Assessing the utility of land sharing and land sparing for birds, butterflies and ecosystem services in lowland England

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Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Background

Globally, the expansion and intensification of agriculture are leading drivers of biodiversity loss and environmental harm. As the human population grows in size and wealth, a key question is how to reconcile food production with the maintenance and recovery of biodiversity and ecosystem services.

The land sharing-sparing framework provides a heuristic approach for evaluating the environmental consequences of contrasting regional land-use scenarios all producing the same quantity of agricultural produce.

Empirical evidence collected across several regions of the world suggest that more species would benefit from land sparing (in which the extent of farmland is minimised through high-yield farming, thus sparing more seminatural habitat) than from land sharing (in which the intensity of farmland is minimised through lower-yield farming, with no spared seminatural habitat). Recent research on birds in two regions of lowland England (The Fens and Salisbury Plain) supports a mixed, 'three-compartment sparing' strategy, in which high-yield farming spares land for both semi/natural habitat and low-yield farmland.

Natural England's interest in this area encompasses the need to understand how land use might be configured to conserve biodiversity and ecosystem benefits more effectively whilst maintaining food production at the levels required by society. This research was commissioned to build on previous work by the research team with the particular aim of exploring further the potential benefits of the 'three-compartment sparing strategy':

- Is three-compartment sparing compatible with improving environmental outcomes such as global warming potential and diffuse pollution (nitrogen and phosphorus export)?

- Is three-compartment sparing supported in other regions of lowland England (The Cotswolds and Low Weald) and for butterflies as well as birds?

The outputs may be used to inform design and development of agri-environment policies and delivery approaches.

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Assessing the utility of land sharing and land sparing for birds, butterflies and ecosystem services in lowland England

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Summary

Agriculture is a major driver of biodiversity loss and environmental degradation, so understanding how to reconcile food production with the maintenance of biodiversity and ecosystem services presents a critical challenge.

The land sharing-sparing framework provides a heuristic approach for evaluating the environmental consequences of contrasting regional scenarios which – crucially – produce an equal quantity of agricultural produce. Empirical evidence collected for several taxa across several regions of the world suggest that more species would benefit from land sparing (in which the extent of farmland is minimised through high-yield farming) than from land sharing (in which the extent of farmland is maximised through lower-yield farming). Our recent research on birds in two regions of lowland England supports a mixed, 'three-compartment sparing' strategy, in which high-yield farming spares land for both seminatural habitat and low-yield farmland.

In this report, we first extend our work in The Fens and Salisbury Plain to consider spatially-explicit land-use scenarios, for which we quantify breeding bird population size, global warming potential (GWP), and nitrogen (N) and phosphorus (P) export. Second, we explore the sensitivity of our results to different species prioritisations. Third, we replicate our original analysis in two new regions (The Cotswolds and Low Weald), for butterflies as well as birds.

For birds in The Fens and Salisbury Plain, our spatially-explicit scenarios reinforce our original conclusions, providing support for intermediate–extreme land sparing or three-compartment sparing. Land-sparing strategies also reduced GWP, especially (in The Fens) when peat soils were restored to wet fen. Results for N and P export were more complex, but a land-sparing strategy minimised N export in The Fens and P export in both regions. Quadruple-win strategies (i.e. those which improved all four environmental outcomes) always involved an increase in the area of spared land, either through intermediate, extreme or three-compartment sparing. The spatial arrangement and habitat composition of spared land influenced most outcomes, especially N and P export.

In general, our conclusions were insensitive to the weightings applied to different bird species. In particular, our conclusions held for species threatened at the national (BoCC and IUCN Red List), European and Global scale. However, species making up the Farmland Bird Indicator and, in Salisbury Plain, those identified as 'endemic' (n = 3) preferred strategies closer to extreme land sharing.

The firm conclusion for birds and butterflies in The Cotswolds and Low Weald (as well as for birds in The Fens and Salisbury Plain) is that three-compartment sparing represents a consistently reliable approach, through which a region can deliver a range of food production targets at the same time as conserving both farmland-avoiders and farmland-adapters. For the avoidance of confusion, three-compartment sparing is not intermediate between land sharing and land sparing, because it involves high-yield farming. Instead, it is a land-sparing strategy which incorporates some shared low-yield farmland.

We identify four key questions to consider before applying three-compartment sparing in practice: 1) how much land should be devoted to low-yield farming versus spared semi/natural habitat?; 2) what kind(s) of semi/natural habitat should be promoted on spared land?; 3) what kind(s) of farming systems should be promoted as low-yield farmland?, and 4) how should high-yield farmland be managed?

We also identify three pressing policy challenges: 1) mechanisms to support sustainable yield growth; 2) mechanisms to incentivise large-scale and long-term conservation on private land, potentially across land-holding boundaries, and 3) mechanisms to link yield growth to habitat restoration.

Finally, we suggest several outstanding conservation science needs.

Section 1: Introduction

Background to land sharing and sparing

Agriculture is a major driver of biodiversity loss and environmental degradation (Tilman *et al.* 2017), yet food production is critical for human wellbeing, and some threatened species now depend on habitats that are a by-product of agricultural activities (Wright, Lake & Dolman 2012). A key question is therefore how to reconcile food production with the maintenance of biodiversity and ecosystem services. Importantly, any action which reduces local food production risks exporting agricultural demand and the associated environmental degradation elsewhere.

Two contrasting strategies have been proposed through which an explicit food production target could be delivered across a focal region: *land sharing* and *land sparing* (Green 2005). Land sharing involves the integration of conservation and food production on the same land. In order to maintain overall production, the lower yields typical of such wildlife-friendly practices must be compensated for by increasing the total area of farmland at the expense of unfarmed natural or semi-natural habitats. In contrast, land sparing involves the separation of land devoted to conservation (referred to henceforth as 'spared land') from land devoted to food production ('farmland'); by farming at higher yields, the food production target can be achieved whilst maximising the area of un-farmed natural or semi-natural habitat within a region.

The difference between sharing and sparing can be interpreted in part as a matter of scale (Ekroos *et al.* 2016): land sharing promotes small patches of (semi-)natural habitat within farmed landscapes, whilst land sparing promotes bigger patches of habitat which are largely separated from agricultural activities. Land sharing also implies less intensive management of the productive areas of a landscape, for example through reduced agrochemical use

or lower stocking density. Here, we define 'spared' land as units of (semi-)natural habitat larger than 1 km^2 in size; smaller habitat features are therefore part of the farmed landscape. The 'yield' of farmland reflects the aggregate harvest across all farmland including small unproductive habitat features; increasing the area of unfarmed habitat within a farmed landscape therefore implies reducing the overall yield (but see e.g. Pywell *et al.* 2015).

Under extreme land sharing no land is spared from agriculture, allowing the regional food production target to be delivered at the lowest feasible yield. Under extreme land sparing, the maximum yield is produced from all farmland such that the area of spared land is maximised. A continuum of intermediate strategies exists between the extremes of sharing and sparing, across which the yield of farmland and the area of spared land increases (**Fig 1.1a**).

In addition to the continuum of strategies between extreme sharing and sparing, *mixed* strategies are conceivable too (Butsic & Kuemmerle 2015; Geschke *et al.* 2018). Whilst the sharing-sparing continuum involves binary (or 'two-compartment') strategies, a useful extension to this simple model involves the introduction of a third land-use compartment of lower-yielding farmland (**Fig. 1.1b**; Finch *et al.* 2019). In addition, the spared compartment can comprise 1 km^2 units of different natural or semi-natural habitat types, such as woodland and semi-natural grassland, which may be managed using techniques which resemble traditional (but extremely low-yielding) farming methods (Macchi *et al.* 2013; Finch *et al.* 2019).

Still, these discrete, non-spatial strategies represent substantial simplifications of the real world. An additional extension could involve designing spatially-explicit land-use scenarios which reflect sparing or sharing whilst incorporating real-world constraints and visions.

Fig. 1.1. Illustration of (**a**) the sharing-sparing continuum and (**b**) three-compartment sparing. Each vertical column represents a distinct food production scenario of constant area (*y*-axis), all of which deliver the same amount of food overall.
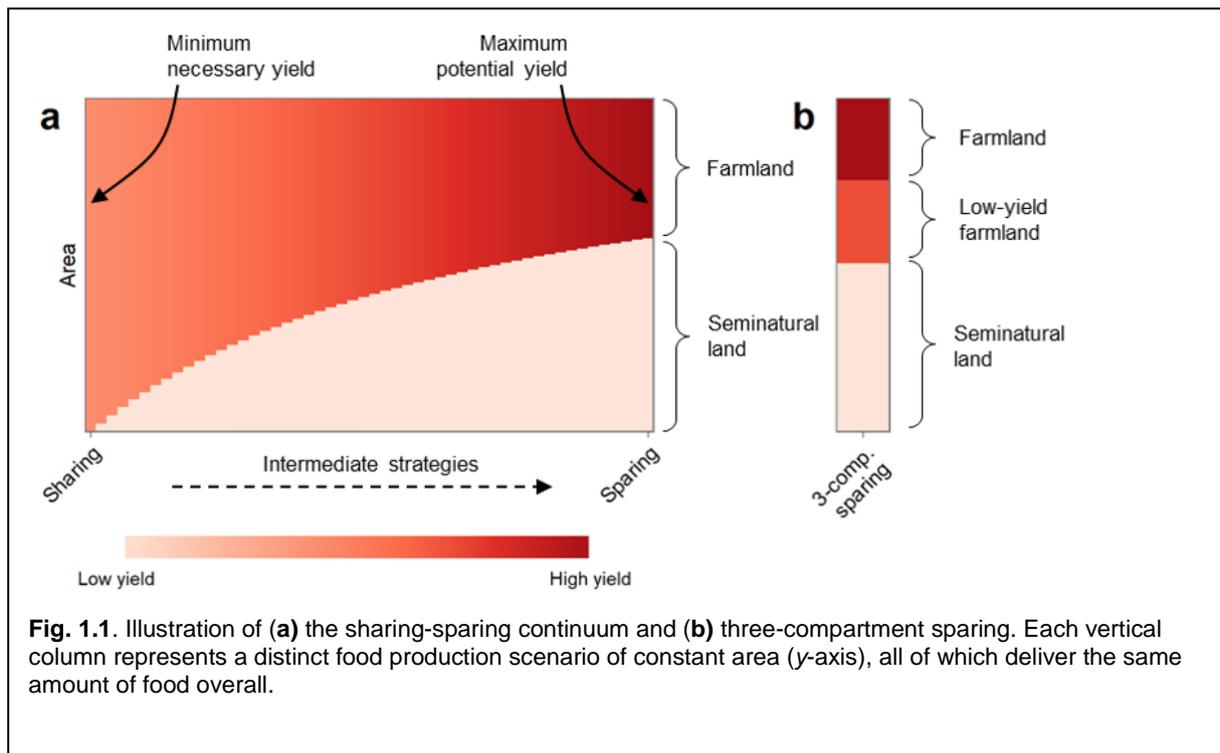
Regardless of the nature of the land-use scenario (two-compartment, three-compartment, spatially explicit), our analytical approach (after Phalan *et al.* 2011) involves predicting the regional population size of each focal species according to the species- and region-specific relationship between population density and agricultural yield. Empirical data on these two variables (across 1-km squares) are used to fit species-specific density-yield curves, which can take a wide range of non-linear shapes and are used to predict the average population density of a species given the yield of a 1-km square. We recognise that yield is not the sole driver of variation in population density, and that yield is influenced by a range of factors each of which may impact species populations differently. In some cases it might be possible to increase (or decrease) population density without affecting yield (Pywell *et al.* 2015); furthermore, some species might exhibit very weak density-yield relationships. The strength of our approach is that it explicitly models the trade-off (or synergy) between food production and conservation outcomes; where density-yield relationships are weak

then the sharing-sparing debate is largely irrelevant.

Biodiversity versus food production is clearly not the only pairwise trade-off of importance in this context. Provisioning services such as timber (Edwards *et al.* 2014) or housing (Collas *et al.* 2017) may take the place of food as the 'yield' component of the density-yield curve, whilst environmental outcomes such as carbon storage might replace density (Williams *et al.* 2017; Williams *et al.* 2018). Other environmental outcomes such as recreation or nutrient run-off are inherently spatial and are unlikely to follow simple deterministic relationships with yield; instead, these outcomes are quantifiable only when scenarios are presented spatially.

Our overarching question – how to optimise the *production* of food across a defined landscape – is largely separate from questions relating to *demand* for food, such as reducing food waste and shifting patterns of consumption. Whilst no realistic projections of future global food demand suggest anything other than a substantial increase compared to the present (World Resources Institute 2018), assessing the

merits of alternative sharing, sparing, intermediate and mixed approaches is still relevant even if overall food demand falls. And, while we should ultimately aim to minimise the environmental costs of *global* food production, we focus here on more tractable *regional* scenarios. Under this approach, we implicitly assume that any region should produce a defined contribution towards meeting global food demand, or else risk exporting environmental costs elsewhere by increasing demand for imported produce.

Previous work

Previous studies which have used density-yield relationships to evaluate discrete sharing-sparing scenarios have largely favoured land sparing (Onial 2010; Phalan *et al.* 2011; Hulme *et al.* 2013; Dotta 2014; Feniuk 2015; Kamp *et al.* 2015; Dotta *et al.* 2016; Williams *et al.* 2017). That is, most wild species are predicted to have larger regional populations under extreme land sparing than under any intermediate or extreme land sharing strategy. This is because, for most species, unfarmed habitat maximises population density, which declines rapidly as yields increase. These findings hold across several regions (Ghana, Uganda, India, Mexico, Uruguay, Kazakhstan, Poland) and taxa (birds, trees, dung beetles, butterflies, grasses, sedges and daisies).

As part of a joint RSPB & University of Cambridge project, we evaluated the sharing-sparing continuum for breeding birds in the East Anglian peaty fens and the chalklands of Salisbury Plain. Study areas were restricted to a narrow range of comparable soil types to support the assumption that observed agricultural yields could be attained anywhere within each landscape. To the best of our knowledge, this work represented the first evaluation of the sharing-sparing continuum for intense agricultural landscapes typical of north-west Europe. Here, a long history of disturbance from agriculture has resulted in a small and fragmented stock of natural habitat, meaning that many sparing-preferring species may have already been lost (if not nationally, then at least regionally). Additionally, a suite of farmland-dependent species which are likely to do poorly under extreme land sparing (Lamb *et al.* 2019) has undergone recent population declines and is currently of high conservation concern (Eaton *et al.* 2015).

Phase 1 of this project involved evaluating discrete scenarios reflecting the sharing-sparing continuum, in addition to a novel three-compartment sparing strategy (**Fig 1.1**). We used species- and region-specific density-yield curves to predict, for each scenario, the regional population size of 101 breeding bird species in the Fens and 83 in Salisbury Plain. We found that in The Fens, land sparing would maximise the predicted regional population size of more species than would land sharing, but that three-compartment sparing would maximise the average regional population size across all species. In Salisbury Plain too, land sparing outperformed land sharing, but an intermediate strategy was optimal overall, and three-compartment sparing was almost as good. At higher levels of regional food production, three-compartment sparing maximised the average regional population size across all species in both regions. This work is published in *Conservation Biology* (**Annex 1**) and forms the foundation of *Module 1B*.

Phase 2 involved the development of spatially-explicit land-use scenarios for the same two study regions, reflecting hypothetical but plausible real-world versions of land sharing and land sparing. These more sophisticated scenarios allowed us to quantify global warming potential in addition to breeding bird population size. This work is currently unpublished and forms the foundation of *Module 1A*.

Project objectives

The present project builds on our previous research, and is divided into two modules:

- Through *Module 1* we advance our work in The Fens and Salisbury Plain by:
  - A) quantifying diffuse pollution (nitrogen and phosphorus export) for the spatially-explicit sharing-sparing scenarios (**Section 2**), and
  - B) considering how alternative species prioritisations alter our conclusions regarding the response of breeding birds across the sharing-sparing continuum (**Section 3**).

- Through Module 2 we develop new case studies, fitting density-yield curves for birds and butterflies in The Cotswolds and Low Weald, and evaluating the consequences for biodiversity of non-spatial sharing-sparing scenarios (**Section 4**).

Section 2: Spatially explicit scenarios (Module 1A)

Introduction

Land is finite, yet demand is growing for the services it provides. Global crop demand, for example, is projected to double between 2005 and 2050 (Tilman *et al.* 2011), and climate goals will be missed without the widespread adoption of negative emissions technologies, many of which are land-hungry (Smith *et al.* 2016). At the same time, habitat loss and degradation are the dominant drivers of extinction risk globally (Tilman *et al.* 2017). Understanding how to allocate land for the sustainable delivery of multiple and often competing goals is therefore a major societal challenge (Benton *et al.* 2018).

Across most of the world, farming is the dominant human land use, and the land sharing-sparing framework (Green 2005) provides a heuristic for understanding the trade-off between agricultural production and biodiversity conservation. Early assessments of the land sharing-sparing framework (e.g. Phalan *et al.* 2011; Hulme *et al.* 2013) evaluated 'binary' food production strategies with land units assigned to one of only 2 land-use types: uniform farmland (with yield increasing from sharing to sparing) and unfarmed habitat (with area increasing from sharing to sparing). More recent evaluations have considered 'mixed' strategies with 3 or more land-use types, combining elements of both land sparing and land sharing (Geschke *et al.* 2018; Finch *et al.* 2019). Response-yield curves have also been fitted for above-ground carbon instead of biodiversity (Williams *et al.* 2017; Williams *et al.* 2018), and 'yields' have been measured for non-agricultural products such as timber (Edwards *et al.* 2014) and human population density (Geschke *et al.* 2018). These studies all illustrate that the regional delivery of multiple goals is usually maximised by some degree of landscape compartmentalisation, sparing 'conservation

land' from the typically negative effects of agriculture, forestry or development.

