost to biodiversity have been explored in forestry for as long as in farming (for recent reviews see Warman, 2020; Betts *et al.*, 2021). Through the 1980s, long-running concerns about the negative impacts of high-yield conventional logging led to the concept of new forestry (Franklin, 1989). Essentially analogous to land-sharing agriculture, this has in turn diversified into an array of approaches including extensive management, multiple-use forestry, variable retention forestry, ecological forest management and reduced impact logging. These variously emphasize retaining more diverse stands, older and dead trees and fallen logs, relying on natural regeneration, reducing chemical inputs, and extending harvesting cycles – all with the aim of emulating natural disturbance regimes, and increasing the value of productive forests for biodiversity and ecosystem services (Lindenmayer *et al.*, 2012). Yet as with agriculture many species are absent from these shared landscapes: there is widespread evidence that old-growth forests are of irreplaceable importance for biodiversity (Paillet *et al.*, 2010; Gibson *et al.*, 2011; Barlow *et al.*, 2016; Betts *et al.*, 2017; Nagel *et al.*, 2017; Eckelt *et al.*, 2018). Retaining large unharvested stands while meeting timber demand is a considerable challenge, given that extensive management may achieve as little as one-fortieth the yield of highly managed forestry (Betts *et al.*, 2021).

One influential proposal to address this problem is triad management (Fig. 9). First set out by Seymour & Hunter (1992), this is conceptually equivalent to three-compartment sparing, and proposes deploying intensively managed, high-yield plantations (Brockerhoff *et al.*, 2008; Paquette & Messier, 2010) in some areas to make space for both far lower-yielding extensive management and unharvested old-growth stands elsewhere in the landscape. Simpler solutions involving plantations and old-growth blocks (analogous to two-compartment sparing) have also been suggested (Boscolo & Vincent, 2003; Warman

& Nelson, 2016). What amounts to two-compartment land sparing has been adopted in New Zealand where, with >70% of native forests now protected, almost all timber is now supplied by exotic pine plantations (Ministry for Primary Industries, 2015). Triad management, on the other hand, has proved popular in parts of Canada and northern USA, although the amount of forest assigned to the different compartments appears to be based largely on political rather than scientific considerations (MacLean *et al.*, 2009; Betts *et al.*, 2021).

Some modelling simulations suggest that mixed, triad-themed solutions might outperform conventional and extensive solutions (and for some metrics, two-compartment sparing) in reconciling timber demand and environmental concerns (Côté *et al.*, 2010; Tittler *et al.*, 2012). However, these conclusions are based on limited proxies for biodiversity outcomes, such as area under old growth and the size of forest patches. As argued by Betts *et al.* (2021), the sharing/sparing framework – using direct measurements of how individual species' abundances vary with yields to estimate landscape-wide outcomes of contrasting scenarios matched for total production – offers a conceptual basis for more rigorous evaluation. However, obtaining the necessary data, in particular across the full production cycle of harvested forests, is very difficult. To date, few analyses have gathered sufficient information to construct such analyses.

