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Title: Evaluating spatially explicit sharing-sparing scenarios for multiple environmental outcomes

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Abstract:

1. Understanding how to allocate land for the sustainable delivery of multiple, competing objectives is a major societal challenge. The land sharing-sparing framework presents a heuristic for understanding the trade-off between food production and biodiversity conservation by comparing region-wide land use scenarios which are equivalent in terms of overall food production.
2. Here, for two contrasting regions of lowland England (The Fens and Salisbury Plain), we use empirical data and predictive models to compare a suite of spatially explicit scenarios reflecting the full range of the sharing-sparing continuum, including mixed scenarios which combine elements of both sharing and sparing. We evaluate a range of outcomes (bird populations, global warming potential (GWP), nitrogen and phosphorus pollution and outdoor recreation), in order to identify approaches to regional land use planning with the potential to deliver multiple societal benefits.
3. Land-sharing scenarios (which reduce the dominance of productive agricultural land in farmed areas and the area of larger unfarmed areas) result in negative outcomes, particularly for birds and GWP. In contrast, many land-sparing scenarios (including mixed scenarios which increase the area of lower-yield farmland alongside larger unfarmed areas) resulted in improvements in all or most outcomes, although for recreation and nutrient export differences between scenarios were modest.
4. Importantly, environmental outcomes also depended on the spatial arrangement of spared land, the types of natural or semi-natural habitat promoted on spared land, whether some lower-yield farmland is delivered alongside larger unfarmed areas, and the overall region-wide food production target.
5. *Policy implications*. Our study suggests that the negative environmental consequences of high-yield farming (at least those considered here) can be outweighed by its potential land-

sparing benefits. However, for high-yield agriculture to realise its full land-sparing potential, explicit policies such as certification or payments for ecosystem services are required to ensure sustainable yield growth alongside habitat conservation. Our study also highlights the importance of mitigating projected increases in food demand.

Keywords: Land sparing; land sharing; conservation; agriculture; birds; global warming potential; diffuse pollution; recreation

Introduction

Earth's land area is finite, yet demand for land-derived products and services is growing (Tilman, Balzer, Hill & Befort 2011; Smith *et al.* 2016). At the same time, habitat loss and degradation – driven primarily by agriculture – are the dominant drivers of global biodiversity loss (IPBES 2019). Understanding how to allocate land for the sustainable delivery of multiple competing goals is therefore a major societal challenge (Benton *et al.* 2018).

The land sharing-sparing framework presents a heuristic for understanding the trade-off between food production and biodiversity conservation by comparing a range of contrasting land use strategies, each delivering the same explicit region-wide food production target (Green, Cornell, Scharlemann & Balmford 2005). Extreme land sharing (where food and wildlife are delivered from the same places) involves farming an entire region at the lowest yield necessary to deliver the food production target, whilst extreme land sparing (where food and wildlife are largely separated) involves farming at the highest attainable yield to spare unfarmed habitat (in units at least 1 km^2 in size, as a general rule of thumb; Phalan *et al.* 2011). A range of intermediate strategies exist between these two extremes. Empirical evidence based on species-specific relationships between population density and agricultural yield suggests that most species – especially those with smaller region-wide populations now than prior to the advent of agriculture – would achieve largest populations under land sparing (reviewed in Balmford, Green & Phalan 2015; Luskin, Lee, Edwards, Gibson & Potts 2018).

Early assessments of the sharing-sparing framework (e.g. Phalan, Onial, Balmford & Green 2011; Hulme *et al.* 2013) compared food production strategies in which units of land are assigned to one of two types: uniform farmland (the yield of which increases from sharing to sparing) or unfarmed habitat (the area of which increases from sharing to sparing). More recently, mixed strategies have been considered which combine elements of both sparing and sharing (Geschke, James, Bennett & Nimmo 2018; 'three-compartment sparing' in Feniuk, Balmford & Green 2019 and; Finch *et al.* 2019). Beyond agriculture-biodiversity trade-offs, response-yield curves have also been parameterised for above-ground carbon (Williams, Phalan, Feniuk, Green & Balmford 2018), timber yield (Edwards *et al.* 2014) and housing (Geschke *et al.* 2018).

The application of spatially explicit scenarios within the sharing-sparing framework (e.g. Law *et al.* 2015; Runting *et al.* 2019) brings several possible advances. First, spatially explicit scenarios are potentially more realistic; a range of land types can be considered, rather than the two or three considered above, whilst accounting for geographical constraints. Spatial scenarios are also likely to increase engagement with local stakeholders and decision makers, especially when existing land use visions are incorporated. Finally, the supply of and demand for some ecosystem (dis-) services such as outdoor recreation and diffuse pollution is inherently spatial, so can only be quantified when scenarios are represented spatially.

Here, for two regions of lowland England (**Fig. 1**), we develop a suite of spatially explicit scenarios, each meeting a defined region-wide energetic food production target (**Fig. 2**). Our scenarios reflect the continuum between extreme sharing and sparing, including intermediate strategies as well as ‘three-compartment sparing’, under which high-yield farming frees up land for both lower-yield farmland and large unfarmed areas (Feniuk *et al.* 2019; Finch *et al.* 2019). For each scenario, we estimate: the region-wide population size of 105 breeding bird species; net global warming potential; nitrogen and phosphorus export; and outdoor recreation welfare value. We describe the responses of these five outcomes across the sharing-sparing continuum, and identify strategies which deliver multiple environmental benefits.

Materials and methods

Study area

Our study regions comprise two contrasting National Character Areas in the English lowlands (**Fig. 1**). The Fens (3,826 km^2) is an ancient wetland, now drained and dominated by arable farmland. Salisbury Plain and West Wiltshire Downs (hereafter Salisbury Plain, 1,223 km^2) hosts a large expanse of semi-natural chalk grassland, surrounded by mixed farmland. Both regions are multifunctional, containing both productive agricultural land and semi-natural habitats of high conservation value, and are thus candidates for modification under sparing or sharing strategies. However, differences in topography, geology and land use history present the opportunity to explore the consequences of similar strategies in different regional contexts.