While these studies have been parameterised using real-world data, the scenarios they evaluate have been simple and largely non-spatial. In contrast, the development of spatially-explicit land-use scenarios brings several potential advances. First, spatially-explicit scenarios have the potential to be more realistic. Because land-use is a continuous attribute rather a discrete one, placing any existing landscape on the sharing-sparing continuum requires substantial simplification (e.g. averaging all 'farmland' into a single uniform land-use; **Fig. 1.1**). Spatially explicit scenarios can instead illustrate the steps through which alternative scenarios are derived from current land-use, whilst accounting for geographical constraints such as soil properties, topography and land designations. Such scenarios are also likely to generate more traction with local stakeholders and decision makers, especially if scenarios incorporate existing land-use visions. Additionally, some ecosystem services and dis-services such as diffuse pollution are inherently spatial, so can only be evaluated when scenarios are represented as maps.

Here, for The Fens & Salisbury Plain, we develop and evaluate a range of spatially-explicit land-use scenarios, each meeting an explicit regional food production target. Scenarios are derived from current land-use, and reflect a range of increasingly extreme land-sparing and land-sharing strategies. For each scenario, we then use (1) density-yield curves to estimate the regional population size of 105 breeding bird species; (2) land-use-specific emissions factors to estimate net global warming potential; and (3) a spatially-explicit model of nutrient retention to estimate diffuse pollution by nitrogen and phosphorus. We quantify the response of these environmental outcomes across the sharing-sparing continuum, and identify scenarios which deliver multiple benefits.

Methods

Study area

We focus on two contrasting regions (National Character Areas, or NCAs) in the English lowlands: The Fens is a region of drained wetlands now dominated by arable farmland, and Salisbury Plain and West Wiltshire Downs ('Salisbury Plain') is characterised by rolling chalk grassland and mixed farmland.

Specifically, we restricted our analysis to 1-km squares dominated (>50% cover) by peaty soil types in The Fens ('Raised bog peat soils', 'Fen peat soils' or '…soils with … a peaty surface') and chalky soil types in Salisbury Plain ('Freely draining lime-rich loamy soils' or 'Shallow lime-rich soils over chalk or limestone'; Farewell *et al.* 2011), to ensure that different land-uses were in principle substitutable between squares.

In The Fens, for the purposes of estimating crop composition and greenhouse gas emissions (see below), we additionally classified each square according to the depth of remaining peat and the properties of the underlying parent material. We identified 1-km squares where the dominant soil class was "Raised bog peat soils" or "Fen peat soils" as *peat*. All other squares (where historic peat deposits have wasted to "…soils with…a peaty surface") were classified as either *skirt loam* or *skirt clay* 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

All scenarios maintained the current area of land in each region, across which a range of food production targets ($P = 0.75, 0.875, 1.0, 1.125$ and 1.25, expressed relative to 2015 production) were met through contrasting land-use scenarios. We focus primarily on $P = 1$ (but see **Appendix 1E** for results at other values of P).

Business as Usual

The *Business as Usual* scenario, from which all other scenarios were derived, is based on a 50-m raster dataset incorporating *Land Cover Map 2015* ('*LCM2015*'; Rowland *et al.* 2017) and *CEH Land Cover® plus: Crops 2015* ('*crops2015*') data, using LCM2015 for pixels with no crops2015 data. For simplicity, we modified this land-use raster as follows:

- All arable crops were combined as 'arable' (we later calculated the 1-km square-specific combination arable crops – see below)
- Urban and suburban land-uses were combined as 'built'
- In The Fens, the small area of coniferous woodland was treated as broadleaf woodland, and the small area of saltmarsh was treated as neutral grassland
- In Salisbury Plain, the small area of neutral grassland, heather grassland and heather was treated as calcareous grassland

Next, we transformed the land-use raster such that all 1-km squares were either spared or farmed. In The Fens, spared blocks were identified as all nature reserves ≥1 km², whilst in Salisbury Plain spared blocks were identified as all contiguous areas of woodland, calcareous grassland and inland rock ≥1 km². Having identified these spared blocks, we classified core overlapping 1-km squares as spared and non-core overlapping squares as farmed, and modified their land-use composition as illustrated in **Fig. 2.1**.

Each spared 1-km square was then classified as either fen or wet grassland in The Fens or chalk grassland or woodland in Salisbury Plain, based on the dominant land cover. Within each spared habitat type we averaged land-use composition across all squares, removing the small area of built land and, in The Fens, replacing improved grassland with neutral grassland. Finally, for squares overlapping spared blocks (i.e.
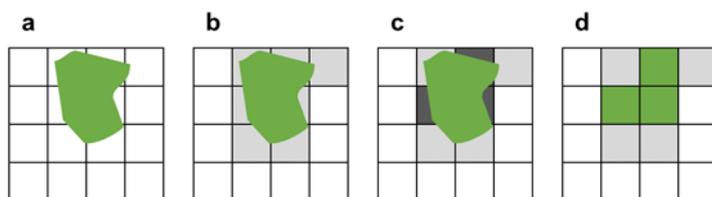
Fig 2.1 Graphical illustration showing how blocks of spared land were transformed to fit the regular 1-km grid. **a** identify spared blocks (green polygon) and calculate land-use composition. **b** identify 1-km squares which overlap spared block (light grey). **c** classify 1-km squares as 'spared' (dark grey) in descending order of overlap area, until the number of spared squares matched the area of each block (rounded to the nearest whole km^2) **d** apply land-use composition of spared polygon to spared squares (green), and apply land-use composition of non-spared portions of overlapping squares (visible light and dark grey areas in **c**) to non-spared overlapping squares (grey in **d**)

grey shaded squares in **Fig 2.1b**, including squares ultimately classified as spared (dark grey in **Fig 2.1c**) and farmed (light grey in **Fig 2.1c**)), we used a simple algorithm to update the 50-m land-use raster to reflect the modified land-use composition of each square (**Appendix 1A**). Non-overlapping squares (white in **Fig. 2.1b**) were classified as farmed and their land-use configuration was unchanged.

To estimate food production we first estimated the region-specific per-hectare yield of each land-use type in GJ edible energy following Finch *et al.* (2019). For arable, we calculated the square-specific composition of arable crops, expanding the area of each square by a 200 m buffer in The Fens and a 1100 m buffer in Salisbury Plain to account for the fact that crops move between parcels throughout the rotation (see Finch *et al.* 2019 for details). For pixels classified as 'arable other' we assumed the region-specific (and, in The Fens, soil-specific) composition of arable crop types not mapped by CEH *crops* using Defra gridded June census data (agcensus.edina.ac.uk). We then used the Farm Business Survey (Duchy College Rural Business 2017) to estimate the average regional yield of each arable crop. We converted harvested produce to edible products (using published feed conversion ratios for produce used as livestock feed; Cassidy *et al.* (2013)), and derived production from grazed land-uses based on published estimates (Tallowin & Jefferson

1999; Cassidy *et al.* 2013). After summing the production within each square (expressed per ha of unbuilt land) we applied a common regional correction factor to account for the area of uncropped features unaccounted for in satellite derived land-use maps. These corrections were based on the linear relationship ($R^2 > 0.98$) between yield estimated using 'remote' land-use areas and land-use areas 'clipped' to exclude uncropped areas for a subset of 1-km squares ($n = 28$ in The Fens, 23 in Salisbury Plain). *Business as Usual* production was thus determined by summing the total production across all squares.

To estimate the potential land-use of each square under alternative scenarios, we also calculated:

- For squares with less than 10% arable land, the proportional area of arable crops across all squares within 5 km, averaged with an inverse distance weighting (distances measured from centroid to centroid). This was used to determine the characteristics of new arable land under land sparing (see below);
- For squares with less than 10% non-arable land, the proportional area of non-arable land-uses across all squares within 5 km (calculated as above with an inverse-distance-weighted average). This was used to determine the

characteristics of new non-arable land under land sharing;

- For currently spared squares, the proportional land-use composition across all farmed squares within 5 km (calculated as above with an inverse-distance-weighted average). This was used to determine the characteristics of new farmed squares under land sharing.

Each alternative scenario involved modifying *Business as Usual* by either adding or removing a pre-defined number of spared 1-km squares, and then adding or removing arable 50-m pixels from farmed squares such that total regional production matched the production target (**Fig. 2.2**, **Fig. 2.3**).

Land sparing scenarios

Land sparing implies an increase in the number of spared squares, compensated for (where $P \geq 1$) by an increase in average farmland yields. We generated land sparing scenarios by sequentially converting farmed squares to spared ones.

The order in which we converted farmed squares, and the habitat type to which new spared squares were restored, varied according to a range of 'priority scenarios'. By default, and unless otherwise stated, we spared squares in ascending order of 2015 food production (thus minimising the opportunity cost of land sparing) and restored new spared squares to the habitat type of the nearest currently spared square (*Least cost*). Under the *Adjacent* scenario we first prioritised restoration in ascending order of distance to nearest currently spared square. For each region, three additional priority plans were developed, reflecting local priorities and visions. In The Fens, these were: *Fens4Future* in which squares >50% covered by the 'Fens for the Future' target areas for habitat restoration (Fens for the Future 2012) were prioritised first for restoration to the habitat type of the nearest currently spared square; *Deep peat*, in which squares >50% covered by peat soil were prioritised first for restoration to fen; and *Washland* in which squares >50%

covered by a 500 m buffer of all waterbodies (rivers, canals and surface water transport; Environment Agency 2014) were prioritised first for restoration to wet grassland. In Salisbury Plain, the priority plans were: S*teppingStones*, in which squares >50% covered by the 'Stepping Stones' Nature Improvement Area plan were first prioritised for restoration to the habitat type of the nearest currently spared square; *Groundwater* in which squares >50% covered by a groundwater source protection zone (Zone 3, total catchment; Environment Agency 2015) were prioritised first for restoration to woodland; and *Chalk stream* in which squares >50% covered by a 1000 m buffer of all chalk stream SSSIs (River Till and River Avon System, boundaries from Natural England) were prioritised first for restoration to chalk grassland.

Each new spared square thus acquired the average land-use composition (and yield) of the corresponding habitat type. To compensate for the loss of food production owing to the conversion of farmed squares to spared semi-natural habitat, we converted non-arable 50-m pixels in farmed squares to arable at random, until total regional production matched the production target. The yield of each new arable pixel reflected the square-specific composition of arable crops (or, for squares with <10% arable land, the inverse-distance-weighted average composition within 5 km, as described above). Built land, inland rock and freshwater were protected from conversion to arable. We used a simple algorithm to update the 50-m land-use raster to reflect these changes (**Appendix 1A**).

Land sharing scenarios

In contrast to land sparing, land sharing implies a reduction in the number of spared squares, allowing (where $P \leq 1$) a reduction in average farmland yields. We generated land sharing scenarios by sequentially converting spared squares to farmed ones in descending order of potential yield
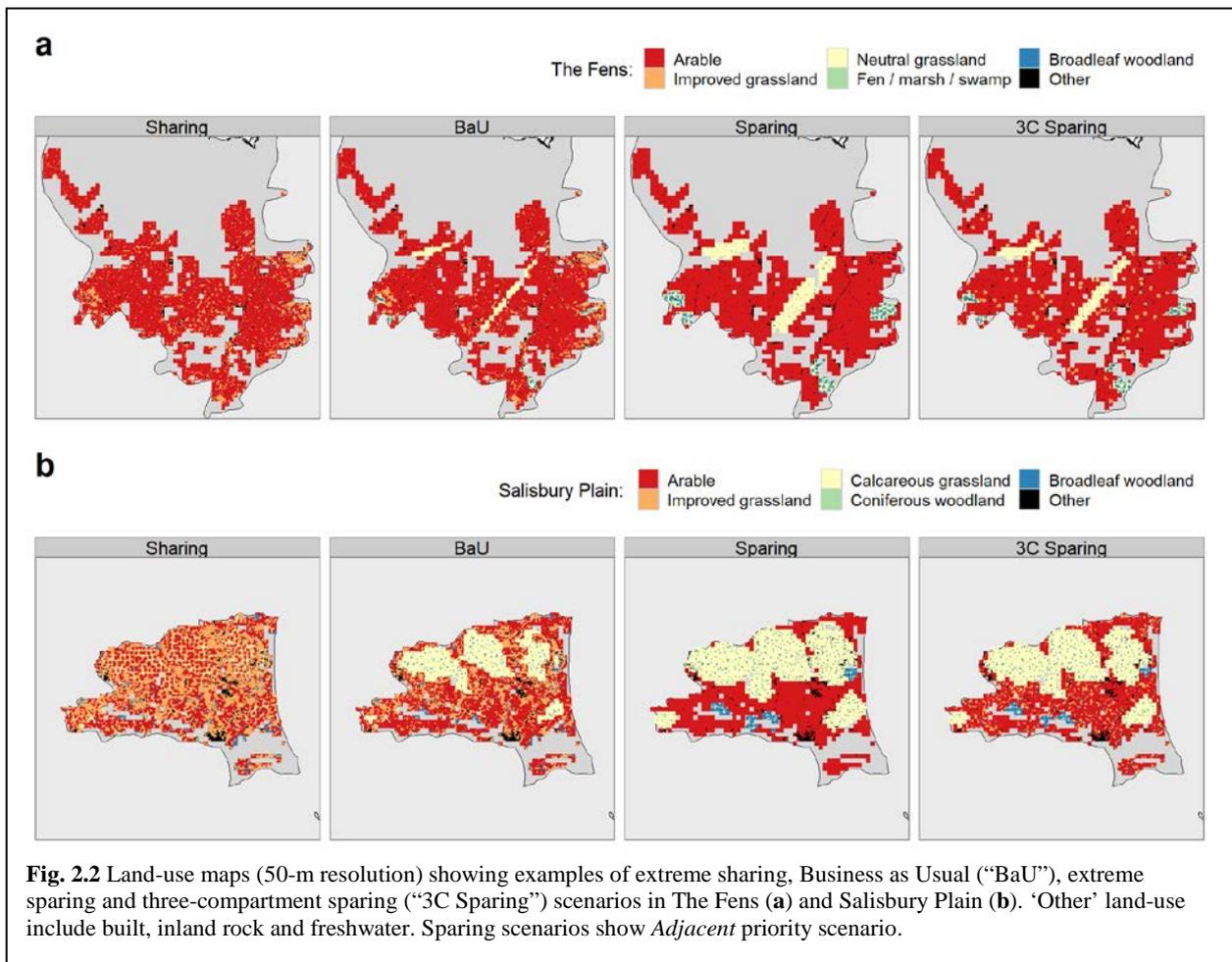
Fig. 2.2 Land-use maps (50-m resolution) showing examples of extreme sharing, Business as Usual ("BaU"), extreme sparing and three-compartment sparing ("3C Sparing") scenarios in The Fens (**a**) and Salisbury Plain (**b**). 'Other' land-use include built, inland rock and freshwater. Sparing scenarios show *Adjacent* priority scenario.

(according to the potential land-use composition calculated above), starting with spared squares immediately adjacent to farmland. To reduce farmland yields following the conversion of spared squares to farmed ones, we converted arable 50-m pixels in farmed squares to non-arable at random, until total regional production matched the production target. The land-use of new non-arable pixels was selected randomly, weighted according to the square-specific composition of non-arable land-uses (or, for squares with <10% non-arable land, the inverse-distance-weighted average composition within 5 km, as described above) but ignoring built, inland rock and freshwater. We used a simple algorithm to update the 50-m land-use raster to reflect these changes (**Appendix 1A**).