Among those studies that do include direct measures of biodiversity, several are limited by surveying just a few species, pooling abundance values across species, or not reporting yield (Calkin *et al.*, 2002; Yoshii *et al.*, 2015; Yamaura *et al.*, 2016; Mestre *et al.*, 2020). Of the analyses that quantify the abundance of large numbers of species across a wide yield spectrum, two studies – on 53 dung beetle species in Pará, Brazil (França *et al.*, 2017) and on 176 birds, 56 dung beetles and 214 ants in Borneo (Edwards *et al.*, 2014) – both suggest simple two-compartment sparing would outperform sharing. A third study based on 91 more commonly sampled Amazonian butterflies suggests that triad-style management, with a mix of
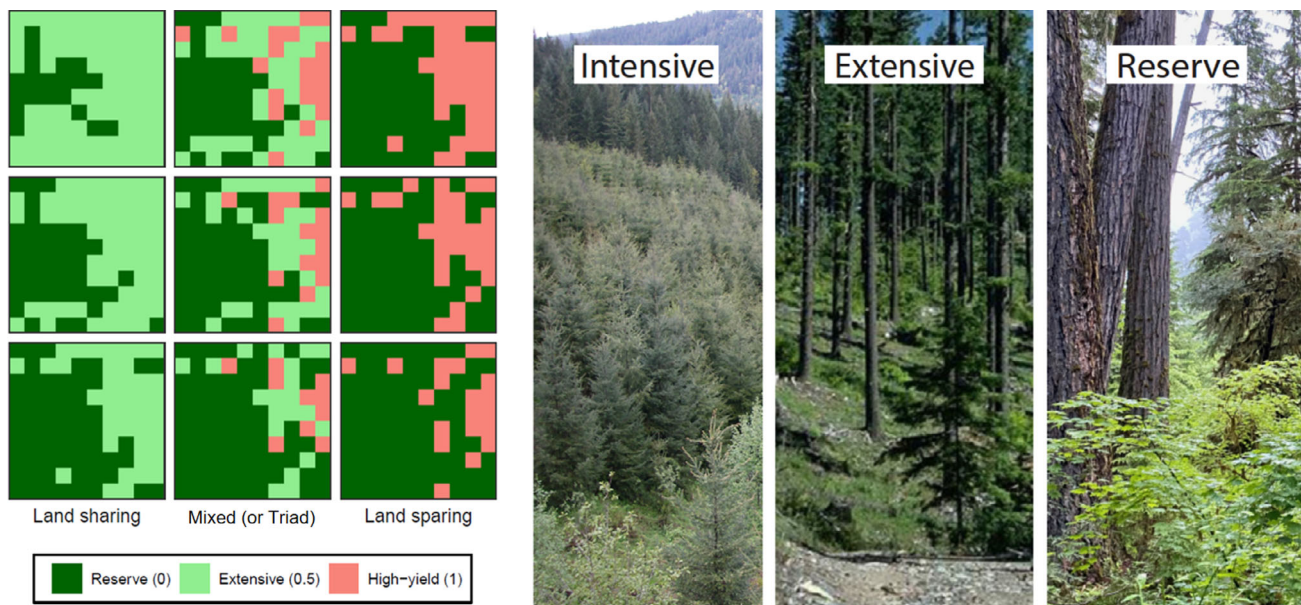
Figure 9 Sharing/sparing in forestry. Hypothetical sharing, mixed (or triad) and extreme sparing landscapes (on left) differ in their proportions of reserve forest, extensively managed low-yield areas and intensively managed high-yield plantations (relative yields in brackets). All landscapes within a row produce the same total harvest, with harvests increasing from the bottom to top rows. Figure first published in Betts *et al.* (2021) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

plantations, reserves and extensive management may perform better than simple sparing (Montejo-Kovacevich *et al.*, 2018). Most recently, a study based on expert estimates of the sensitivity to management of large mammals, three species groups of bats and five high priority habitat types has again identified as optimal mixed solutions involving selective logging, protected areas and plantations, with substantially more area assigned to high-yield plantations and no-take forests than at present (Runting *et al.*, 2019).

The scarcity of relevant analyses and their varied conclusions to date suggest further fieldwork drawing on the sharing/ sparing framework would be helpful (Betts *et al.*, 2021). As well as data characterizing how species' densities vary with timber yield, several additional issues may be important in identifying how to meet future demand for wood products at least environmental cost. Consideration needs to be given to differences in harvesting schedules (Ward & Erdle, 2015) and in uses and hence values of timber from plantations compared with natural forests; simple aggregate measures of harvest may mask these important distinctions. Second, a model exploring the estimated effects of widely varying management practices within individual land-uses suggests these may be substantial (Runting *et al.*, 2019); more field data on the outcomes of management regimes would evidently be helpful. Third, where new plantations are established is clearly key; benefits from sparing may be considerably increased if plantations are created on already-cleared land rather than within still-forested areas (Griscom *et al.*, 2018). Last and perhaps most importantly, the overall impact of different management regimes for biodiversity may depend not so much on their relative values as forests, but on variation in their vulnerability to clearance.

In regions with strong environmental governance, the risk of conversion may be very low. However, Griscom *et al.* (2018) show that if the risk of deforestation of unmanaged lands is high, and extensive management regimes reduce the risk of conversion relative to conventional logging, extensive systems may outperform sparing approaches. Further studies incorporating empirical estimates of how the prevailing management regime drives the probability of forest conversion are clearly needed.