We restricted each study region to 1-km squares dominated (>50% cover) by peaty soils in The Fens (n = 1,128) and chalky soils in Salisbury Plain (n = 1,026), to ensure that alternative land covers were, in principle, substitutable (Finch *et al.* 2019). In The Fens, for the purposes of quantifying crop composition and greenhouse gas fluxes (see below), we classified 1-km squares where the dominant soil class was ‘raised bog peat soils’ or ‘fen peat soils’ (Farewell, Truckell, Keay & Hallett 2011) as *peat* (**Fig. 1b**). Remaining squares (where peat deposits have degraded to ‘loamy and sandy soils with naturally high groundwater and a peaty surface’) were classified as either *skirt clay* or *skirt loam* according to whether the parent material was clay-like (with ‘unconsolidated marine’ origin, dominant mineralogy 60%+ clay, and dominant grain <2 mm diameter) or loam-like (a catch-all category incorporating all other non-clay-dominated parent materials; from Lawley 2011).

Land use scenarios

Each regional scenario was constrained to deliver an explicit food production target (P, expressed relative to 2015 production). We focus primarily on $P = 1$, but see **Supporting Information** for other values of P.

Business as Usual

The *Business as Usual* scenario, on which all alternative scenarios are based, is formed from a 50-m raster dataset incorporating *Land Cover Map 2015* (‘*LCM2015*’; Rowland *et al.* 2017) and *CEH Land Cover® plus: Crops 2015* (‘*crops2015*’) data, with *LCM2015* used for pixels with no *crops2015* data. For simplicity, we modified land use as follows: arable crops were combined as ‘arable’ (we later calculated the proportion of each arable crop in each 1-km square); urban and suburban land uses were combined as ‘built’; in The Fens, the small area of coniferous woodland (0.002% of the study area) was treated as broadleaf woodland, and the small area of saltmarsh (0.109%) as neutral grassland; in Salisbury Plain, the small areas of neutral grassland (< 0.001%) and heather grassland and heather (0.003%) were treated as calcareous grassland. We additionally modified the land use map such that all 1-km squares were either entirely ‘spared’ or ‘farmed’, based on overlap with nature reserves and natural and semi-natural land covers (see **Supporting Information** and **Fig. S1**).

We estimated food production following Finch *et al.* (2019) based on region- and land use specific per-hectare yields (GJ human edible energy; (see **Supporting Information**). For arable land, we calculated the composition of arable crops in each 1-km square, then estimated the average regional yield of each arable crop using the Farm Business Survey

(Duchy College Rural Business School 2017). Production from grazed land uses was based on published estimates (Tallowin & Jefferson 1999; Cassidy, West, Gerber & Foley 2013). These yield estimates were strongly correlated with equivalent values derived from direct farm surveys in both The Fens (d.f. = 25, r = 0.94, p < 0.001) and Salisbury Plain (d.f. = 18, r = 0.94, p < 0.001; Finch *et al.* (2019)). We expressed the yield of each square per hectare of unbuilt land, and summed this across all 1-km squares within each region to calculate *Business as Usual* production.

Land-sparing scenarios

Land sparing involves an increase in the area of spared land, compensated for by an increase in average farmland yields (though when $P < 1$, compensatory increases in farmland yields are not necessary under some intermediate sparing scenarios). We present a range of land-sparing scenarios between *Business as Usual* and extreme sparing (under which farmed squares contain no woodland or grassland and the area of spared land is thus maximised). We generated land sparing scenarios by sequentially converting a pre-defined number (in discrete increments) of farmed squares to spared ones

The order in which farmed squares were spared, and the habitat type to which they were restored, varied according to five regional 'priority scenarios', representing a mix of real and hypothetical land management plans (**Fig. 3**). Under the *Least cost* scenario, and unless otherwise stated, we spared farmed squares in ascending order of 2015 food production (such that higher-yielding squares were typically protected from conversion to spared land), converting these to the habitat type of the nearest currently spared square. Under the *Adjacent* scenario we restored 1-km squares in ascending order of distance to nearest currently spared square (such that existing spared areas grew in size, with farmed squares distant from currently spared areas being protected from conversion). For each region, three additional scenarios were developed to reflect local priorities and visions. In The Fens, these were: (1)

Fens4Future, in which we first restored squares >50% covered by the ‘Fens for the Future’ target areas (Fens for the Future 2012), which identify priority areas for restoring some of the historic wetland habitat; (2) *Deep peat*, in which we first restored squares >50% covered by peat soil (as opposed to wasted peat), converting these farmed squares to permanently wet fen to protect the remaining peat resource ; and (3) *Washland* in which we first restored squares >50% covered by a 500 m buffer around all waterbodies (rivers, canals and surface water transport; Environment Agency 2014), converting these farmed squares to wet grassland as a possible flood mitigation solution. In Salisbury Plain, the priority plans were: (1) *SteppingStones*, in which we first restored squares >50% covered by the ‘Stepping Stones’ Nature Improvement Area plan, which maps priority areas for connecting existing patches of semi-natural habitat; (2) *Groundwater*, in which we first restored squares >50% covered by a groundwater source protection zone (Zone 3, total catchment; Environment Agency 2015), converting these farmed squares to woodland as a possible action for mitigating pollution of aquifers which supply drinking water; and (3) *Chalk stream*, in which we first restored squares >50% covered by a 1000 m buffer around all chalk stream Sites of Special Scientific Interest (the River Till and River Avon System), converting these farmed squares to chalk grassland as a possible action for mitigating diffuse pollution of aquatic ecosystems.

Each new spared square was assigned the average land use composition and yield of the corresponding restored habitat type. To increase food production on the remaining farmed squares we converted randomly selected 0.25-ha units of woodland or grassland to arable land until total region-wide production matched the production target. The yield of new arable land was determined by the square-specific composition of arable crops (or, for squares with <10% arable land, the average proportional composition of arable crops across all squares within 5 km, with each square weighted according to the inverse of the distance to the focal square).