Three-compartment sparing

For extreme sparing scenarios (i.e. where all non-arable pixels have been converted

to arable, and the area of spared land is maximised) we generated corresponding 'three-compartment sparing' scenarios in which a fixed number of farmed squares (equal to the number of spared squares) were converted to 'low-yield farmland'. The yield of low-yield farmland was set to 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 yield higher than the target yield of low-yield farmland), achieving the necessary yield reduction by replacing arable pixels with non-arable pixels, as described above for land sharing. In order to maintain overall production, we then sequentially converted pairs of spared and low-yield farmland squares to high-yield farmland, until total production matched *P*. As above, we used a simple algorithm to update the 50-m land-use raster to reflect
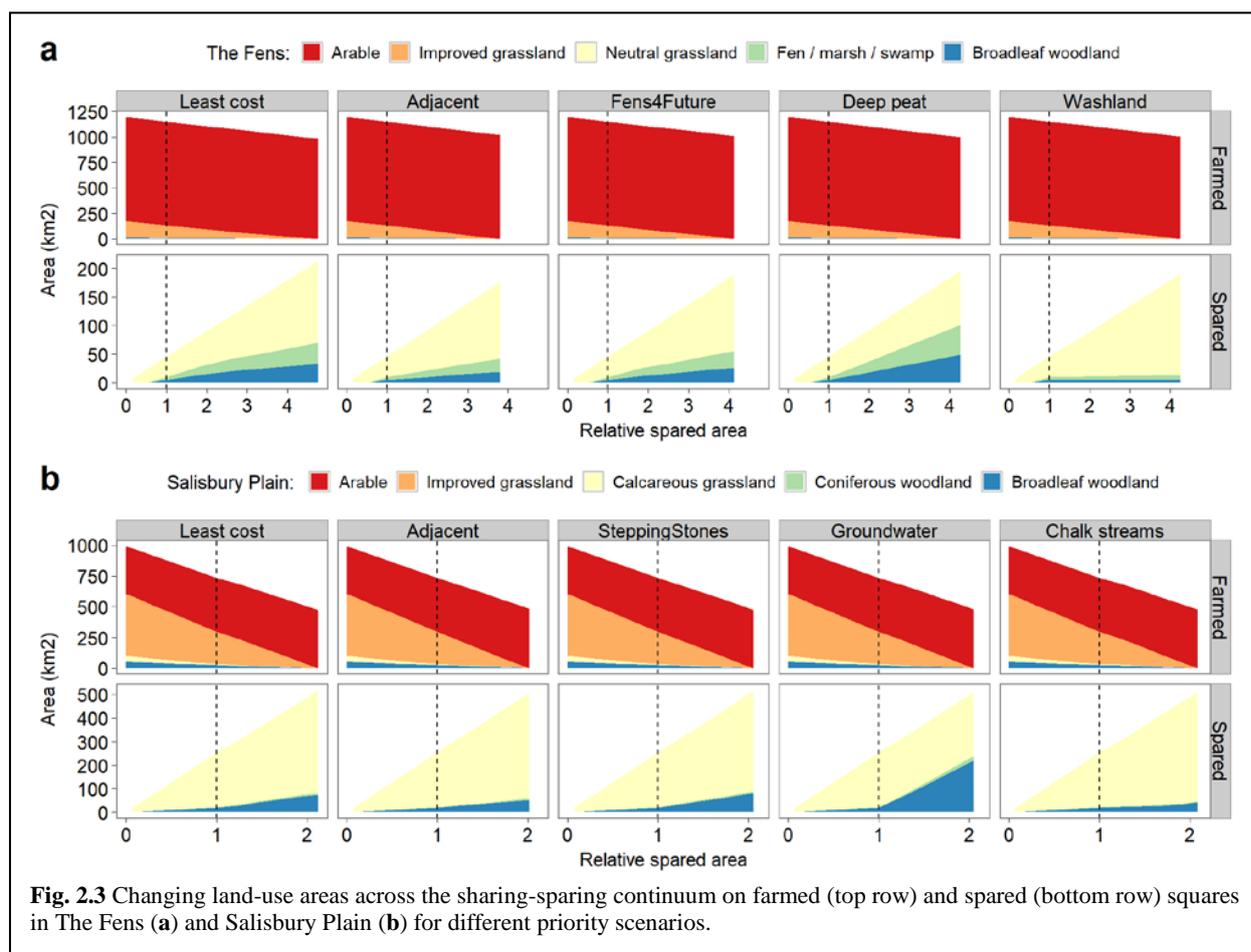
Fig. 2.3 Changing land-use areas across the sharing-sparing continuum on farmed (top row) and spared (bottom row) squares in The Fens (**a**) and Salisbury Plain (**b**) for different priority scenarios.

these changes (**Appendix 1A**). To summarise, three-compartment sparing scenarios contained an equal number of spared (fen or wet grassland in The Fens, chalk grassland or woodland in Salisbury Plain) and low-yield farmland squares, but fewer spared squares than under extreme land sparing.

Yield Growth

So far, our scenarios include no change in per hectare yields of agricultural land-uses; production increases on farmed squares arise through an increase in the proportion of arable land within farmed squares. However, depending on biophysical, technical and socioeconomic factors, yield growth of up to 1.3% per annum may be achievable (Lamb *et al.* 2016b). The environmental consequences of increasing production through land-use change (i.e. increasing the proportion of arable land within farmed squares) *versus* per hectare yield growth may differ. Rather than substituting land-use change with yield growth, we use yield

growth to extend our extreme sparing scenarios, to evaluate a land-sparing upper limit (methods in **Appendix 1C**, results in **Appendix 1F**).

Bird population sizes

We used the species- and region-specific density-yield curves developed by Finch *et al.* (2019) to estimate the regional population size of breeding bird species under each scenario. These curves were fitted to data from 34 farmland and fen sites in The Fens and 108 farmland and chalk grassland sites in Salisbury Plain, primarily representing 1-km Breeding Bird Survey squares (Harris *et al.* 2017). Density-yield curves were used to predict density (and thus population size) in farmed squares (of varying yield) and spared squares (fen or chalk grassland). We used comparable data (representing point estimates of habitat-specific density, rather than density-yield curves) to estimate densities in wet grassland and woodland, and in The Fens

Table 2.1. Rare species of fen and/or wet grassland absent from Breeding Bird Survey sites. The final two columns represent arbitrary density estimates (either present or absent) for fen and wet grassland.

Common name	Scientific name	Fen	Wet grassland
Spotted Crake	*Porzana porzana*	1	1
Corncrake	*Crex crex*	0	1
Garganey	*Anas querquedula*	1	1
Golden Oriole	*Oriolus oriolus*	1	0
Pintail	*Anas acuta*	0	1

we assumed an arbitrary relative density of 1 in wet grassland and/or fen for five additional species listed in **Table 2.1**. These species were undetected at bird survey sites, but there is good evidence that they bred in The Fens during our study period (Holling & The Rare Breeding Birds Panel 2014; 2015; 2016; and 2017).

For farmed squares with a yield greater than the maximum yield of sites used to parameterise density-yield curves, we extrapolated density-yield curves to estimate yield-specific population densities. However, for species for which the density-yield curve was increasing at the highest-yield survey sites, we assumed no additional increase in density beyond the maximum recorded in those sites. In addition, we applied a penalty to these high-yielding sites, so that the predicted density was reduced proportionally to the difference between the yield of the site and the maximum yield of bird survey sites (i.e. for a site with yield 10% higher than the maximum yield of bird survey sites we reduced predicted density by 10% compared to that predicted by the density-yield curve).

In total, we estimated the population size of 96 species in The Fens and 76 species in Salisbury Plain (excluding species detected at only 1 farmland survey site, for which density-yield curves were deemed less reliable). We summarised population change as the geometric mean ratio between each scenario and the *Business as Usual* scenario, averaged across all species. We also calculated the geometric mean ratio separately for species estimated to have smaller populations under a pre-agricultural baseline than under a food production scenario ('winners') and those estimated to have smaller populations under all food production scenarios than under the pre-agricultural baseline ('losers'; after Finch *et al.* 2019, and assuming a 50:50 ratio of fen and wet grassland in The Fens and chalk grassland and woodland in Salisbury Plain, at P = 1).

Global warming potential

We estimated the net annual global warming potential (GWP_{100}) of each scenario compared to *Business as Usual*, based on the total area of each land-use. Greenhouse gas fluxes associated with land-use were assumed to be annually constant, and included greenhouse gas emissions from fertiliser application, livestock (manure and enteric fermentation), and (in The Fens) drained organic soil, and carbon sequestration from biomass accumulation in woodland and (in The Fens) peat formation. Greenhouse gas fluxes associated with land-use change (compared to *Business as Usual*) were annually variable, representing either the diminishing loss or gain of soil carbon in mineral-based soils or (in the Fens only), methane spikes following re-wetting. Annually variable fluxes were annualised over a 50-year period, assuming a 0% discount rate.

Emissions factors (tonnes CO_2eq per hectare) were generally estimated using IPCC Tier 1 methodologies, as described in **Appendix 1B**. GWP was summed across

each region and expressed relative to *Business as Usual*, where values less than 1 reflect an overall reduction in net greenhouse gas emissions compared to 2015 land-use.

Nutrient export

We estimated nitrogen (N) and phosphorus (P) export using the InVEST nutrient-delivery ratio (NDR) model (v 3.5.0 Sharp *et al.* 2018), applied to all watersheds which intersect our study regions in The Fens and Salisbury Plain (**Fig. 2.4**). The NDR model is a spatially-explicit model which describes the movement of nutrients through three-dimensional space. The landscape is divided into pixels, with each pixel assigned a land-use and each land-use assigned a nutrient loading (i.e. N and P application rates, kg ha^{-1} yr^{-1}) and a corresponding nutrient retention efficiency (representing the proportional retention of N or P, largely determined by vegetation properties). This loading follows a 'flow path' (according to a digital elevation model) into a watercourse. Delivery factors are calculated for each pixel based on the properties of pixels belonging to the same flow path (e.g. slope, retention efficiency, etc.). Total nutrient export is then computed by summing the pixel-level nutrient contributions. In general, a pixel's nutrient export increases with increasing nutrient load, slope and runoff, and decreases with increasing retention efficiency, though these effects are modified by the properties of the flow path.

We used CEH's Integrated Hydrological Digital Terrain Model (IHDTM, 50-m horizontal resolution, units = m; Morris & Flavin 1990) and interpolated average total observed annual precipitation for 2005–2015 (1-km resolution, units = mm; Tanguy *et al.* 2016). The IHDTM was modified by filling to eliminate sinks (cells with undefined drainage direction, being lower than all surrounding cells) and combined with a digital watercourse network (Moore, Dixon & Flavin 1994) to ensure accurate routing of flow paths along known watercourses.

We first calibrated the NDR model using current (2015) land-use, derived from a combination of *LCM2015* and *crops* as described above. Each 50-m pixel was thus assigned to one of 18 land-use categories, with each 1-km square's 'arable' area associated with a (potentially) unique composition of arable crops.

For each of the 17 non-arable land-uses, and for each square's arable area (reflecting an area-weighted average of the composition of different arable crops within that square) we estimated N and P loading and retention coefficients. For each LCM landcover we used loading and retention rates for N and P as described in Redhead *et al.* (2018). For arable, we estimated the crop-specific loading and retention rates for N and P as follows. The 2013 British Survey of Fertiliser Practice (Defra 2014) reports an overall application rate on arable land of 138 kg ha^{-1} for N and 25 kg ha^{-1} for P_2O_5 across England & Wales. The equivalent applications rates in Wessex (for Salisbury Plain) are 120 (0.87 relative to England & Wales) and 22 (0.88) and in Anglia (for The Fens) they are 144 (1.04) and 33 (1.32). Redhead *et al.* (2018) used nutrient loading rates on arable land of 35.2 kg N ha^{-1} and 1.52 kg P ha^{-1}, implying that 26% and 14% of applied N and P, respectively, are 'loaded' into the environment. We took crop-specific N and P application rates for England & Wales from the British Survey of Fertiliser Practice (2013) and corrected these according to the regional relative application rates described above. We then calculated loading rates by multiplying N and P application rates by 0.26 and 0.14, respectively.

Following Redhead *et al.* (2018), we set critical flowlength to 50 m (the resolution of the input land-use raster), the threshold accumulation parameter to 1000 and the Borselli *k* parameter to 2, and assumed no subsurface flow.

Fig. 2.4. Catchments (black) and watercourses (white) intersecting focal 1-km squares (grey) in The Fens (**a**) and Salisbury Plain (**b**).

Fig. 2.5 Relationship between modelled (x-axis) and measured (y-axis) nitrogen and phosphorus export for catchments in The Fens and Salisbury Plain. Black line shows linear regression fit (shaded ribbon = S.E.), and dashed line shows 1:1, on log-log scale. For nitrogen, slope estimate = 1.0 ± 0.12 ($R^2 = 0.91$); for phosphorus, slope estimate = 1.1 ± 0.13 ($R^2 = 0.88$).

We validated these parameter values using measured nutrient and flow data from catchments within our study regions. Data used for validation were derived from the UK Environment Agency's Water Information Management System (WIMS). Because these data represent measured nutrient concentrations, we located WIMS sites with coincident information on river flow from the National River Flow Archive (NRFA; Fry & Swain 2010). Total annual nutrient load per year was calculated from the WIMS and NRFA data for each catchment using the Beale Ratio Estimator equation, an established method for extrapolating loads from intermittent measurement data. Further details on estimating total nutrient loads from WIMS and NRFA data can be found in Redhead *et al.* (2018). The correspondence across catchments between export modelled using NDR and estimated from measured data was extremely strong (**Fig. 2.5**), giving confidence that the NDR will reliably quantify relative differences in nutrient export between scenarios.

Finally, we substituted the 2015 land-use raster with each alternative scenario's land-use (holding land-use in cells outwith our focal 1-km squares at 2015 values), and ran the NDR model with all other parameters as described above. We calculated the total pixel-level export of N and P across all pixels (including those outwith our focal 1-km squares; **Fig. 2.4**), and expressed this relative to *Business as Usual*.

Results

At current production ($P = 1$), extreme land sharing resulted in (by definition) a complete loss of spared habitat, facilitating a 4% and 26% reduction in mean farmland yields compared to *Business as Usual* in The Fens and Salisbury Plain, respectively (**Fig. 2.2**, **Fig. 2.3**, **Fig. 2.6**). By contrast, extreme land sparing (under the *Least cost* scenario) resulted in a 377% increase in spared area in The Fens (facilitated by a 17% increase in mean farmland yields), and a 112% increase in spared area in Salisbury Plain (facilitated by a 57% increase in mean farmland yields; **Fig. 2.6**). These differences reflect the differing current area of spared land in the two regions (47 km^2 in The Fens, 257 km^2 in Salisbury Plain; **Fig. 2.2**). Regional priority scenarios resulted in slightly less spared land under extreme sparing compared to *Least cost* (**Fig. 2.6**), and differed in the ratio of habitats represented on new spared land (**Fig. 2.3**, **Fig. 2.5**), as well as the location of new spared land. By definition, three-compartment sparing restored a smaller area of spared semi-natural habitat compared to extreme sparing (**Fig. 2.6**).

Birds

In both regions, geometric mean relative population size was maximised under scenarios which increased the area of spared land (except for *Washland* in The Fens, for which all alternative scenarios resulted in average population declines; **Fig. 2.7**).

In The Fens, geometric mean relative population size peaked under either extreme land sparing (*Deep Peat*) or three-compartment sparing (*Least cost* and *Fens4Future*), with mean population size 34–68% higher compared to *Business as Usual,* depending on the priority scenario (**Fig. 2.7**). Across all priority scenarios, *Deep Peat* (in which fen is promoted over wet grassland on spared land) performed best. In Salisbury Plain, geometric mean relative population size peaked under three-compartment sparing regardless of the priority scenario, with mean population size 6–28% higher compared to *Business as Usual*, depending on the priority scenario (**Fig. 2.7**). The next-best scenario was an intermediate land-sparing strategy, with mean population size 1–14% higher compared to *Business as Usual*.

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, for all priority scenarios except *Washland* in The Fens (**Fig. 2.8**). Extreme sparing resulted in average populations 85–169% and 10–64% higher compared to *Business as Usual* in The Fens (excluding *Washland*) and Salisbury Plain, respectively (**Fig. 2.8**).