Seafood production

In 1883 Huxley famously rejected pleas for fisheries regulation, stating 'I believe, then, that the cod fishery... and probably all the great sea fisheries, are inexhaustible: that is to say that nothing we do seriously affects the number of fish. And any attempt to regulate these fisheries seems... to be useless' (Huxley, 1884). We now know that Huxley was wrong. How to go about harvesting what people want from the sea at least cost to nature has become at least as contested a question as how best to limit the impact of agriculture. Again, there are suggestions that the sharing/sparing framework might prove helpful (McGowan *et al.*, 2018; Renwick *et al.*, 2020). The search for fresh solutions to marine fisheries management is motivated by observations that since the mid-1990s, global landings from capture fisheries have been stagnant (FAO, 2020) or perhaps even in decline (Pauly & Zeller, 2016); that 34% of reported stocks are now overfished (FAO, 2020); and that without improvements to management this fraction will rise dramatically by 2050 (Costello *et al.*, 2016; Worm, 2016). These concerns about harvest sustainability, alongside worries

about fishery impacts on non-target species, have led to wide-spread calls for the very significant scaling-up of Marine Protected Areas (MPAs) – in effect, for sparing large portions of the ocean (Worm et al., 2009; Lubchenco & Grorud-Colvert, 2015; O'Leary et al., 2016; Sala & Giakoumi, 2018).

In response, MPA coverage has expanded dramatically, from ~0.6% of global ocean area in 1990 to ~7% currently (Lubchenco & Grorud-Colvert, 2015; Marine Conservation Institute, 2021; Protected Planet, 2021), of which ~2.7% comprises fully or highly protected MPAs (the focus of the rest of this discussion). When they are well managed, no-take marine reserves are clearly capable of reducing the local impacts of fishing and hence recovering populations of both target and non-target species within their boundaries (Halpern, 2003; Worm et al., 2006; Lester et al., 2009; Edgar et al., 2014; Gill et al., 2017). Moreover, dispersal of larvae and adults through reserve boundaries means that where a target species is overfished, its protection within MPAs can boost overall harvest too (Hilborn et al., 2004; White & Costello, 2014; Hilborn, 2018; Botsford et al., 2019; Cabral et al., 2020). Hence, unlike in farming or forestry, the dispersal of target populations means that removing part of an area from harvesting need not necessarily diminish what is available to be harvested across the entire seascape (Levin et al., 2009).

However, when a fishery is not overexploited, spillover through MPA boundaries is generally considered to be insufficient to compensate for closing the site to fishing, so (everything else being equal) overall harvest is reduced (Hastings & Botsford, 1999; Hilborn, 2014, 2018; Botsford et al., 2019; but see White et al., 2008; Edgar et al., 2018). This has an important consequence. The same overall offtake can now only be met by increasing fishing intensity beyond the reserve (Levin et al., 2009), leading to potentially negative consequences for target and non-target populations as a whole (Hilborn, 2013, 2018). This situation is analogous to the observation that, for a given level of food or timber production, terrestrial reserve establishment leads to increased pressure on non-reserved land. In line with the MacKay Principle, assessing the overall effects of MPAs thus requires accounting for how much they displace fishing effort elsewhere.

The alternative to sparing via no-take MPAs is in effect sea sharing – with no zero-take reserves, but with strictly enforced regulations restricting total or seasonal effort, with restrictions on the use of different gear types, and so on. Proponents argue modifying effort this way can reduce fisheries' negative impacts on overall biodiversity at lower cost to target species offtake than can a combination of strict MPAs and otherwise lightly regulated fishing (Hilborn, 2018; Hilborn et al., 2020b). Recent tests of this proposition, however, have drawn contrasting conclusions. Using data for the USA's West Coast groundfish fishery, Hastings et al. (2017a) suggest that reducing impacts on sensitive non-target species may be achieved at less cost to target species harvest through the complete closure of some of the fished area than through area-wide restrictions on effort. Hilborn (2017) argues instead that the increase in fishing effort beyond MPAs that would be needed to maintain overall offtake may make this approach economically unfeasible (but see Hastings et al., 2017b). In a second study, Hilborn

et al. (2020a) conclude that implementing no-take MPAs would be an inefficient approach to limiting harmful bycatch in the Bering Sea and Aleutian Islands, and along the California coast. Here, because non-target species known to be of concern are patchily distributed and differ in their vulnerability to different gear types, localized restrictions on gear use could in principle achieve substantial mitigation of impacts at very limited cost to offtake, without the use of strict MPAs. It is not clear how far these results would hold, however, if broadened to consider many hundreds of non-target species, with each gear type then likely to impact some vulnerable species in every location.