Land-sharing scenarios

In contrast to land sparing, land sharing involves a reduction in the area of spared land, allowing (where $P \leq 1$) a reduction in average farmland yields. We present a range of land-sharing scenarios between *Business as Usual* and 'extreme sharing' (under which no spared squares remain and the average yield of farmed land is thus minimised). We generated land sharing scenarios by sequentially converting a pre-defined number (in discrete increments) of spared squares to farmed ones in ascending order of distance to farmed squares. The land-use and yield of converted squares was determined according to the average proportional land use composition across all currently farmed squares within 5 km, with each square weighted according to the inverse of the distance to the focal square. When spared squares were tied on distance to farmed squares, we converted those with the highest potential yield first.

To maintain overall production across farmed squares, we randomly selected 0.25-ha units of arable land and converted these to woodland or grassland until total region-wide production matched the production target. The land use of new non-arable 0.25-ha units was selected randomly, weighted according to the square-specific proportional composition of woodland or grassland (or, for squares with <10% non-arable land, the average proportional composition across all squares within 5 km, with each square weighted according to the inverse of the distance to the focal square).

Three-compartment sparing

For each extreme sparing scenario, we generated an equivalent 'three-compartment sparing' scenario in which a fixed number of farmed squares (equal to the number of spared squares) was converted to 'low-yield farmland'. The yield of low-yield farmland was fixed at the region-specific median yield at which species with hump-shaped density-yield curves reach peak density (see Finch *et al.* 2019). We randomly converted farmed squares to low-yield farmland (considering only those squares with yields higher than the level defining low-yield farmland), achieving the required yield reduction as described above for land sharing. In order to maintain overall production, we then sequentially converted pairs of spared and low-yield farmland 1-km squares to (high-yield) farmland, until total production matched the region-wide production target. Three-compartment sparing scenarios thus contained an equal number of spared and low-yield farmland squares, but with a smaller area of spared semi-natural habitat than under the corresponding extreme sparing scenario.

Bird population size

We used the density-yield functions developed by Finch *et al.* (2019) to predict the region-wide population size of each breeding bird species under each scenario. Density-yield functions were parameterised using data collected from 140 surveys at 34 sites in The Fens and 397 surveys at 108 sites in Salisbury Plain (primarily 1-km Breeding Bird Survey squares; Harris *et al.* (2019)). We used these species- and region-specific functions to estimate, for each scenario, the region-wide population size of 96 species in The Fens and 76 species in Salisbury Plain (excluding species detected at only one farmland survey site, for which population density estimates were deemed less reliable). We summarised predicted population change as the geometric mean ratio across species between each scenario and the *Business as Usual* scenario. We also calculated the geometric mean ratio separately for species predicted to achieve smaller populations under a pre-agricultural baseline than under any sharing-sparing scenario (‘winners’) and those predicted to have smaller populations under all sharing-sparing scenarios than under a pre-agricultural baseline (‘losers’; see **Supporting Information**).

Global warming potential

We estimated the net annual global warming potential of each scenario based on the total area of each land use and land-use transition. Greenhouse gas fluxes associated with ongoing land use were assumed to be annually constant, and included emissions from fertiliser application

(N_2O), livestock (N_2O and CH_4) and woodland removal (CO_2), in addition to carbon sequestration from biomass accumulation in woodland. For peat soils in The Fens, we derived emissions factors for CO_2, CH_4 and N_2O from drained and wet land uses, including a temporary methane spike following re-wetting (**Table S6**).

To quantify greenhouse gas fluxes associated with land-use *change*, we created a 50×50 m land use raster for each scenario, from which pixel-level land-use changes (compared to *Business as Usual*) were computed. The procedure for creating this land use raster is described in **Supporting Materials**. Greenhouse gas fluxes associated with land-use change are not annually constant, so were annualised over a 50-year time period, reflecting the importance of near-to-medium-term emissions from a policy perspective.

Most emissions factors (CO_2 equivalents, expressed as warming potential over 100 years, GWP_{100}) were estimated using IPCC Tier 1 methodologies, as described in **Supporting Materials**. We summed net GWP_{100} across all land within each region, and expressed this relative to *Business as Usual*, where values <1 reflect a net reduction in global warming potential compared to 2015 .

Nutrient export

We estimated nitrogen and phosphorus export using a spatially explicit nutrient delivery ratio (NDR) model (InVEST v 3.5.0 Sharp *et al.* 2018), applied to all watersheds which intersect our study regions (**Fig. S2**). The NDR model (see **Supporting Materials**) describes the movement of nutrients through a three-dimensional landscape divided into pixels, with each pixel assigned a land-use-specific nutrient loading (i.e. application rate) and nutrient retention efficiency. Each pixel’s nutrient loading flows downhill into a watercourse, and nutrient export is defined as the total quantity of nitrogen or phosphorus reaching the watercourse.

We calibrated and executed the NDR model as described by Redhead *et al.* (2018), running the model for each scenario-specific 50×50 m land use raster (as described above for greenhouse gas fluxes) and holding land use in cells outside our focal 1-km squares (but within the focal catchments) at 2015 values. We summed total nitrogen and phosphorus export across all pixels within focal 1-km squares (representing 13% of the entire catchment in The Fens and 37% in Salisbury Plain), expressed relative to total export under *Business as Usual*.

Recreation

Recreation value was derived from an empirically-derived recreation demand model (Outdoor Recreation Valuation (ORVal); (Day & Smith 2018)), utilising data from the Monitor of Engagement with the Natural Environment survey (2009–2016). Adopting the repeated random utility framework (Morey, Rowe & Watson; McFadden 1973), ORVal seeks to understand how adult residents of England and Wales make daily decisions regarding their choice of outdoor recreation trips given their characteristics and the environmental and other qualities of the outdoor recreation opportunities accessible to them from their home location (see **Supporting Materials** for full description). ORVal estimates the total recreational value of a spatially explicit land use scenario given the distribution and socio-economic composition of people and the distribution and quality of recreation sites. Recreation sites are defined as access points to existing public rights of way; recreation opportunities are altered by modifying the land cover associated with each site. We focus here on the total welfare value of outdoor recreation (a monetary estimate of the benefits that members of society attribute to the recreation experiences afforded to them by accessible outdoor recreation sites), but also present results for total number of visits (**Supporting Materials**), both expressed relative to the *Business as Usual* scenario.