Among species classified as winners (40% of species in The Fens, 58% in Salisbury Plain), extreme land sharing maximised geometric mean relative population size in The Fens, where average populations were 5% higher compared to *Business as Usual* (**Fig. 2.9**). In contrast, geometric mean relative population size of winners was maximised by three-compartment sparing in Salisbury Plain (15–17% increase; **Fig. 2.9**).
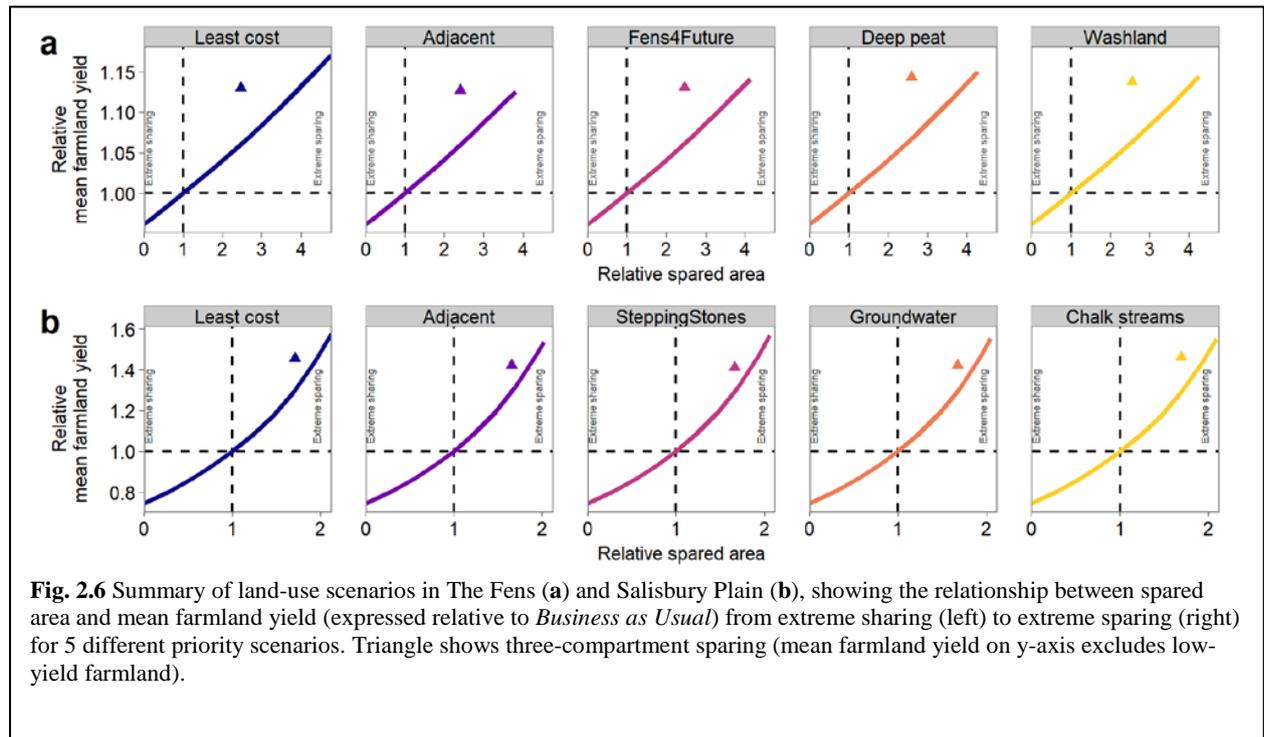
Fig. 2.6 Summary of land-use scenarios in The Fens (**a**) and Salisbury Plain (**b**), showing the relationship between spared area and mean farmland yield (expressed relative to *Business as Usual*) from extreme sharing (left) to extreme sparing (right) for 5 different priority scenarios. Triangle shows three-compartment sparing (mean farmland yield on y-axis excludes low-yield farmland).
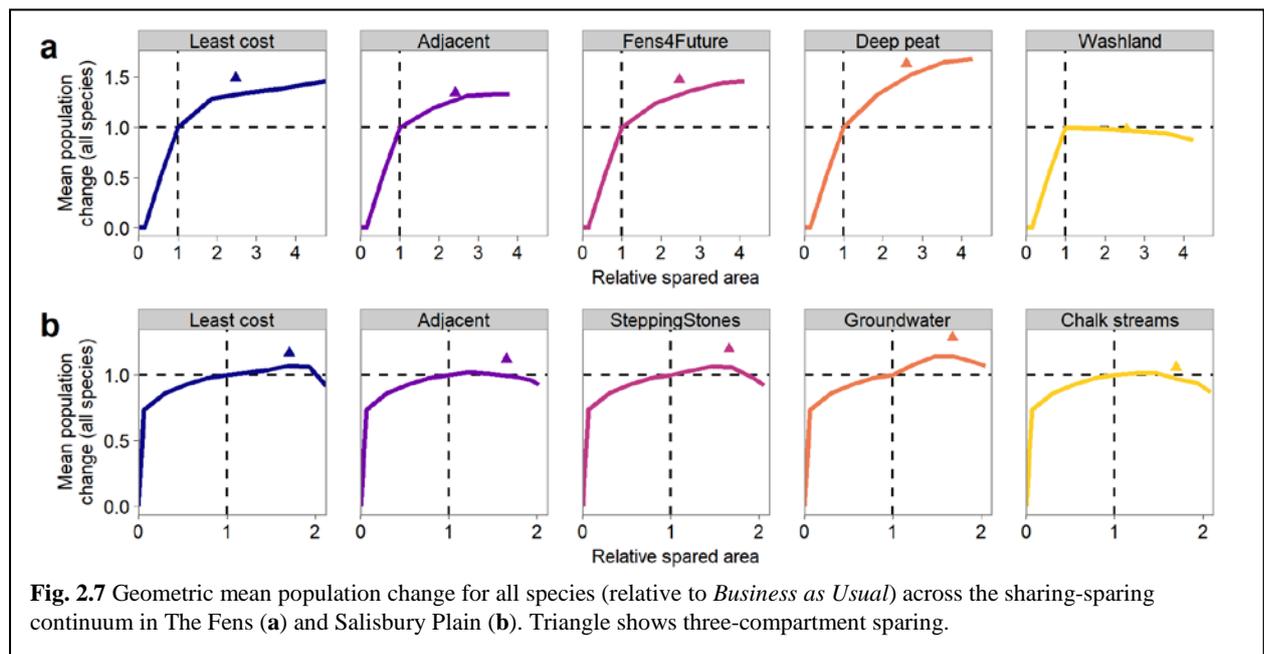
Fig. 2.7 Geometric mean population change for all species (relative to *Business as Usual*) across the sharing-sparing continuum in The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.
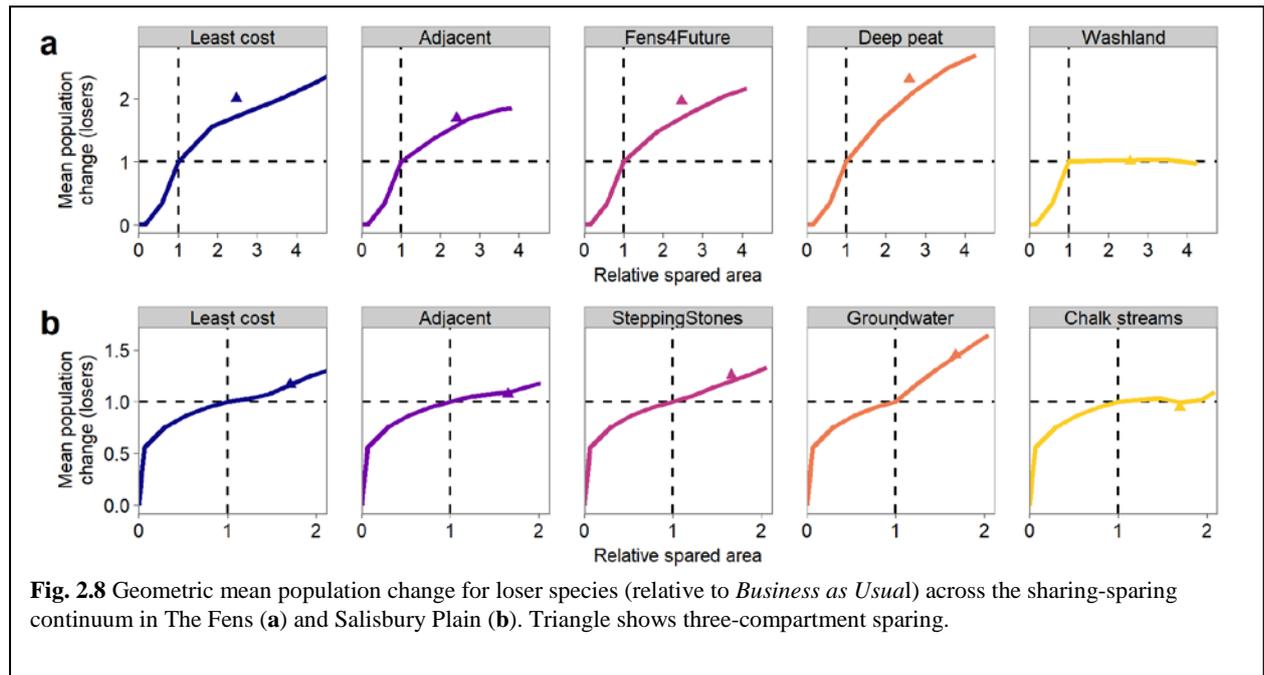
Fig. 2.8 Geometric mean population change for loser species (relative to *Business as Usual*) across the sharing-sparing continuum in The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.
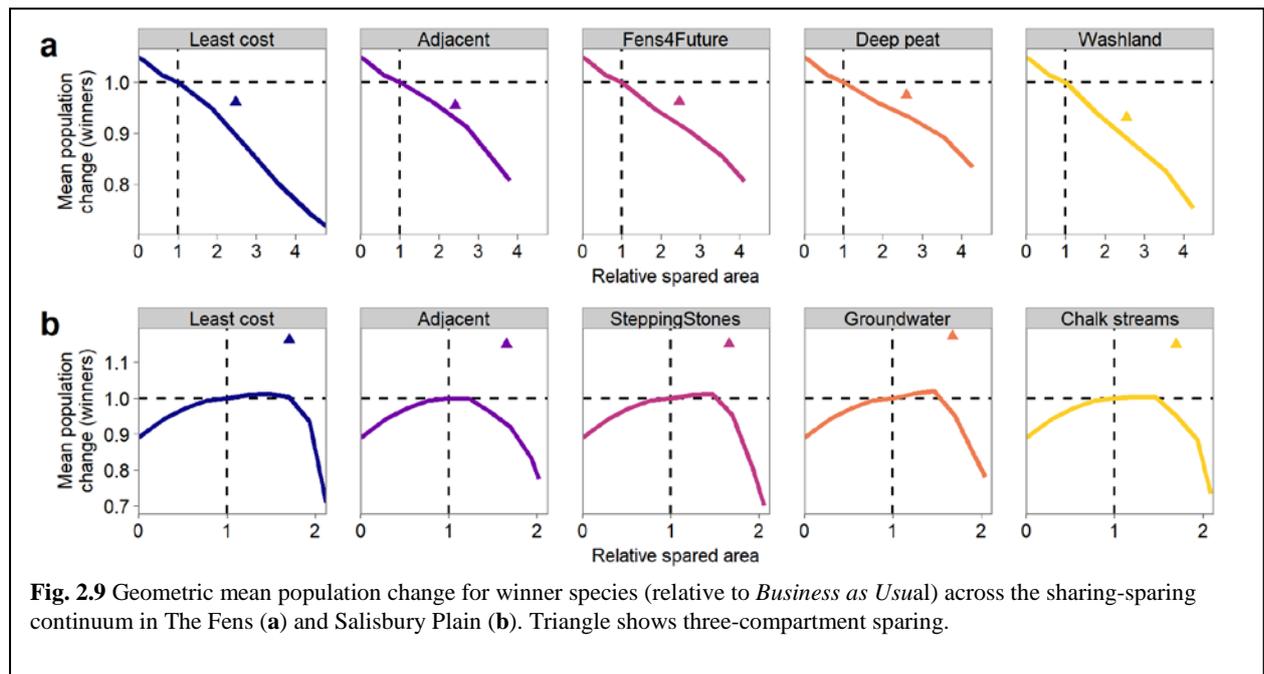
Fig. 2.9 Geometric mean population change for winner species (relative to *Business as Usual*) across the sharing-sparing continuum in The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.

Global warming potential

In both regions, land sharing resulted in a net increase in total regional GWP, driven by the loss of carbon sequestered in spared habitats (and, in The Fens, the draining of wet organic soil). In contrast, land sparing typically reduced GWP, with sequestration from habitat restoration on spared land (and re-wetting of organic soil in The Fens) outweighing the additional emissions associated with higher-yield farming (**Fig. 2.10**).

In The Fens, there was variation between different priority scenarios in the response of GWP across the sharing-sparing continuum, largely reflecting the fate of organic soils. The *Deep peat* scenario (and, to a lesser extent, *Fens4Future*), in which peat soils were prioritised for restoration to wet fen, resulted in strong reductions in net GWP under extreme sparing (41% reduction compared to BaU under *Deep peat*), whereas scenarios which restored wet grassland or which continued to cultivate peat soils resulted in higher net GWP (**Fig. 2.10**). In Salisbury Plain, the response of GWP across the sharing-sparing continuum was consistently negative (i.e. more land sparing = lower GWP), but the *Groundwater* scenario (prioritising woodland over chalk grassland)

reduced GWP to the extent that net GWP was negative under extreme land sparing (**Fig. 2.10**).

These conclusions were robust to uncertainty in the emissions factors used (**Appendix 1D**).

Nutrient export

The response of nitrogen and phosphorus export across the sharing-sparing continuum varied substantially between regions and priority scenarios. In The Fens, N export was minimised under land sharing for *Adjacent*, *Washland* and *Fens4Future*, (though extreme land sparing came close for *Washland* and *Fens4Future*) but land sparing for *Least cost* and *Deep peat* (**Fig. 2.11**). In Salisbury Plain, land sharing minimised N export under all priority scenarios, but average N export under land sparing varied substantially between scenarios (**Fig. 2.11**). Overall, N export was lowest under *Least cost* extreme land sparing in The Fens and under land sharing in Salisbury Plain.

Phosphorus export showed a similar response to N in The Fens, but not in Salisbury Plain, where it was minimised under land sharing for *Adjacent,* but under various land sparing strategies under all other priority scenarios (**Fig. 2.12**). Overall,

Fig. 2.10 Net GWP (relative to *Business as Usual*) across the sharing-sparing continuum in The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.
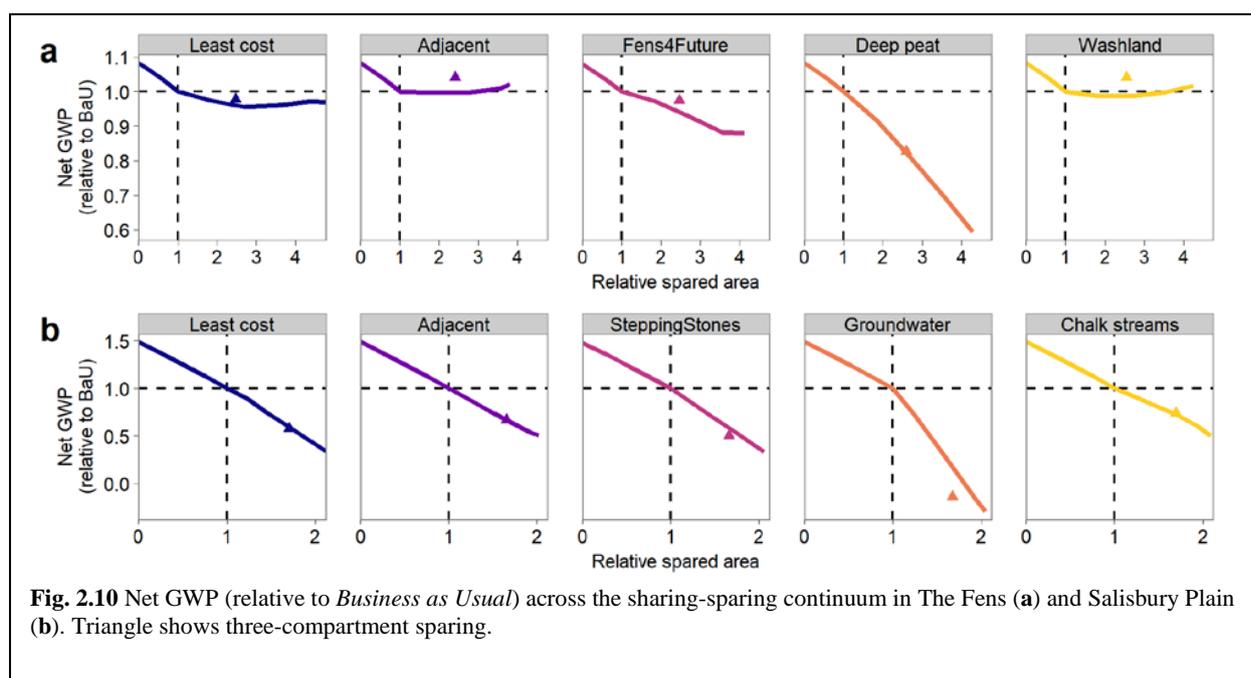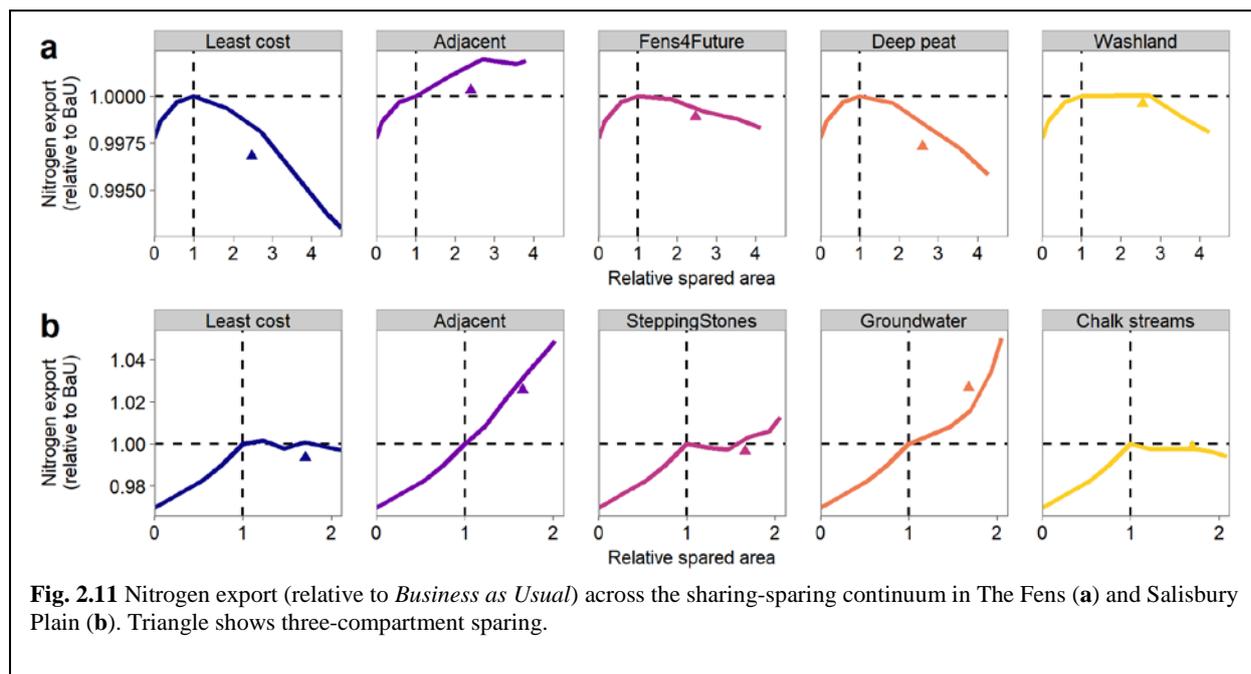
Fig. 2.11 Nitrogen export (relative to *Business as Usual*) across the sharing-sparing continuum in The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.
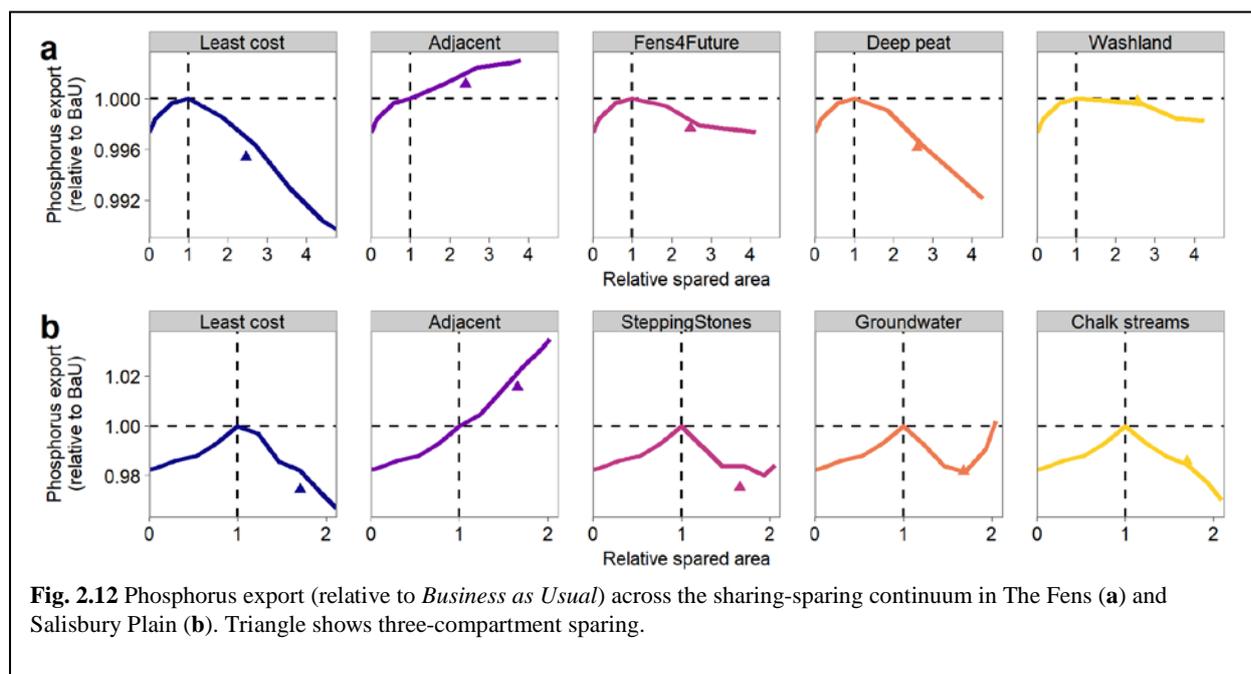
Fig. 2.12 Phosphorus export (relative to *Business as Usual*) across the sharing-sparing continuum in The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.