As with debates over sustainable forestry, this lack of resolution suggests that a re-examination of the MPA issue through an explicit sharing/sparing framework may be helpful (McGowan et al., 2018; Renwick et al., 2020). However, even more than for farming or forestry, assessing region-wide impacts of diverse harvesting regimes on a broad suite of non-target as well as harvested populations is a challenging proposition. Carefully parameterized modelling is probably the only practical approach. This will require information not just on immediate fishing-induced mortality of target and non-target species but on the impacts of fishing on the carrying capacity of species' habitats, on the density-dependence of key life history stages, on dispersal between areas under different fishing regimes, and on interspecific interactions. It will also be important to explore the consequences of contrasting management systems for fishing effort and profit as well as for food security, management costs, employment and the extent of illegal fishing (White et al., 2008; Wolff, 2015; Lubchenco et al., 2016).

One study has made a start. McGowan et al. (2018) built a three-compartment optimization model to explore which combination of three simplified management regimes (reserved or no-take, open-access or unmanaged, and managed) would maximize biomass of a single fished species (a tiger prawn) while meeting a minimum level of harvest within a constrained management budget. The results are particularly sensitive to the available budget (Fig. 10a). Because the authors' estimate that fisheries management is more costly per unit area than reserve management, at lower budgets the biomass of the fished species is maximized in sparing seascapes (comprising reserved and open-access waters). A mixed strategy, involving well-managed (i.e. shared) portions of seascape too, only becomes optimal once the budget is sufficient that spending on more no-take areas would mean the minimum harvest threshold can no longer be met (McGowan et al., 2018). In suggesting simple sparing may be appropriate even when considering just one fished species, these model findings are interesting. However, they are unavoidably preliminary: the model assumes uniform dispersal and includes no non-target taxa or interactions among species. It would seem worthwhile to develop this approach through more sophisticated models, but their necessary complexity and the scarcity of suitable data for their parameterization suggest this will be difficult.

One final consideration is aquaculture, which is now responsible for >27% of all seafood production (and 45% of freshwater and marine production combined; FAO, 2020). One

could perhaps interpret this as the most extreme version of sparing, with its adoption analogous to the switch from terrestrial hunter-gathering to farming. By reducing demand for wild-caught fish, aquaculture could in principle lower the environmental costs of meeting a given level of seafood demand (Tidwell & Allan, 2001; Kok *et al.*, 2020). One recent study has even suggested that because aquaculture species are more efficient feed converters than livestock, greatly expanding aquaculture to meet a disproportionate fraction of world's rising demand for animal protein could substantially lessen demand for new crop and grazing land too (Froehlich *et al.*, 2018; Fig. 10b). In reality, aquaculture takes multiple forms.