Aggregate response across outcomes

To synthesise the response of all five variables across scenarios, we designed a simple scoring system which accounts for both the magnitude and direction of changes. We scored outcomes equal to *Business as Usual* as 0, those showing a 0–10% 'improvement' (higher value for birds and recreation value, lower value for GWP_{100} and nutrient export) as 0.1, those showing a 10–25% improvement as 0.25, and those showing a >25% improvement as 0.5. We assigned opposite scores to outcomes which showed a deterioration, then calculated, for each scenario, the mean score across all five outcomes. Note that each outcome is quantified independently.

Results

At current production levels ($P = 1$), the complete loss of spared habitat under extreme sharing facilitates a 4% and 26% reduction in mean farmland yield compared to *Business as Usual* in The Fens and Salisbury Plain, respectively (**Fig. 4a**, **Fig. 4g**). Under extreme sparing (*Least cost*), farmland yields increased by 17% and 57% facilitating a 377% (from 47 to 224 km^2) and 112% (from 257 to 545 km^2) increase in the area of spared land in The Fens and Salisbury Plain, respectively.

Bird population size

In both The Fens and Salisbury Plain, geometric mean relative population size was maximised under a land-sparing scenario, whereas land sharing resulted in average population declines compared to *Business as Usual* (except for *Washland* scenarios in The Fens, for which average population size was always lower than under *Business as Usual*; **Fig. 4b**, **Fig. 4h**).

In The Fens, geometric mean relative population size was maximised under either extreme land sparing (*Deep Peat*) or three-compartment sparing (*Least cost*, *Adjacent* and *Fens4Future*), with average populations 34–68% larger across scenarios than under *Business* *as Usual*(**Fig. 4b**). Extreme land sparing under the *Deep Peat* scenario (in which fen is promoted on spared land) resulted in largest average bird population increases. In Salisbury Plain, geometric mean relative population size was maximised under three-compartment sparing, with mean population size 6–27% larger across scenarios than under *Business as Usual* (**Fig. 4h**). Three-compartment sparing under the *Groundwater* scenario (in which woodland is promoted on spared land) resulted in the largest average bird population increases.

Among species classified as losers (61% of species in The Fens, 40% in Salisbury Plain), extreme land sparing maximised geometric mean relative population size in both regions (except for *Washland* in The Fens; **Fig. S4**). For species classified as winners, geometric mean relative population size was maximised under extreme land sharing in The Fens and three-compartment sparing in Salisbury Plain.

For loser species in both regions and winner species in The Fens geometric mean relative population size was higher at lower production targets (**Fig. S5**). For winner species in Salisbury Plain, however, geometric mean relative population size was higher at higher production targets, and the best strategy shifted from intermediate sparing towards land sharing at higher production targets (**Fig. S5**).

Global warming potential

In both regions, land sharing resulted in an increase in net GWP_{100} caused by the loss of carbon sequestered in spared habitats and, in The Fens, the continued cultivation of peat soil. In contrast, land sparing typically reduced GWP_{100} (**Fig. 4c**, **Fig. 4i**). These conclusions were robust to emissions factor uncertainty (**Fig. S6** and **S7**).

In The Fens, there was substantial variation in the response of GWP_{100} under land sparing between priority scenarios, largely owing to differences in the fate of peat soils. The *Deep* *peat* scenario (and, to a lesser extent, *Fens4Future*), in which peat soils were permanently rewetted, resulted in a 43% reduction in net GWP_{100} under extreme sparing compared to *Business as Usual*, whereas scenarios which restored wet grassland or which continued to cultivate peat soils increased GWP_{100} (**Fig. 4c**). In Salisbury Plain, land sparing consistently reduced GWP_{100}. Extreme land sparing under the *Groundwater* scenario (which promoted woodland over chalk grassland) minimised GWP_{100} overall, resulting in negative net emissions (**Fig. 4i**). In both regions, but especially in The Fens, GWP_{100} was lowest at low production targets (**Fig. S8**).

Nutrient export

Land sharing reduced nitrogen and phosphorus export in both regions, whereas the consequences of land sparing for nutrient export varied markedly between regions and priority scenarios. The magnitude of change relative to *Business as Usual* was small in all cases, perhaps due to total nutrient inputs being essentially constant between scenarios.

Extreme land sparing under the *Least cost* scenario performed well in both regions, minimising nitrogen and phosphorus export in The Fens (4% and 5% reduction, **Fig. 4d**, **Fig. 4e**) and phosphorus export in Salisbury Plain (7% reduction, **Fig. 4k**), whilst extreme land sharing minimised nitrogen export (7% reduction, **Fig. 4j**). In contrast, extreme land sparing under the *Adjacent* scenario performed poorly in both regions, resulting in increases in both nitrogen and phosphorus export. Nutrient export was lowest at low production targets, with variation in nutrient export between production targets far exceeding variation across the sharing-sparing continuum (**Fig. S9** & **Fig. S10**).

Recreation

In both regions, increasingly extreme land sharing resulted in a small increase in both the total welfare value of outdoor recreation (**Fig. 4f**, **Fig. 4l**) and the total number of recreational visits

(**Fig. S11**). The consequences of land sparing for recreation varied between regions and, to a lesser extent, between priority scenarios. In The Fens, recreation value and visits were maximised under land sparing scenarios, with extreme land sparing under the *Least cost* scenario resulting in the highest total welfare value, closely followed by the *Deep peat* scenario. In Salisbury Plain, both value and visits declined under extreme land sparing, but intermediate land sparing (especially under the *Adjacent* scenario) resulted in an increase in recreation value. Overall, both metrics of recreation were maximised under extreme land sparing in The Fens (up to a 37% increase in recreation value) but extreme land sharing in Salisbury Plain (up to a 4% increase). This pattern persisted regardless of the region-wide production target, though the value of outdoor recreation was highest at low production targets (**Fig. S12**).