P export was lowest under *Least cost* extreme land sparing in both regions (**Fig. 2.12**).

Quadruple-win strategies

There were several strategies which resulted in improvements in all four outcomes compared to *Business as Usual* (i.e. geometric mean relative population size > 1, relative GWP < 1, relative N export < 1, and relative P export < 1). In both regions, these 'quadruple-win' strategies involved a shift towards land sparing (**Fig. 2.13**).

Quadruple wins were delivered by intermediate–extreme land sparing and three-compartment sparing under *Least cost*, *Fens4Future* and *Deep peat* in The Fens, and by intermediate and three-compartment sparing under *Least cost*, *SteppingStones* and *Chalk streams* in Salisbury Plain (**Fig. 2.13**).

Discussion

The response of our 4 environmental outcomes (birds, GWP, N export and P
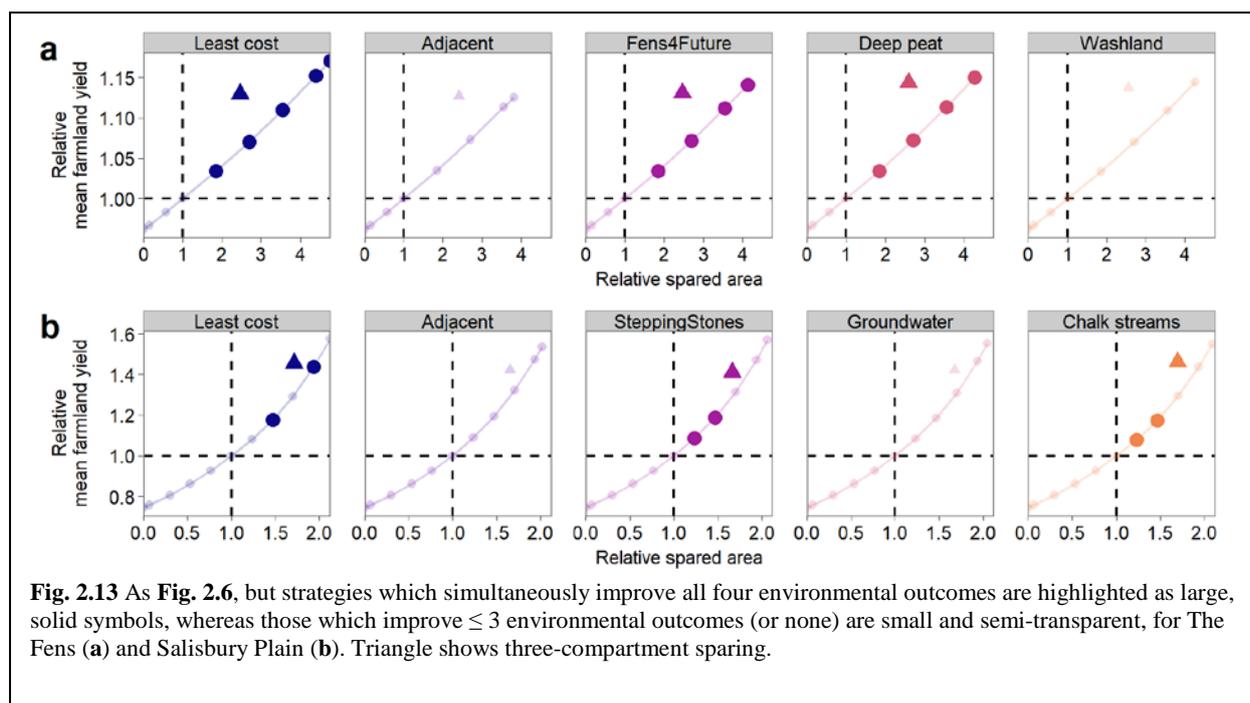
Fig. 2.13 As **Fig. 2.6**, but strategies which simultaneously improve all four environmental outcomes are highlighted as large, solid symbols, whereas those which improve ≤ 3 environmental outcomes (or none) are small and semi-transparent, for The Fens (**a**) and Salisbury Plain (**b**). Triangle shows three-compartment sparing.

export) across the sharing-sparing continuum – and among different regional priority scenarios – was variable. Nonetheless, several strategies – all involving a shift towards land sparing – delivered improvements in all four outcomes, relative to *Business as Usual*. These quadruple-win strategies included intermediate–extreme land sparing and three-compartment *sparing* in The Fens, and intermediate (but not extreme) land sparing and three-compartment sparing in Salisbury Plain.

For birds, this study supports our previous conclusions based on discrete, non-spatial scenarios (Finch *et al.* 2019). Increases in geometric mean population size relative to *Business as Usual* are predicted under extreme land sparing in The Fens, and intermediate land sparing and three-compartment sparing in both regions. Loser species showed a consistent positive response across the sharing-sparing continuum, whilst the response of winner species varied between regions, with loser species achieving maximum geometric mean relative population size under land sharing in The Fens but intermediate land sparing in Salisbury Plain.

In The Fens, loser species (and thus all species on average), saw higher geometric mean relative population size under *Deep peat* (which promoted fen over wet grassland), whereas *Washland* (promoting wet grassland over fen) performed poorly. This corroborates our previous findings, in which a 2:1 ratio of fen to wet grassland on spared land outperformed a 1:1 or 1:2 ratio (Finch *et al.* 2019). This is unsurprising, given the higher species richness of fen (a complex mosaic of reed swamp, wet woodland and open water) compared to wet grassland (which, nonetheless, supports breeding populations of several species of high conservation concern, including Black-tailed Godwit *Limosa limosa*, Lapwing *Vanellus vanellus* and Snipe *Gallinago gallinago*).

The consequences of land sharing and land sparing for global warming potential were consistent across all priority scenarios in Salisbury Plain, with net GWP increasing (i.e. worsening) under land sharing and reducing (i.e. improving) under land sparing, especially when woodland was promoted on spared land. In contrast, there was substantial variation in GWP between priority scenarios in The Fens. Scenarios which promoted wet grassland over fen resulted in higher net GWP, because wet

grassland contributes little to carbon sequestration through peat formation. In addition, strategies which prioritised land sparing on remaining peat soil avoided the substantial carbon emissions associated with their continued cultivation.

For nitrogen and phosphorus export, the best strategy depended as much on the priority scenario as on whether a sharing or sparing strategy was adopted.

In both regions the *Adjacent* priority scenario resulted in highest nitrogen and phosphorus export under extreme land-sparing. Under this scenario, existing spared areas were expanded, leading to a strong polarisation between discrete areas of farmed and spared land. In contrast, *Least cost* was among the best-performing scenarios for both nutrients under extreme land sparing. Under this scenario, squares are spared according to their 2015 yield rather than any particular spatial pattern, resulting in a haphazard distribution of spared land, along different flow paths. These differences suggest that 1) restored habitat which is adjacent to existing natural habitat may be redundant in terms of nutrient capture, and 2) natural land-covers adjacent to farmland (whether as isolated spared squares or within shared farmed squares) are important for intercepting nutrients before they enter a watercourse. This highlights the importance of constructing spatial land-use scenarios, and suggests that the consequences of land sharing and land sparing *per se* are hard to predict for diffuse pollution. Instead, the strategic placement of natural and seminatural land covers with respect to nutrient sources appears to be just as important. This conclusion may also apply to natural flood management, where the misplacement of river-floodplain restoration can exacerbate flooding by synchronising previously asynchronous flood peaks (Dixon *et al.* 2016).

At higher production targets, most environmental outcomes worsened, although bird species classified as winners

in Salisbury Plain achieved higher geometric mean relative population size at higher food production targets (**Appendix 1E**).

In summary, our results support our previous conclusion that three-compartment sparing maximises bird conservation outcomes in the face of regional food production requirements. In addition, we show that three-compartment sparing (as well as extreme land sparing in The Fens and intermediate land sparing in both regions) could deliver multiple environmental benefits. However, these additional benefits depend on the spatial arrangement of spared land and the types of land cover promoted on spared land.

Our scenarios are designed to represent a range of plausible but increasingly extreme alternative land-use visions for each region. Several factors may constrain the realisation of these scenarios in practice. In The Fens, wetland restoration is complicated by access to water during the late spring and summer months. We were unable to estimate the potential availability of water for wetland restoration, though we note that the Ouse Washes is currently in an unfavourable state due to an *excess* of water in spring, which could potentially be diverted elsewhere. The topography of The Fens also presents an engineering issue; any re-wetting project must avoid negative impacts on neighbouring farmland.

In Salisbury Plain, our extreme land-sharing scenarios are unlikely to be compatible with military training requirements, as the majority of the currently spared area is currently used for military training exercises. Land sparing, in contrast, involves an increase in the area of chalk grassland, leveraged through a reduction in the area of improved grassland within farmland; this may require changes to husbandry practices, because the livestock which currently graze the chalk grassland are supported by improved grassland during winter months.

Section 3: Considering species importance (Module 1B)

Introduction

In order to evaluate the relative merits of land sharing and sparing, we previously estimated the regional breeding population size of 101 bird species in The Fens and 83 in Salisbury Plain for a range of food production scenarios spanning the sharing-sparing continuum, as well as for 'three-compartment' sparing (Finch *et al.* 2019; **Fig. 1.1**). To summarise results across species, we calculated (for each scenario) the geometric mean relative population size. Across all species, geometric mean population change was maximised under three-compartment sparing (followed by intermediate–extreme land sparing) in The Fens and under intermediate sparing (followed by three-compartment sparing) in Salisbury Plain (Finch *et al.* 2019). Under this approach, all species contribute equally to the geometric mean. Clearly, however, some species are of higher conservation priority than others. Various measures have been developed to identify species of conservation importance or priority.

In the UK, the *Birds of Conservation Concern* (*BoCC*) assessment places species on Green, Amber and Red lists reflecting increasing levels of conservation concern, measured against standardised criteria (Eaton *et al.* 2015). Other *Red Lists* follow guidelines issued by the International Union for Conservation of Nature (IUCN) in assessing extinction risk at national (Great Britain; Stanbury *et al.* 2017), continental (Europe; BirdLife International 2015) and global (BirdLife International 2018) scales. Geographic range size is also a strong predictor of extinction risk among vertebrate species (Ripple *et al.* 2017), and is often used as a measure of conservation priority (Bibby 1999). Governments can also identify lists of important species, such as the Section 41 (England) and Section 42 (Wales) list of priority species under the

NERC Act 2006, though these typical use similar criteria to the other listings.

Species, and the environmental conditions with which they are associated, are not distributed uniformly across space. When evaluating regional scenarios, species for which the focal region is especially important – endemic species being the most extreme case of this – should perhaps therefore be given priority. *The Bird Atlas 2007–11* (Balmer *et al.* 2013) produces estimates of relative breeding abundance for all 10-km squares across Great Britain, which can be used to estimate the proportion of the total British breeding population of any species supported by a focal region. According to these data we estimate, for example, that The Fens supports a high proportion of the national breeding population of species such as Spotted Crake *Porzana porzana* (72%), Common Crane *Grus grus* (45%) and Bittern *Botaurus stellaris* (26%), whereas Salisbury Plain supports important numbers of Stone-curlew *Burhinus oedicnemus* (43%), Corn Bunting *Emberiza calandra* (7%) and Quail *Coturnix coturnix* (6%). We define these species as having high 'endemism' scores, though we recognise that none are strictly endemic.

In this module, we explore whether accounting for species conservation status, range size, or endemism influences our conclusions regarding the consequences of land sharing and land sparing for breeding birds in The Fens and Salisbury Plain.

Additionally, we develop a more flexible approach to the three-compartment model. Previously, under 'three-compartment sparing', we set the yield of high-yield farmland to the observed regional maximum; the area of low-yield farmland to the area of spared (semi-)natural habitat; and the yield of low-yield farmland to the median yield at which species with hump-shaped density-yield curves reach peak density (**Fig. 1.1b**). Here, we develop food production strategies in which these scenario parameters are free to take any

feasible value (i.e. any value which meets the production target). We identify the optimal strategy as that which maximises overall geometric mean population change, then explore how this optimum strategy changes for different species groups.

Methods

Study system, data collection, and scenario design/evaluation

This module is a direct extension of our previous work (Finch *et al.* 2019). We use the same study regions (The Fens and Salisbury Plain), the same species density-yield relationships and (initially) the same food production scenarios (as illustrated in **Fig. 1.1**), for which we estimated the regional population size of each breeding species in each region.

Species weightings

For each breeding species (101 in The Fens, 83 in Salisbury Plain) we weighted species differently based on the following attributes:

1. *BoCC*, where green = 1, amber = 2 and red = 3 (Eaton *et al.* 2015)
2. *GB Red List*, where least concern = 1, near threatened = 2, vulnerable = 3, endangered = 4 and critically endangered = 5 (based on assessments of breeding populations; Stanbury *et al.* 2017)
3. *European Red List*, using the same scores as for the GB Red List (BirdLife International 2015)
4. *Global Red List*, using the same scores as for the GB Red List (BirdLife International 2018)
5. *Global Range* in km^2 (extent of occurrence during the breeding season, from BirdLife International (2018)).
6. *Endemism*, the proportion of the total British breeding population of each species supported by each region, divided by the number of 10-km squares overlapping each region (thus correcting for the different size of the two regions; Balmer *et al.* 2013)

Based on these scores, we computed geometric mean relative population size for each scenario following two alternative weighting approaches, and compared these to the unweighted, 'all species' geometric mean.

First, we used ordinal/continuous weightings, based on the raw scores described above (using the inverse of range size for *Global Range*), to calculate a weighted geometric mean. Under this approach, all species contribute to the overall mean, but species with higher scores (threatened species, those with high endemism scores, or small global ranges) are given more weight. So, for example, under the *BoCC* scores, red-listed species have three times as much influence on the geometric mean as green-listed species.

Second, we established a binary weighting, in which 'low-priority' species (those classified as green or least concern; with an endemism score < 0.2; or with global range > 20 million km^2) were given a weighting of 0 and all other species were given a weighting of 1. This approach is equivalent to calculating the geometric mean for subsets of priority species, with low-priority species excluded altogether. We identified a further three subsets of species:

7. *Winners*, species identified by Finch *et al.* (2019) as having larger populations under any agricultural scenario than under a hypothetical pre-agricultural baseline.
8. *Losers*, species identified by Finch *et al.* (2019) as having smaller populations under all agricultural scenarios than under a hypothetical pre-agricultural baseline.
9. *FBI*, the 19 species representing the UK Farmland Bird Indicator (Gregory, G. Noble & Custance 2004).

We also tested the sensitivity of our results to the arbitrary thresholds used to identify endemic (0.1, 0.2 or 0.3) or small-range (15, 20 or 25 million km^2) species.

Optimising the three-compartment model

In addition to evaluating the scenarios in **Fig. 1.1** developed by Finch *et al.* (2019), we defined for each region a much broader range of 'three-compartment' strategies. We defined, for each region, P as the current regional food production (GJ per ha), Y_{max} as the maximum observed yield across 1-km squares, Y_{spared} as the mean yield of spared land (reflecting a small amount of meat production, and calculated assuming a 50:50 ratio of fen and wet grassland in The Fens and chalk grassland and woodland in Salisbury Plain), A_{spared} as the current total area of spared land and A_{total} as the total area.