Its environmental impacts thus vary widely depending, among other things, on the location of facilities (inshore, offshore, on land; Belton *et al.*, 2020); and on whether the cultivated species is fed on plants, on wild-caught fish (in which case aquaculture might increase rather than diminish fishing impacts), or indeed is unfed (Willer & Aldridge, 2020). Assessing these diverse alternatives will require quantification not just of local impacts of aquaculture operations but estimation and summation of the effects of sourcing feed. As with farming, the impacts of aquaculture on food security and on livelihoods – especially of small-scale fishers – also demand careful scrutiny (Belton *et al.*, 2016; Golden *et al.*, 2016).
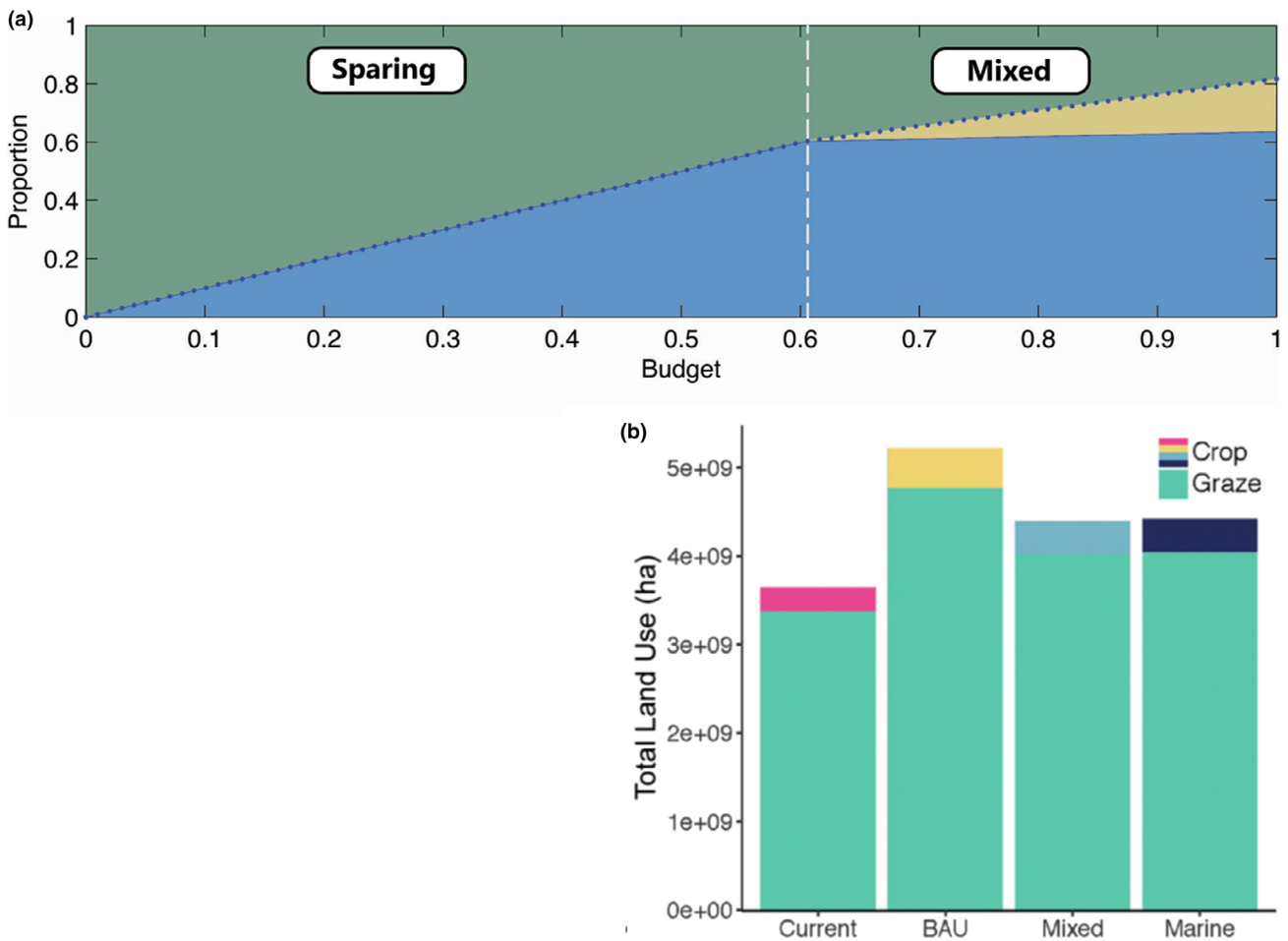

Figure 10 Sharing/sparing in seafood production. (a) Result of a three-compartment optimization analysis aimed at maximizing the biomass of a single fished species within budget and minimum harvest constraints. At lower budget levels, simple two-compartment sparing comprising only open-access (green) and reserved (blue) areas is optimal. At higher budget levels, mixed solutions including well-managed (yellow) areas become optimal. The data were first published in McGowan *et al.* (2018). (b) The theoretical potential for aquaculture to spare land from farming. Switching growth in meat consumption to aquaculture could spare an area roughly twice the size of India from farmland. Bars show the global area of land under grazing and crop production currently, under a business-as-usual projection for consumption by 2050, and under scenarios in which all increased meat consumption 2018–2050 is provided by aquaculture (either mixed freshwater/marine, or simply marine); the different colours used for cropland have no significance. Figure first published in Froehlich *et al.* (2018) [Colour figure can be viewed at zslpublications. onlinelibrary.wiley.com.]

So how can we spare a planet?