Aggregate response across outcomes

In both regions, land sharing resulted in a negative average score, primarily due to strong deteriorations in bird population size and GWP_{100} (**Fig. 5**). Maximum scores were achieved under extreme land sparing in The Fens (*Least cost*, *Fens4Future* and *Deep peat* in particular) and intermediate land sparing in Salisbury Plain (*Least cost*, *SteppingStones* and *Groundwater* in particular). Three-compartment sparing delivered a positive mean score across all five priority scenarios in both regions.

Discussion

Several scenarios – always involving a shift towards land sparing – delivered improvements in four or more outcomes compared to *Business as Usual*. However, outcomes also depended on the spatial arrangement of spared land, the types of natural or semi-natural habitat promoted on spared land and whether some lower-yielding farmland was ‘spared’ alongside natural and semi-natural habitat. Broadly, scenarios which promoted the restoration of fen on peat soils in The Fens, and the restoration of woodland in Salisbury Plain performed well, because these habitats support more bird species than alternative habitats and deliver relatively high rates of carbon sequestration. For nutrient export and recreation value *Least Cost* scenarios almost always outperformed *Adjacent* scenarios, suggesting that large aggregations of spared areas are suboptimal for some ecosystem (dis-) services.

Although agricultural intensification is a key driver of wildlife declines (e.g. Donald, Sanderson, Burfield & van Bommel 2006), our results suggest that the negative consequences of high-yield farming on birds can be outweighed if its potential land-sparing benefits are realised, especially when low-yield farmland is 'spared' in addition to natural and semi-natural habitat. Other studies, generally based on simpler, non-spatial scenarios, have also found support for scenarios which incorporate elements of land sharing into land-sparing scenarios (Montejo-Kovacevich *et al.* 2018; Feniuk *et al.* 2019; Finch *et al.* 2019). An important caveat is that our alternative-future scenarios do not explicitly account for the temporal dynamics in the development of new habitats, nor their colonisation by bird communities.

Global warming potential decreased under most land sparing scenarios, highlighting the importance of large-scale habitat restoration for carbon sequestration. In The Fens, scenarios which promoted land sparing on remaining peat soils avoided the substantial carbon emissions associated with their continued cultivation, with the restoration of this land to permanently wet fen resulting in further reductions in GWP_{100}. This supports findings from national-scale analyses which have highlighted the importance of both restoring degraded peat soils and creating space for carbon-sequestering natural and semi-natural habitats (Lamb *et al.* 2016; Thomson *et al.* 2018).

Differences in nutrient export between scenarios were modest, with larger differences between alternative sparing scenarios. Extreme land sparing under the *Least cost* scenario delivered a patchy distribution of spared land intercepting multiple nutrient flow paths, and was consistently high performing. In contrast, extreme land sparing under the *Adjacent* scenario resulted in a strong polarisation between large blocks of farmed and spared land, and performed poorly in both regions. This suggests that restored habitat which is adjacent to existing spared land may be redundant in terms of nutrient capture, but that semi-natural land covers adjacent to farmland are important for intercepting nutrients. The consequences for diffuse pollution of the sharing-sparing continuum *per se* are thus difficult to predict. Instead, the strategic placement of nutrient-intercepting land with respect to nutrient-exporting land may be more important.

Disentangling the drivers of the recreational changes predicted under different scenarios is challenging, with the consequences of any change in landcover depending on how close that location is to human population centres, and how well served those populations are by alternative recreation experiences. In the Fens, land sparing is associated with increases in the area of semi-natural habitats which are in short supply under *Business as Usual*, generating gains in recreation value that outweigh the losses precipitated from removal of improved grassland in farmed areas. Since woodland is generally the most preferred land cover, the two scenarios which result in the largest expansion of wet woodland (*Deep Peat* and *Least Cost*), also deliver the greatest increases in recreation value. In Salisbury Plain, where semi-natural habitats are already relatively extensive, the incremental benefits of additional semi-natural habitats diminish towards extreme sparing, whilst the incremental losses from the increasing dominance of arable land in farmed areas increases. Additionally, due to use for military training, existing recreation sites are relatively sparse in the currently spared parts of Salisbury Plain, so the recreational impact of the expansion of agricultural land covers here under land sharing is perhaps limited. These results highlight the importance of considering spatial variation in both the supply of and demand for ecosystem services.

Our illustrative scenarios are designed to represent a range of plausible alternative regional land use visions, though practical constraints and potential unintended consequences may limit their realisation. In The Fens, wetland restoration is complicated by limited water availability during late spring and summer, whilst the flat topography presents a challenge for re-wetting projects to avoid negative impacts on neighbouring land. Hydrological models could be integrated with our spatially-explicit scenarios to better understand these issues. More generally, our scenarios ignore social and economic factors. Delivering semi-natural habitat on private land – whether as small-scale features as is common under existing agri-environment schemes, or as larger blocks under land sparing – requires incentives to compensate land managers for incurred management costs and income forgeone (Hanley, Banerjee, Lennox & Armsworth 2012).

We accomplished increases in farmland yields by increasing the arable component of farmed 1-km squares. Whilst we believe that such changes are technically feasible in our study regions – all focal 1-km squares were matched on soil type, so different land uses should be theoretically substituable – higher yields might instead (or additionally) be achieved by selecting higher-yielding cultivars and breeds, increasing (or optimising) the application of fertilisers, or adopting improved soil and pest management (e.g. Mitchell & Sheehy 2018). We avoided explicitly evaluating these alternative practices due to difficulties in quantifying their consequences for our focal outcomes, but in **Supporting Materials** we explore the consequences of leveraging yield growth to extend our extreme land sparing scenarios. We assume that increases in crop yield and stocking density result in proportional increases in agricultural emissions; this assumption may be optimistic, though conversely it could be argued that efficiency gains could reduce the environmental costs of higher-yield farming (Balmford *et al.* 2018; The Royal Society 2019). That the yield of wheat and other crops has stagnated across Europe (Ray, Ramankutty, Mueller, West & Foley 2012) suggests that improved crop breeding and agronomic practices will be necessary to deliver land sparing through crop yield growth.