Our scenarios include (up to) three types of land. 'Farmland' is present in all scenarios, and is the highest-yielding land type, with yield ranging up to Y_{max}. 'Spared natural habitat' is the lowest-yielding land type, with yield fixed at Y_{spared}. 'Spared low-yield farmland' is always higher-yielding then spared natural habitat and lower-yielding than farmland. We constrained all scenarios to maintain current regional food production (P), generating all feasible areas and yields of the three land types.

Following Finch *et al.* (2019) we then evaluated each strategy by calculating the geometric mean population change across all species (relative to a simplified representation of the present day) and identified the 'optimal strategy' as that which maximised this value. Finally, we identified optimal strategies for geometric means calculated using each of the nine binary weightings described above, as well as across all species.

Results

Species weightings

In most cases, weighting the geometric mean had little effect on the response of population size across the sharing-sparing continuum (**Fig. 3.1**). Weighting according to species conservation status resulted in a similar response to the unweighted mean in both regions, with the best scenario (where 'best' = the strategy which maximises geometric mean relative population size) being three-compartment sparing in The Fens and an intermediate sparing strategy (followed closely by three-compartment sparing) in Salisbury Plain. Weighting by endemism score had a more marked effect, amplifying the benefits of extreme two-compartment sparing in The Fens, and dampening the magnitude of the response across the sharing-sparing continuum in Salisbury Plain (where intermediate / three-compartment sparing remained the best strategy). In Salisbury Plain, weighting by global range size had a similar dampening effect.

Calculating the geometric mean across smaller subsets of species (equivalent to a binary weighting) resulted in larger divergences from the 'all species' response, especially (and unsurprisingly) for groups represented by few species (**Fig. 3.2**). Still, in The Fens three-compartment sparing was always the best (or close to the best) strategy except for winners and FBI species, for which strategies close to land sharing maximised mean relative population size. In Salisbury Plain, when considering only threatened species or species with small global ranges, the best intermediate strategy shifted slightly towards extreme land sparing, with three-compartment sparing still performing almost as well. In contrast, FBI species and those with high endemism scores achieved highest mean relative population size under extreme land sharing.

As we increased the arbitrary threshold at which species were defined as having a small range (from 15 to 25 million km^2) the mean response converged on the mean response of all species (**Fig. 3.3**). Changing the arbitrary threshold at which we defined species as 'endemic' (0.1, 0.2 or 0.3) had no effect in Salisbury Plain, where the same three species were always represented (**Fig. 3.4**). In The Fens, as the threshold was reduced (thus including more species),

the mean response converged on the mean response of all species.

compartments, with a larger spared compartment than present in both regions
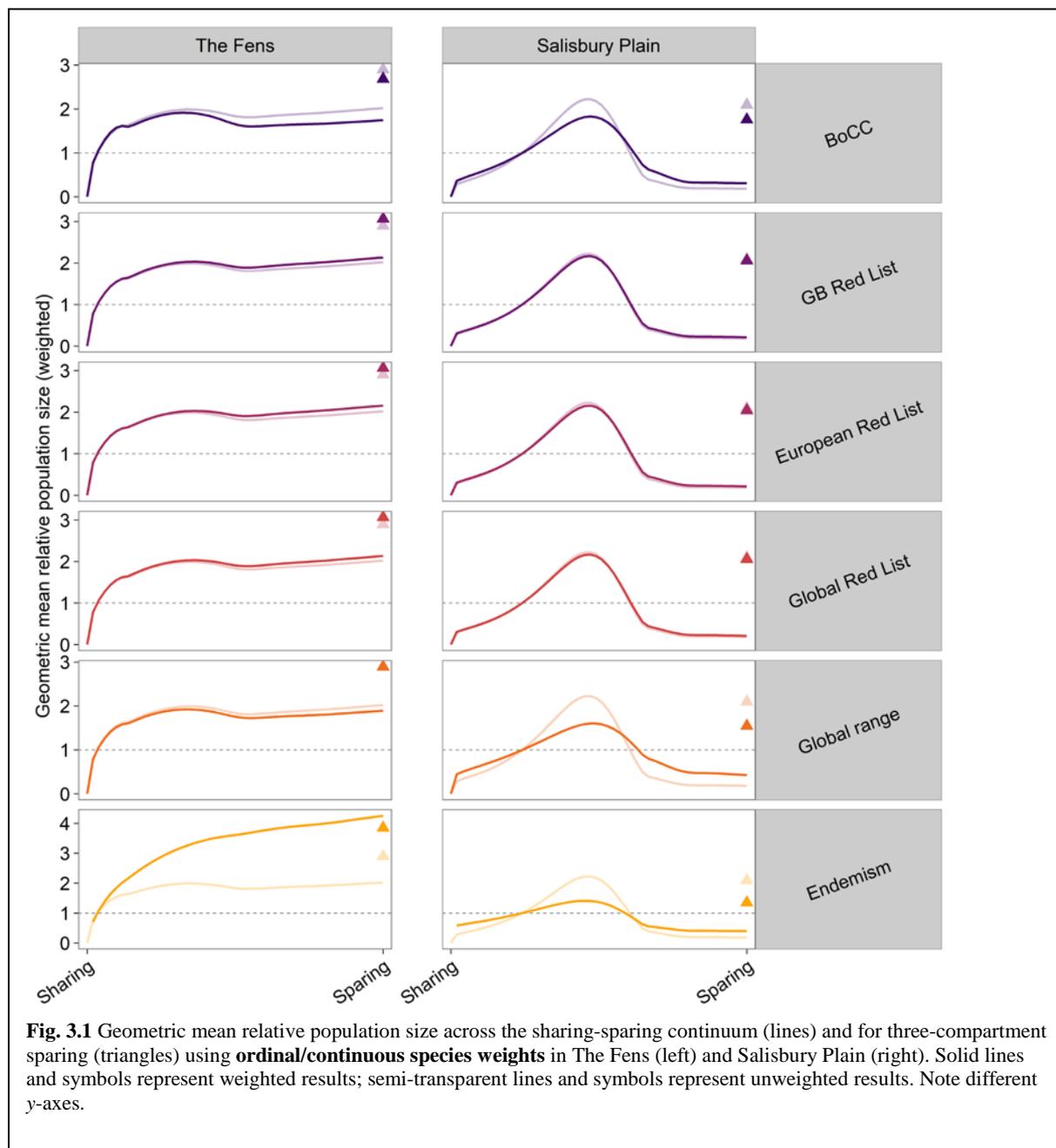
Fig. 3.1 Geometric mean relative population size across the sharing-sparing continuum (lines) and for three-compartment sparing (triangles) using **ordinal/continuous species weights** in The Fens (left) and Salisbury Plain (right). Solid lines and symbols represent weighted results; semi-transparent lines and symbols represent unweighted results. Note different *y*-axes.

Optimal scenarios

All results described so far reflect the 2-compartment sharing-sparing continuum and a simple three-compartment sparing strategy (**Fig. 1.1**). However, density-yield curves can be used to evaluate a much wider range of scenarios, reducing the constraints imposed by the simple sharing-sparing continuum. Under this more flexible approach, the strategy which maximises the 'all species' geometric mean included three

(**Fig. 3.5**).

In The Fens, the yield of the main farmed compartment in the 'all species' optimum scenario was set to Y_{max} (108 GJ ha^{-1}, current average yield = 52 GJ ha^{-1}), with the third compartment occupying 28% of the total area at 29 GJ ha^{-1} (**Fig. 3.5**). In Salisbury Plain, the yield of farmland was 31 GJ ha^{-1} (Y_{max} = 45 GJ ha^{-1}, current average yield = 26 GJ ha^{-1}), and the third-

Fig. 3.2 Geometric mean relative population size across the sharing-sparing continuum and for three-compartment sparing using **binary species weights** in The Fens (left) and Salisbury Plain (right). Solid lines and symbols represent results for each subset with sample sizes noted at the bottom of each panel; semi-transparent lines and symbols represent results for all species. Note different *y*-axes.

compartment was substantially smaller than in The Fens (3% of the total area).

The characteristics of the optimal scenario were broadly consistent across different subsets of species (**Fig. 3.5**). For almost all subsets, the best scenario involved an increase in the area of spared natural habitat compared to present. Exceptions were FBI species, those classified as

winners from agriculture in The Fens and as endemic species in Salisbury Plain.

In The Fens, all other species subsets did best under scenarios where the yield of farmland equalled Y_{max}, with relatively minor differences in the area of spared low-yield farmland. Species classified as losers from agriculture or as endemic required a smaller area of low-yield farmland and a larger area
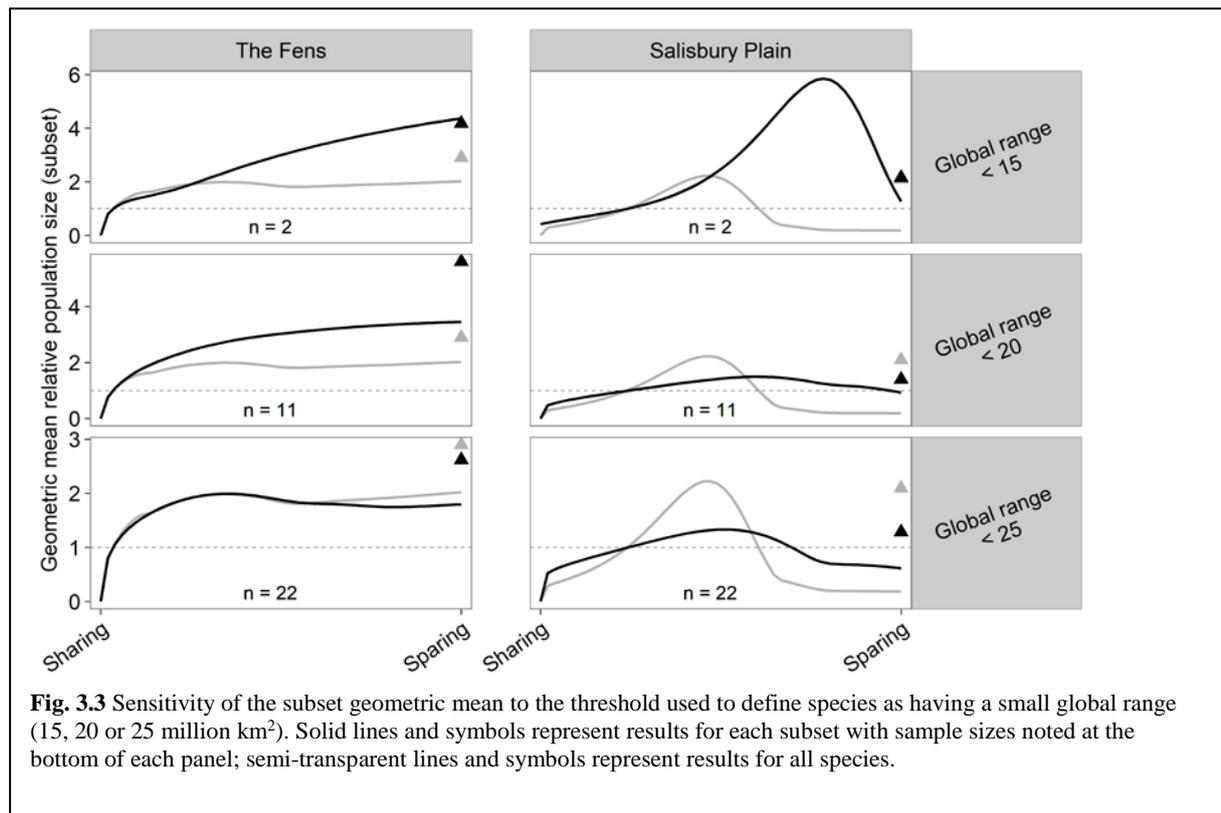
Fig. 3.3 Sensitivity of the subset geometric mean to the threshold used to define species as having a small global range (15, 20 or 25 million km^2). Solid lines and symbols represent results for each subset with sample sizes noted at the bottom of each panel; semi-transparent lines and symbols represent results for all species.
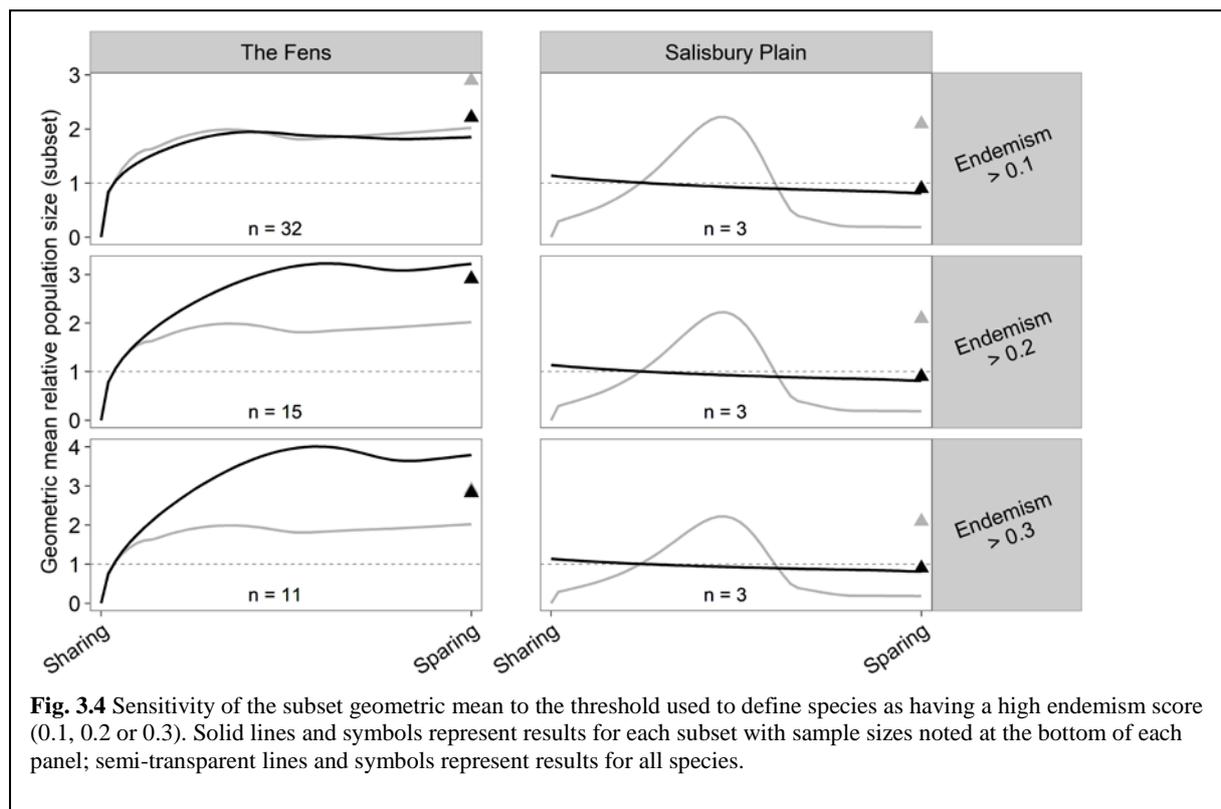
Fig. 3.4 Sensitivity of the subset geometric mean to the threshold used to define species as having a high endemism score (0.1, 0.2 or 0.3). Solid lines and symbols represent results for each subset with sample sizes noted at the bottom of each panel; semi-transparent lines and symbols represent results for all species.

of spared natural habitat than species on the European Red List or with a small global range (**Fig. 3.5**).