There are clearly many questions left to answer. Nevertheless empirical data from sharing/sparing studies in agriculture, in forestry, in urban planning and even in nature-based recreation repeatedly show that very many species – and certainly the majority of those that are specialized or narrowly distributed – are strongly dependent on the continued retention of relatively large areas of natural habitat. Natural vegetation too is clearly of disproportionate value in sequestering and storing carbon. Giving rising human demands, keeping extensive areas free from the cow, the plough and the chainsaw will require increasing yields elsewhere, and will thus diminish the value of areas of production for other species and for ecosystem services. Yet analyses that have quantified this trade-off – across many different goods, production systems and socio-economic contexts – have consistently concluded that these losses are substantially less than the benefits that can accrue through conserving wilder places where nature can continue to thrive. If other species could decide how people meet their needs, it seems that for the most part, they would ask us to concentrate rather than spread our footprint.

So what do these findings mean – for conservationists, for producers, and for governments? For conservationists currently negotiating targets for 2030 and beyond, these results provide strong empirical support for plans for securing biodiversity and nature-based climate mitigation to be ambitious. Calls to protect at least 30% of the land and of the sea by 2030 already have considerable political support (Greenfield & Harvey, 2021), and even bolder targets (Locke, 2013; Wilson, 2016; Dinerstein *et al.*, 2017, 2019) are gaining increasing traction. Yet many would argue such proposals may be counterproductive if they do not simultaneously set out how this dramatic scaling-up of the area assigned primarily to conservation can be delivered alongside other human demands – in particular for food (Balmford & Green, 2017; Büscher *et al.*, 2017; Mehrabi *et al.*, 2018), but also for fuel and fibre. No matter how compelling the conservation case, if ambitious strategies remain largely mute on these more tangible human concerns it seems unlikely their goals will be achieved.

This in turn means that producers and land and sea managers – farmers, foresters, fishers, planners, even architects – have critically important roles in determining the long-term future of the natural world. Several analyses have concluded that there is scope at regional and global scales for meeting rising food demand at the same time as significantly scaling-up habitat conservation. In Brazil for example, the strikingly low yields currently achieved by much of the beef sector suggest that narrowing yield gaps by as little as one-quarter could free-up enough land to meet domestic and export demand for all agricultural and wood products until at least 2040 without any further deforestation (Strassburg *et al.*, 2014). Multiple global-scale exercises confirm that food demand could in principle be met through to the second half of this century while slowing or even reversing natural habitat loss (Bajzelj *et al.*, 2014; Erb *et al.*, 2016; Tilman *et al.*, 2017; Springmann *et al.*, 2018*a*; Folberth *et al.*, 2020; Leclère *et al.*, 2020; Williams *et al.*, 2021). However, in each case this requires both very considerable closure of existing yield gaps and demand-side changes such as marked reductions in food waste and shifts by wealthier consumers towards more plant-based diets.

Last, this inescapable need for demand-side measures along with active policy linkages between yield growth and enhanced habitat protection means that humanity's ability to feed, fuel and house itself sustainably will depend in large measure on government and intergovernmental involvement. This is a major challenge (and one that applies equally to efforts to avert catastrophic climate change). In much of the world, people feel government decisions are increasingly made in the interests of powerful vested interests rather than society as a whole; indeed, the very notion of substantial intervention by national governments appears often to be in retreat. However, as illustrated clearly in the US during the Trump administration, local and regional governments can provide crucial political leadership on environmental issues. Conservation NGOs can work with producers to deliver land sparing (and in some cases already are – Phalan *et al.*, 2016; Table 1). Businesses – particularly those major transnational corporations now in control of very large parts of the farming, fisheries and forestry sectors (Folke *et al.*, 2019) – have increasing power and responsibility to deliver socially and environmentally desirable outcomes. Many of the kinds of land-sparing interventions illustrated in Table 1 can be instigated by businesses. But private actors need to be encouraged by appropriate regulations and incentives; and those enterprises already striving to adopt best practices require the level playing field which stronger regulation provides.

While the COVID-19 crisis is far from over, its widely varying impacts on lives and livelihoods already provide stark messages for how we tackle the extinction and climate crises (Balmford *et al.*, 2020) – underscoring the inescapable importance of good governance; of political leadership that confronts and admits to (rather than ignores) seemingly remote but accelerating existential threats; of policy measures that take a systems approach but also consider individual-level impacts; of paying timely attention to findings from natural and social science; and of solutions that recognize and embrace the necessity of internationally concerted action. We can perhaps hope that these lessons from the pandemic will stimulate a greater appetite among our leaders for ambitious, pro-active, equitable and data-driven responses to the far greater environmental challenges that lie ahead.

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