For high-yield agriculture to realise its full land-sparing potential, explicit policies are required to ensure sustainable food production alongside habitat conservation (Ewers, Scharlemann, Balmford & Green 2009; Phalan *et al.* 2016). These could include novel certification schemes for (groups of) producers who conserve large unfarmed areas or high nature value farming systems (Chandler *et al.* 2013) or multi-tier economic instruments which incentivise productive but sustainable food production in some places and habitat conservation in others (Defra 2020). We caveat that high yields must not compromise future production, and that crop yield resilience may benefit from proximity to semi-natural habitat (Redhead, Oliver, Woodcock & Pywell 2020). That almost all outcomes were improved at lower food production targets highlights the additional importance of mitigating increases in demand for products grown in our study areas, through mechanisms such as waste reduction and dietary change (Lamb *et al.* 2016).

Authors' contributions

TF, RG, WP & AB conceived the study; TF, BD, DM, RF & JR conducted data analysis; TF led the writing and figure production, with contributions from all authors. All authors gave final approval for publication.

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Data Availability Statement

See **Supporting Information** for supplementary methods, results, figures, tables and references.

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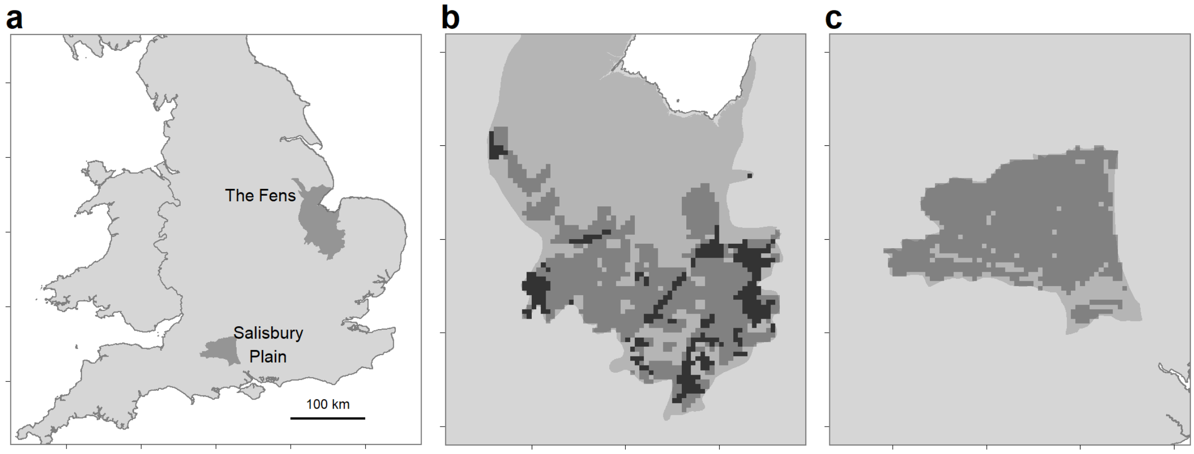

Figure 1 a Location of study regions in southern England, showing National Character Areas of The Fens and Salisbury Plain and West Wiltshire Downs. In **b** (The Fens) and **c** (Salisbury Plain), medium grey shows focal 1-km squares in each region; in **b**, dark grey shows 1-km squares with *peat* soil.