In Salisbury Plain there was more variation in the optimal yield (and relative area) of farmland and low-yield farmland. For species classified as losers from agriculture, the optimal yield of farmland was Y_{max}, and

Fig 3.5 Illustration of optimal configuration at current production for different species groups in The Fens (top) and Salisbury Plain (bottom), compared to *Current* (far left). Numbers along *x*-axis show number of species per group. Black = current maximum observed yield, white = low/zero yield in spared habitats, grey = intermediate yields (see panel).
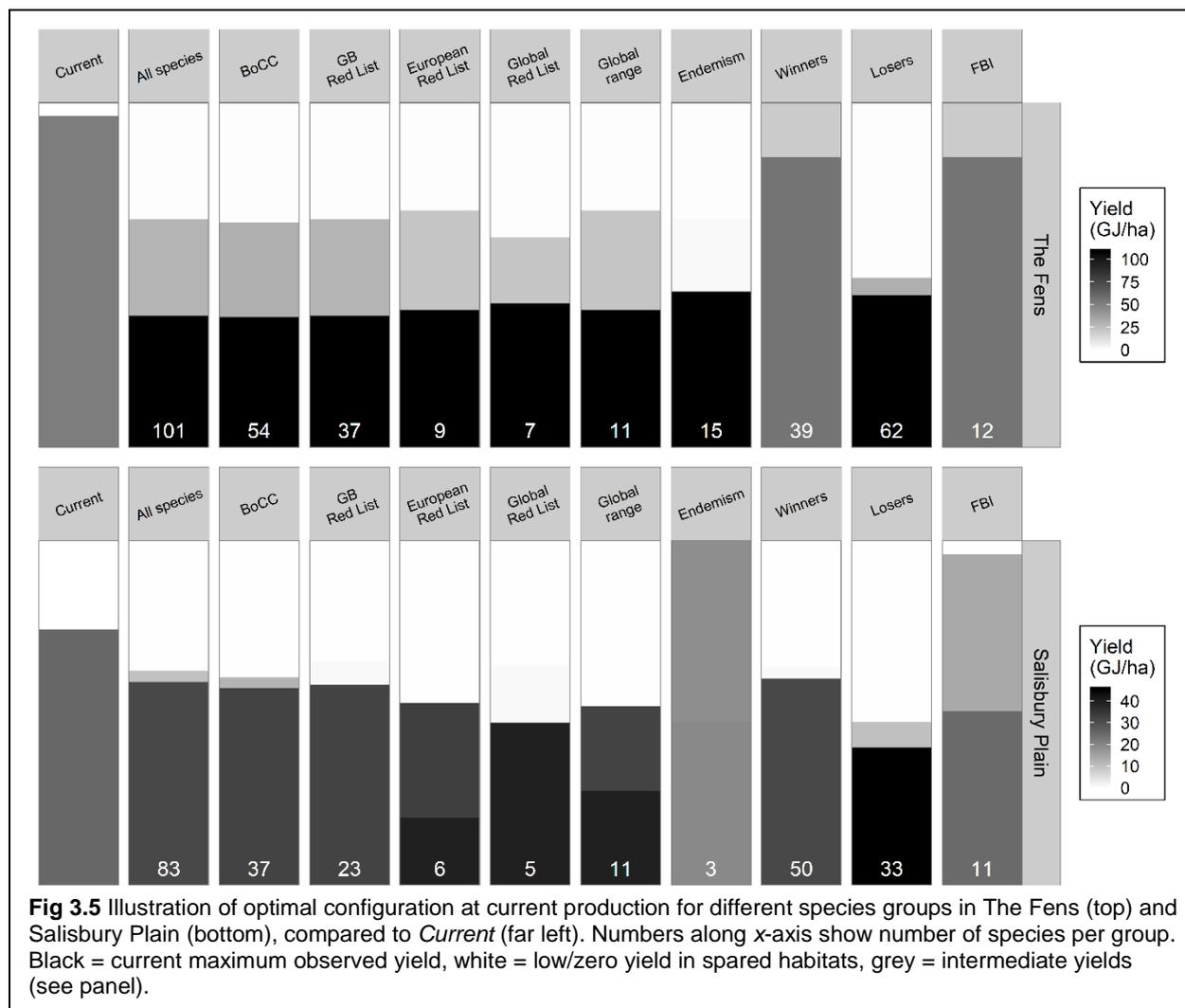
for species on the European and Global Red Lists and with small global ranges the optimal yield of farmland was close to Y_{max}. However, for all other species subsets the optimal yield of farmland was below Y_{max}. For most subsets either the optimal yield of low-yield farmland was close to that of farmland, or the area of low-yield farmland was relatively small. In other words, the requirement for a distinct third compartment was relatively weak (largely because the main farmed compartment was usually below Y_{max}).

Discussion

We suggest that our previous conclusions (Finch *et al.* 2019) are relatively insensitive to different species prioritisations and groupings. Modifying the geometric mean according to continuous species weightings

had, at most, a modest effect on the response of mean relative population size across the sharing-sparing continuum. The binary weighting approach had a more marked effect, but only species groups represented by relatively few species departed substantially from the 'all species' response. Importantly, all our conclusions remain essentially unchanged when considering only threatened species.

By evaluating a wider range of three-compartment scenarios, the relative geometric mean response (across all species) was higher than under any of the scenarios tested previously (i.e. those illustrated in **Fig. 1.1**). Still, the optimal three-compartment scenario in The Fens was very close to the originally-defined three-compartment sparing, and in Salisbury Plain the optimal three-compartment scenario represented a slight

modification (through the addition of a small, very low-yielding third compartment) to intermediate sparing.

The properties of this optimal strategy were relatively consistent across different species groupings, with some exceptions. Thus, whilst our general conclusion – increasing yields on some farmland and sparing other land for conservation – is broadly robust, the characteristics of spared conservation land (natural habitat and low-yield farmland) are more sensitive to the identity of the species groups which are prioritised.

In both regions, species on the Global Red List were among those which benefited most from land sparing (i.e. high yields on farmland combined with a large area of spared natural habitat). These include wetland species such as the near-threatened Black-tailed Godwit *Limosa limosa* and Lapwing *Vanellus vanellus* in The Fens, and grassland / scrub species such as the vulnerable Turtle Dove *Streptopelia turtur* and the near-threatened Meadow Pipit *Anthus pratensis* in Salisbury Plain.

In contrast, farmland specialists (e.g. FBI species), and endemic species in Salisbury Plain (Corn Bunting *Emberiza calandra*, Stone Curlew *Burhinus oedicnemus* and Quail *Coturnix coturnix*) preferred, on average, strategies much closer to land sharing, with less (or no) spared natural habitat and lower farmland yields. This presents an important challenge to our main conclusion; in a national context, Salisbury Plain supports important populations of some species which are expected to benefit, on average, from land sharing. Whilst most species on average benefit from a three-compartment or intermediate sparing strategy, many of these may be supported by conservation in other parts of the country.

Section 4: New case studies: the Cotswolds and Low Weald (Module 2)

Introduction

In The Fens and Salisbury Plain, the strategy which maximised geometric mean relative population size across breeding bird species was (close to) three-compartment sparing. This strategy involves high-yield farming which spares land as a combination of both semi-natural habitat and low-yield farmland (**Fig. 1.1b**). An outstanding question is to what extent this conclusion is generalisable to other regions and taxa. Insects, for example, tend to operate at smaller spatial scales than birds, so may benefit more from land sharing approaches which promote fine-scale habitat features (Ekroos *et al.* 2016), though studies from the tropics suggest that dung beetle populations would be maximised under land sparing (Williams *et al.* 2017). Furthermore, the habitats promoted under land sparing in The Fens and Salisbury Plain are likely to support species which are absent from farmland, but these habitats are arguably atypical of lowland England. Elsewhere, broadleaf woodland is a more typical 'spared' habitat, and many woodland species can persist in farmland where hedgerows and small wooded areas (copses/spinneys) are present. Land sparing may receive less support in such regions.

In this module we test the generality of our previous findings by applying the sharing-sparing model to two new regions (Low Weald and The Cotswolds) and assessing the responses of butterflies as well as birds.

Methods

Study regions

Building on the availability of existing bird and butterfly survey data, we focussed on two regions of southern England: Low Weald and The Cotswolds (**Fig. 4.1**). The Cotswolds is characterised by rolling limestone hills and mixed farmland, whilst Low Weald is clay-dominated and primarily grassland. These regions differ from The Fens and Salisbury Plain in that their baseline habitat is primarily woodland. We considered including relatively sparse bird and butterfly data from High Weald. However, differences in cropping and land use between High and Low Weald suggested that density-yield functions may have differed between these two areas, and we lacked sufficient data to estimate them separately.

We restricted our study to the dominant soil type in each region, excluding squares where it covered less than 50% using the NatMAP soilscape (Farewell *et al.* 2011). In The Cotswolds, the dominant soil is "Shallow lime-rich soils over chalk or limestone", supporting arable and grassland, limestone pastures and lime-rich woodlands. In Low Weald, the dominant soil is moderate fertility "Slowly permeable seasonally wet slightly acid but base-rich loamy and clayey soils", supporting arable, grassland and woodland. The total number of focal 1-km squares is 1513 in The Cotswolds, and 1378 in Low Weald (**Fig. 4.2**).

For each focal square we calculated land-use areas using *LCM2015 (*Rowland *et al. 2017)*. The main 'spared' (semi-)natural land covers in both regions are woodland (broadleaf and coniferous) and semi-natural grassland, but no 1-km squares are currently covered entirely by these land covers in either region. Instead, we identified large (>1km^2) square-shaped (i.e. perimeter [km] / area [km^2] ≤ 5) blocks of woodland and semi-natural grassland, then classified 1-km squares as spared, as illustrated in **Fig. 2.1**. We thus treated large but linear patches of habitat (with high 'edginess') as part of the farmed landscape. According to this definition, there are currently just 13 spared 1-km squares in the Cotswolds (land-use composition = 88% broadleaf woodland, 8% coniferous woodland, 4% calcareous grassland), and 7 in Low Weald (78% broadleaf woodland,

22% coniferous woodland). All other squares were treated as farmed.

Bird density

Breeding Bird Survey

We identified all species with potential breeding populations in each region using the Bird Atlas 2007–11 (Balmer *et al.* 2013), excluding aerial foragers, nocturnal species, introduced species and gulls and terns. We then used UK Breeding Bird Survey (BBS) data to estimate their density in farmland (of varying yield) and woodland.

The BBS involves skilled volunteers recording encounters of adult birds along two transects (each 1 km long, 0.2 km wide) within randomly selected 1-km squares (Harris *et al.* 2017). Two visits are made to each BBS square between early April and late June. Along each transect, each of five 200 m transect sections is assigned to a broad habitat category (woodland, scrubland, semi-natural grassland / marsh, farmland, waterbodies) and adult birds are counted in two distance bands (0–25 m, 25–100 m).

To estimate site-, visit- and species-specific detection probabilities, analysis was conducted at the 200 m transect level, using the number of individual birds of each species detected in each distance band. We supplemented our data with equivalent BBS data from all surveyed squares south of 54°N within England & Wales, then estimated the half-normal detection function for each species, with 'habitat type' and 'visit' as co-variates. The integral of this detection function up to 100 m gives the estimated probability of detecting a species within 100 m of the transect line (Buckland *et al.* 2001; Johnston *et al.* 2014). Site-specific detection probabilities were thus calculated for each species by weighting the habitat-specific detection probability by the proportion of transects sections under each habitat type within each square.

We then used generalised linear models with Poisson error structure and log link function to estimate species-specific

densities in each square. For each species and region, we fitted a regression with the maximum count (from either visit) as the dependent variable and the natural logarithm of the species-, site- and visit-specific 'effective area' (detection probability × transect area [0.4 km^2]) as an offset. The independent variables were the additive effects of 'site' and 'year' (both fixed factors). We then averaged predictions (weighted by 1/SE) for years 2014–17 to estimate mean site-specific species density. This approach accounts for the fact that different sites were surveyed in different years, with the 'year' variable controlling for inter-annual variation in abundance at the regional scale. To increase statistical power for the estimation of these year effects, we supplemented data from our study sites with BBS data from all squares within South East England NUTS1 statistical region for Low Weald and the South West NUTS1 region for The Cotswolds.

Population density in woodland

No BBS squares were covered entirely by woodland (mean woodland cover = 11%, range = 0–64% in The Cotswolds; mean woodland cover = 15%, range = 0–49% in Low Weald), and we were unable to find comparable data from other sources on bird population density in woodland for these regions. In order to estimate population density in large woodland blocks, we therefore used a mixture modelling approach applied to transect-section-level data to estimate species-specific density in woodland. These data are based on 478 and 401 transect sections from 48 and 41 BBS squares in The Cotswolds and Low Weald, respectively.

For each species i and each 200 m transect section j in each year (selecting the visit with the maximum count for each species across all transect sections in a square), we acquired the total number of birds (Y), the effective area (EA, 0.04 km^2 × detection
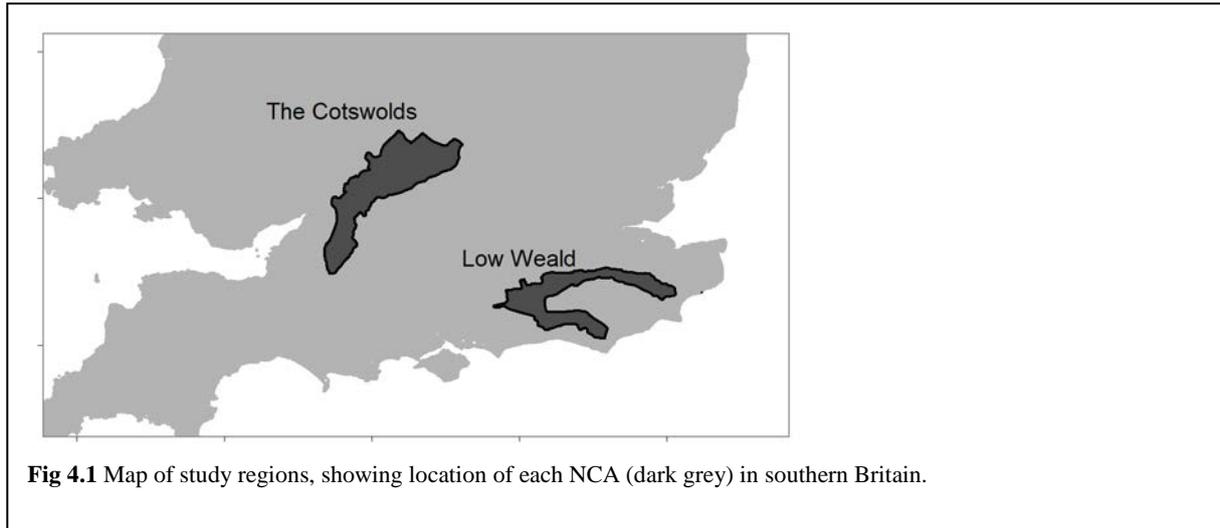
Fig 4.1 Map of study regions, showing location of each NCA (dark grey) in southern Britain.
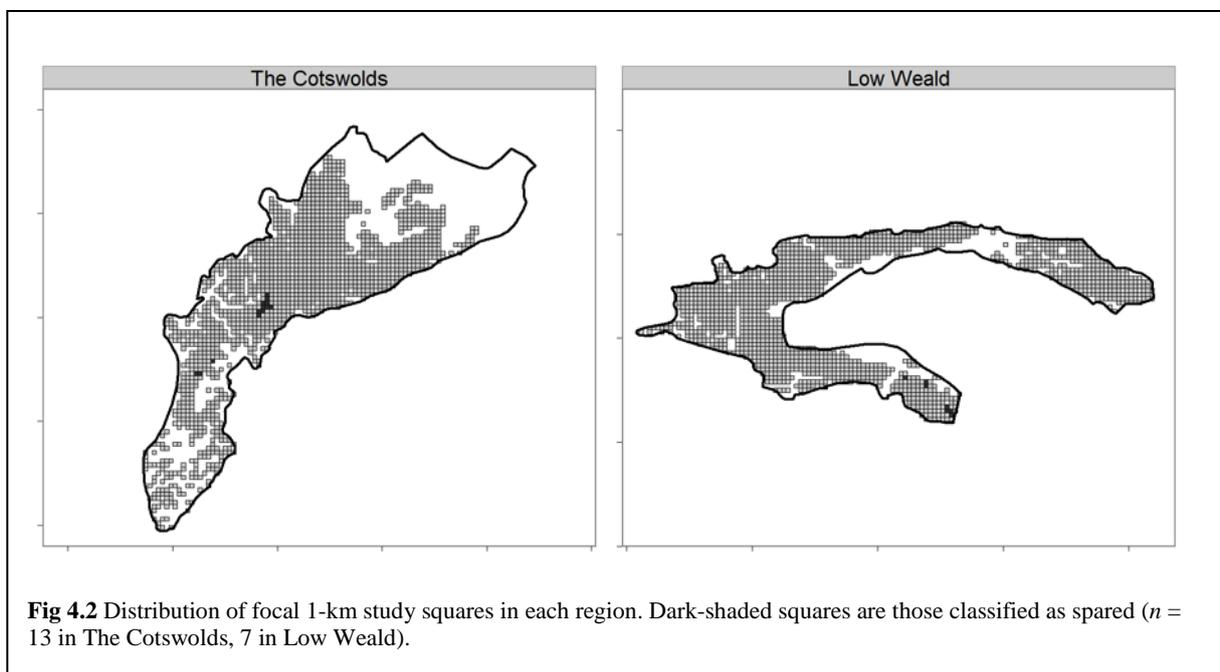
Fig 4.2 Distribution of focal 1-km study squares in each region. Dark-shaded squares are those classified as spared ($n =$ 13 in The Cotswolds, 7 in Low Weald).

probability, based on the broad habitat type associated with each transect section) and the proportional cover of woodland ($P_{woodland}$, broadleaved + coniferous), farmland ($P_{farmland}$, arable + improved grassland), and other land (P_{other}) within the surveyed area of each transect (i.e. 100 m either side) using *LCM2015*.

For each species i, we then fitted a model to all data from 2014–17:

$$\bar{Y}_{ij} = [P_{woodland\,j} \times EA_{ij} \times \exp(k_1)] +$$

$$[P_{farmland\,j} \times EA_{ij} \times \exp(k_2)] +$$

$$[P_{other\,j} \times EA_{ij} \times \exp(k_3)]$$

We estimated parameters k_1, k_2 and k_3 (representing habitat-specific densities) by minimising $\sum \bar{Y}_{ij} - Y_{ij} \times \log(\bar{Y}_{ij})$ with Nelder-Mead optimisation. We defined woodland density as $\exp(k_1)$, and drew 5 samples of this estimate (representing 5 hypothetical woodland 'sites') per species / region using a bootstrap (resampling with replacement) approach.

Population density in scrub

As an alternative to broadleaf woodland (for Low Weald only), we also estimated species population density in scrub. We used data from a 2018 BBS survey of Knepp Estate's 'southern block' (which followed the same field protocol as

described above, except the total transect distance was 6 km). This area represents extensive, early-to-mid successional scrub habitat, managed by low-density, semi-feral livestock. We estimated species-specific densities by dividing the total count (selecting the visit with maximum count for each species) by the species-specific effective area (detection probability in scrub habitat, derived as above × transect length [6 km] × transect width [0.2 km]).