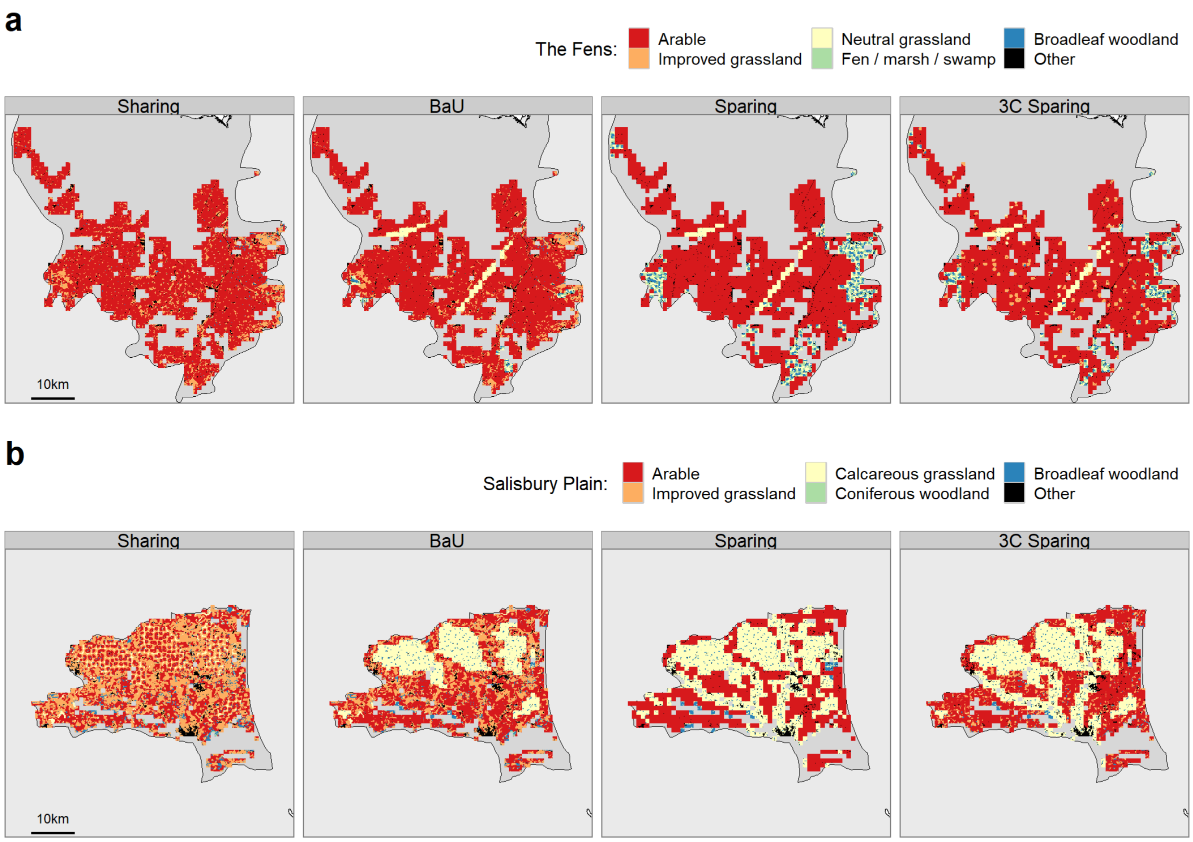

Figure 2 50×50 m land use maps showing examples of alternative scenarios in The Fens (**a**) and Salisbury Plain (**b**). Sparing and three-compartment (3C) Sparing show the *Deep peat* scenario in The Fens and the *Chalk streams* scenario in Salisbury Plain. ‘Other’ land use category includes built land, inland rock and freshwater. BaU = “Business as Usual”, under which land cover remains fixed at 2015 values.

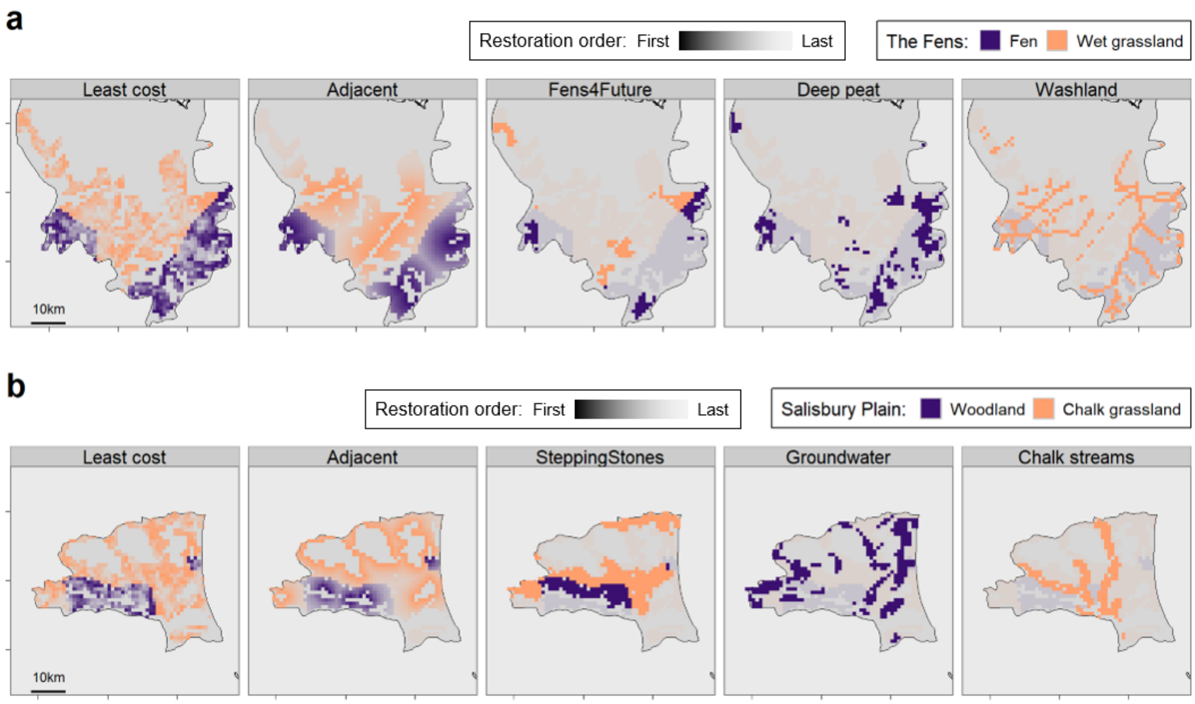

Figure 3 Illustration of five regional priority scenarios in The Fens (**a**) and Salisbury Plain (**b**) showing the order in which farmed squares are converted to spared land (darker filled squares first) and the habitat type to which they are restored (fen or wet grassland in The Fens, woodland or chalk grassland in Salisbury Plain). Grey-shaded squares are either already spared, or are not part of our study. Note that, even under extreme sparing, not all coloured squares will actually be spared (unless $P \approx 0$). See methods for full description of regional scenarios.

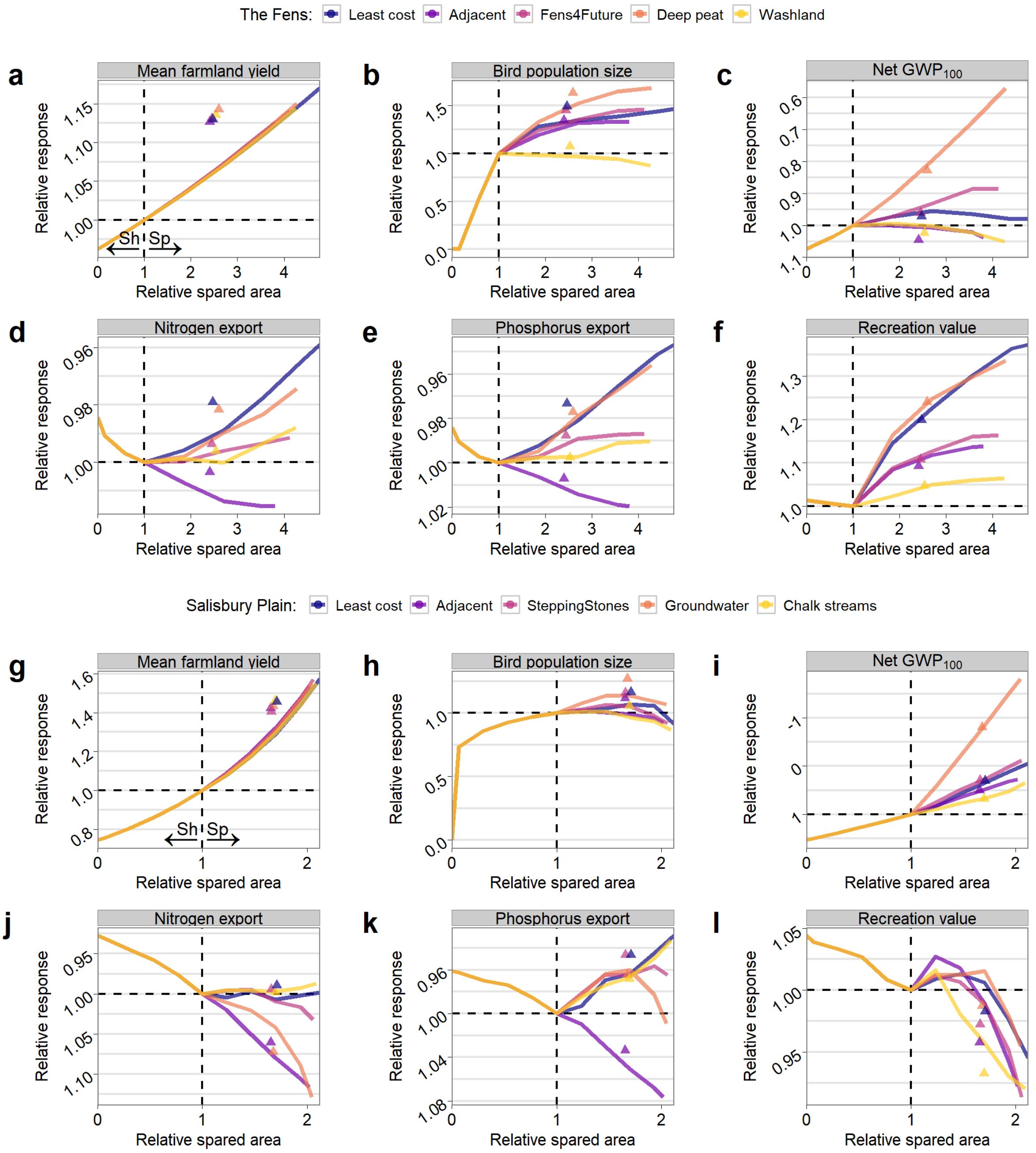

Figure 4 Relative response, compared to *Business as Usual*, of mean farmland yield (**a**, **g**), bird population size (**b**, **h**), net GWP_{100} (**c**, **h**), nitrogen export (**d**, **j**), phosphorus export (**e**, **k**) and recreation value (**f**, **l**) across the sharing-sparing continuum with five alternative land-sparing scenarios in The Fens (**a**-f) and Salisbury Plain (**g-l**). Triangles show three-compartment sparing (mean farmland yield on *y*-axis excludes low-yield farmland). Note that *y*-axes are inverted for GWP_{100}, nitrogen and phosphorus, such that high *y* values reflect

improvements in all outcomes. Scenarios to the left of the vertical dashed line represent land sharing (Sh), whilst scenarios to the right represent land sparing (Sp).

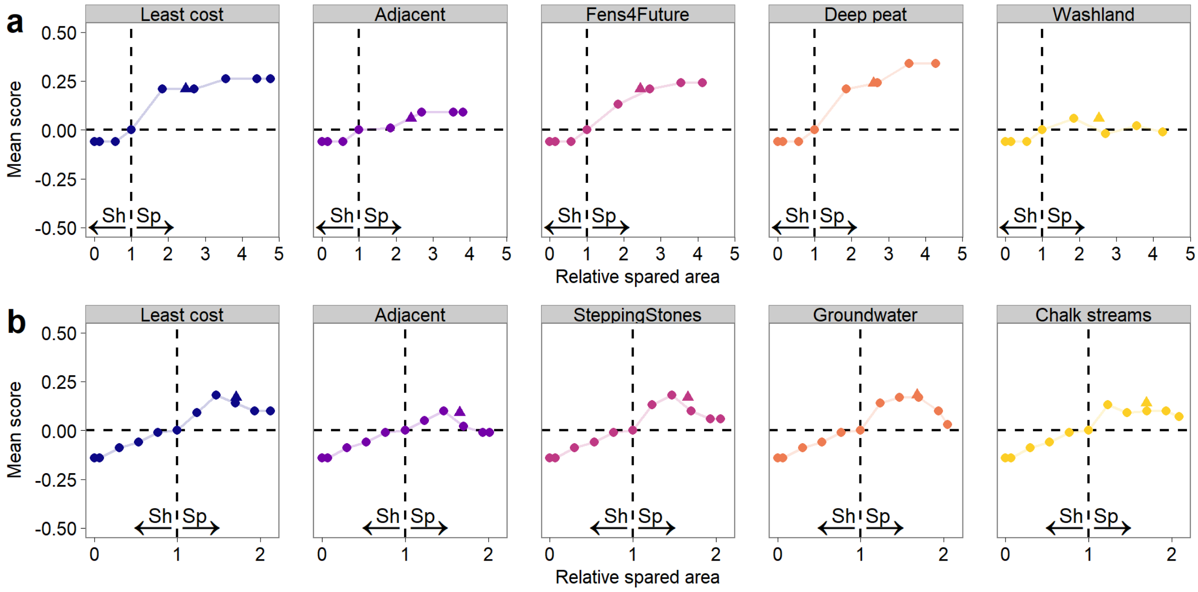

Figure 5 Average response score across five environmental outcomes relative to *Business as Usual* across the sharing-sparing continuum for five alternative regional priority scenarios in The Fens (**a**) and Salisbury Plain (**b**). Triangles show three-compartment sparing. See main text for details of scoring system.