Butterfly density

To estimate site-specific butterfly density, we used data from two national monitoring schemes, the UK Butterfly Monitoring Scheme (UKBMS) and the Wider Countryside Butterfly Survey (WCBS) collected during 2014–17. Both schemes involve walked transects in which skilled volunteers count butterfly species within 2.5 m of the transect line. The UKBMS entails roughly 26 visits per year between April and September at 'self-selected' sites with variable transect length, whereas WCBS involves 2–4 visits per year to randomly selected 1-km squares with a standardised transect length of 2 km (the butterfly equivalent of BBS).

Both surveys produce indices of butterfly abundance (detections per km, per species, per visit). We assume constant detection among habitats, however butterfly activity is strongly seasonal. To account for seasonal variation in butterfly activity, we used species- and year-specific flight curves (based on national WCBS data), which present relative abundance for each week of the year (for 26 weeks from 1st April), scaled such that the sum of all weekly abundance indices = 1 (**Fig. 4.4**, points). We first characterised the 'typical' phenology of each species, by averaging all weekly flight activity data across years 2013–17 (**Fig. 4.4**, red curve) and identifying, for each species, the week of peak flight activity (**Fig. 4.4**, thick grey vertical line). For species with two or more flight peaks, we chose the largest of the peaks within the core WCBS survey period

(27th May – 26th August; **Fig. 4.4** dashed vertical lines). We then identified, for each annual flight activity curve, the peak closest to the week of peak flight activity identified in the multi-year flight activity curve (**Fig. 4.4**, filled point). In other words, multi-year flight activity data were used to identify the general phenology of peak activity, but peaks themselves were identified separately for each year (this is important mainly for species with multiple peaks, for which inter-annual variation in flight activity might result in different parts of the annual cycle being identified as peak activity in different years; see e.g. Wood White in 2017).

For each species and year, surveys conducted during weeks of flight activity less than 5% of flight activity in the peak week were excluded. We then multiplied observed butterfly abundance by the inverse of the ratio between that week's relative flight activity, and the activity of the peak week (such that counts during weeks of low average activity were inflated and counts during peak week were unchanged). For each site, species and year, we then averaged phenology-corrected density across all visits, weighting according to the ratio between that week's predicted activity, and the predicted activity of the peak week (such that estimates of density during weeks of high activity were given more weight). Finally, for each species at each site, we divided each annual abundance estimate by the species-specific national population index (scaled across 2014–17 to mean = 1), and then averaged across all years.

We excluded three migratory species (Painted Lady *Vanessa cardui*, Red Admiral *Vanessa atalanta* and Clouded Yellow *Colias croceus*) whose numbers are primarily determined by factors operating outside of the UK. For Silver-washed Fritillary *Argynnis paphia*, for which flight curves were unavailable, we used flight curves of a surrogate species with similar phenology (Gatekeeper *Pyronia tithonus*).
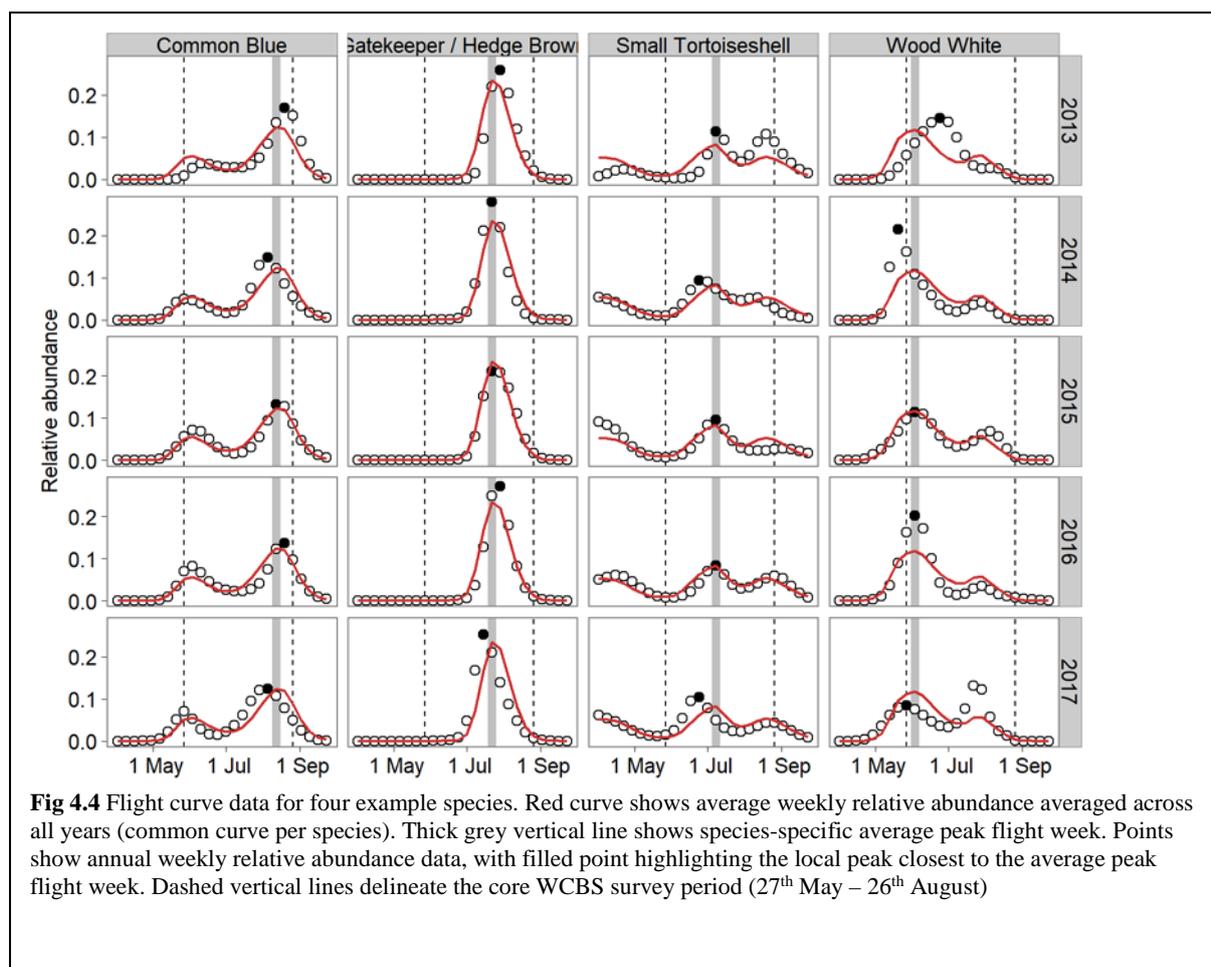
Fig 4.4 Flight curve data for four example species. Red curve shows average weekly relative abundance averaged across all years (common curve per species). Thick grey vertical line shows species-specific average peak flight week. Points show annual weekly relative abundance data, with filled point highlighting the local peak closest to the average peak flight week. Dashed vertical lines delineate the core WCBS survey period (27th May – 26th August)

Yields

To estimate agricultural yield, we first calculated land-use areas for all 1-km squares (including BBS & WCBS sites) and each UKBMS site (the area within 25 m of the transect line) using *LCM2015* (adjusted as described above such that 'spared' areas match the 1-km grid).

We estimated the site-specific combination of crops making up 'Arable and horticulture' using the Rural Payments Agency's 2016 Crop Map of England (*CROME*). We calculated the proportion of each arable crop type (excluding 'mixed crop' and 'fallow') within each site, increasing the area of each site by a 500 m buffer in order to approximate the temporal rotation of crops. We then used regional Farm Business Survey data (Duchy College Rural Business 2017) to estimate region- and crop-specific yields. Following Finch *et al.* (2019), we estimated the edible end-product(s) associated with each crop, and converted

harvested tonnes to edible content (using published feed conversion ratios (Cassidy *et al.* 2013) for end-products fed to livestock).

For grazed land uses (Improved grassland, and semi-natural grassland which included Calcareous grassland, Neutral grassland, Acid grassland, Heather grassland, Heather and Fen, marsh and swamp) we took estimates of land-use-specific fodder production from the literature (10 tonnes DM per ha for improved grassland, 4 tonnes DM per ha for semi-natural grazed land-uses; Tallowin & Jefferson 1999). We then used gridded June Survey data (http://agcensus.edina.ac.uk) to estimate the proportion of forage land used for dairy cattle, beef cattle and sheep per site (data reported at 5-km resolution), excluding dairy cattle on semi-natural grasslands. Finally, we used published feed conversion ratios (Cassidy *et al.* 2013) to convert grass into

edible animal products (i.e. beef, lamb or milk).

We identified land under organic management using Natural England's map of Environmental Stewardship Scheme Agreements ('Organic Entry Level' with or without 'Higher Level Stewardship'). In these areas, we applied yield penalties of 10% for grazed land-uses (following Muller *et al.* 2017), and crop-specific yield penalties for arable crops (after de Ponti, Rijk & van Ittersum 2012). For non-agricultural land-uses (Broadleaf and Coniferous woodland, (Supra)Littoral sediment, Freshwater, Saltwater, Inland rock, Suburban and Urban) we assigned a yield of 0. We then multiplied area by yield for each land-use and summed across each site, dividing by the area of unbuilt land.

Because *LCM2015* is of insufficient resolution to identify small uncropped features, we manually digitised field boundaries using aerial imagery for a sub-set of sites. For these sites, we re-calculated *LCM2015* areas excluding uncropped hedges, margins, fallows and horsiculture, then re-estimated the yield of each square. Based on the region-specific relationship between yields estimated using 'raw' and 'clipped' *LCM2015* areas (The Cotswolds: α = −0.506 ± 0.42, β = 0.905 ± 0.02, R^2 = 0.99; Low Weald: α = 0.201 ± 0.33, β = 0.769 ± 0.02, R^2 = 0.99), we predicted the 'clipped' yield of all sites.

We assumed a yield of 0 in spared woodland and 0.21 GJ per ha on scrub, reflecting 75 tonnes liveweight of meat across Knepp's 3500 acre estate (Barkham 2018; assume 50% is edible = 0.025 tonnes of beef per hectare = 0.21 GJ per ha).

Density yield curves
We fitted density-yield curves for each species in each region following Phalan *et al.* (2011).

For birds, we used data from all BBS squares and the 5 sampled woodland 'sites'. We excluded species detected at < 3 BBS squares, leaving 64 and 67 species

across 48 and 44 BBS squares in The Cotswolds and Low Weald, respectively.

For butterflies we used data from all WCBS squares. Because UKBMS sites typically represent patches of low-yielding seminatural habitat, and UKBMS transects aren't intended to be representative of an entire 1-km square, we deemed yield estimates of UKBMS transects in farmland sites to be unreliable. We therefore excluded UKBMS sites with yield < 10% of the maximum regional yield (the remaining UKBMS sites had an average woodland cover of 76% in The Cotswolds and 95% in Low Weald). As above, we excluded species detected at < 3 sites, leaving 21 and 29 species across 31–33 and 25–27 sites in The Cotswolds and Low Weald, respectively (sample size differs between species due to species-specific flight seasons).

We considered two density-yield models which can describe a wide range of curve shapes:

(A) $\qquad d_i = \exp(b_0 + b_1(x_i^{\alpha}))$

(B) $\qquad d_i = \exp(b_0 + b_1(x_i^{\alpha}) + b_2(x_i^{2\alpha}))$

where d_i is the predicted density of a species at survey site i, x_i is the yield of site i, and b_0, b_1, b_2 and α are parameters estimated from the data. Parameters were estimated by maximum-likelihood using an iterative Nelder-Mead numerical optimisation. Several parameter starting values were used to ensure that the correct solution was found. Following Phalan *et al.* (2011), the value of α was constrained between 0 and 4.6, and all model parameters were constrained such that the maximum predicted density did not exceed 1.5 × the maximum observed density. We additionally constrained model B to avoid a sharp peak at less than 10% of the maximum observed yield, or sharp peaks resulting in more than 90% of the curve being at less than 10% of the peak density (thus avoiding density predictions of 0 at

almost all feasible yields). We selected the model (A or B) with the lowest AIC value.

We explored uncertainty in the shape of each curve by bootstrapping. We selected survey sites at random, with replacement, from each region's pool of survey sites, and fitted the density-yield functions for each species in each bootstrap sample. We repeated this 100 times, calculating species population size and geometric mean population change for each sample.

Scenarios

For each region we designed scenarios reflecting the sharing-sparing continuum for a range of regional food production targets (from 0.25 to 2× current production) and defining all spared land as woodland:

- Land sharing – farming the entire region at the minimum yield necessary to achieve the production target, with no spared land.
- Land sparing – farming at the maximum observed regional yield (across a 1-km square) over the smallest area necessary (whilst still achieving the production target), and sparing the remaining land.
- Intermediate strategies – sparing increasingly more land by farming at an increasingly high yield.
- Three-compartment sparing – with an area of low-yield farmland (set to equal the area of spared woodland) delivering some food production (at a yield set to the median at which species with hump-shaped density-yield curves reach peak density).

For each scenario, we estimated the regional population size of each species using density-yield curves. For birds in Low Weald, we also estimated regional population size for scenarios which varied the composition of spared land, from 100% woodland to 100% scrub, using densities estimated from Knepp for scrub.

For each region and each production target we identified winners as species with a higher population under any production

scenario than in a hypothetical 100% woodland baseline scenario; we identified losers as species with a smaller population under all production scenarios than in a hypothetical 100% woodland baseline scenario. We classified species as winners and losers at each production target, and identified the two-compartment scenario at which each species achieved its highest population size. We then calculated the geometric mean population size (relative to current) across all species (and across winners and losers separately) for each scenario at each production target.

Results

Both regions are currently close to the extreme sharing end of the sharing-sparing continuum. The area of spared land (that is, square-shaped blocks of woodland >100 ha in size) is small (0.9% of total area in The Cotswolds, 0.6% in Low Weald), such that even under extreme sharing (resulting in the total loss of these spared areas) mean farmland yields would decline by only around 1% in each region. In contrast, due to the large difference between current mean yield (16 GJ ha^{-1} in The Cotswolds, 10 GJ ha^{-1} in Low Weald) and the maximum observed yield (36 GJ ha^{-1} in The Cotswolds, 34 GJ ha^{-1} in Low Weald), there is a large (hypothetical) potential for land sparing. If current food production were met by farming at the maximum observed yield then the total spared area could theoretically increase to 55% of the total area in The Cotswolds (×61) and to 71% of the total area in Low Weald (×118). Land sparing reflects, in part, the consolidation of small woodlands into much larger units, as well as a shift towards arable-dominated agriculture.

Vote counting

At current production in The Cotswolds (and assuming all spared land is broadleaved woodland), only 31% of birds and 38% of butterflies achieved maximum population size under land sparing (red colours); 53%

and 52% did best under sharing (blue colours), with the remainder (16% and 10%) doing best under an intermediate strategy (purple colours; **Fig. 4.5**). In Low Weald 42% of birds and 52% of butterflies achieved maximum population size under land sparing; land sharing maximised the population size of 49% of birds and 35% of butterflies, with the remaining species (9% and 14%) doing best under an intermediate strategy (**Fig. 4.5**).

Most butterfly species (62% in each region), and just under half of all bird species (48% in The Cotswolds, 46% in Low Weald) were classified as losers from agriculture, with smaller predicted population sizes under all production scenarios than in the hypothetical pre-agricultural baseline (**Fig.**

4.5, dark colours). Across all regions and taxa, the majority of losers achieved maximum population size under land sparing (**Fig. 4.5** dark red); however, in The Cotswolds, a moderate number of species classified as losers – 36% of birds and 39% of butterflies – did best under land sharing.

Among bird species, just over half were classified as winners (52% of winners in The Cotswolds; 54% in Low Weald), with larger predicted population sizes under a production scenario than in the hypothetical pre-agricultural baseline (**Fig. 4.5**, pale colours). Among butterfly species, winners were in the minority (38% of species in both regions). Across all regions and taxa, the majority of winner species achieved maximum population size under land

Fig. 4.5 Number of bird and butterfly species classified as winners (pale colours, top) and losers (dark colours, bottom) from agriculture and achieving maximum population size under land sparing (reds), land sharing (blues) or an intermediate strategy (purples) across a range of production targets in The Cotswolds (top row) and Low Weald (bottom row). Assumes all spared land is broadleaved woodland. Note that there were no species classified as "Winner, Sparing best" or "Loser, Intermediate best".

sharing (**Fig. 4.5**, pale blue), with the remainder doing best under an intermediate strategy.

Mean relative population size

Across all taxa and regions, loser species showed a linear positive response across the sharing-sparing continuum, with geometric mean relative population size maximised under extreme sparing (**Figs 4.6**, **4.7**, central panels). Winners, by contrast, showed a negative response, with geometric mean relative population size maximised under extreme sharing (**Figs 4.6**, **4.7**, right panels).

Due to the approximately even balance of winners and losers among bird species, the opposite response of these groups across the sharing-sparing continuum, and the somewhat stronger response of winners compared to losers, most strategies

left panels), with strongest declines towards land sparing. Among butterfly species, geometric mean relative population size across all species increased towards land sparing, peaking at intermediate–high levels of land sparing (**Fig 4.7**).

Three-compartment sparing (**Figs 4.6**, **4.7**, box-and-whisker) maximised geometric mean population size (across all species) for both taxa in both regions, though bootstrap confidence intervals were wide and overlapped with intermediate sparing, especially for butterflies.

Changing the production target

For all taxa and regions, higher production targets resulted in more species being classified as losers, and a greater
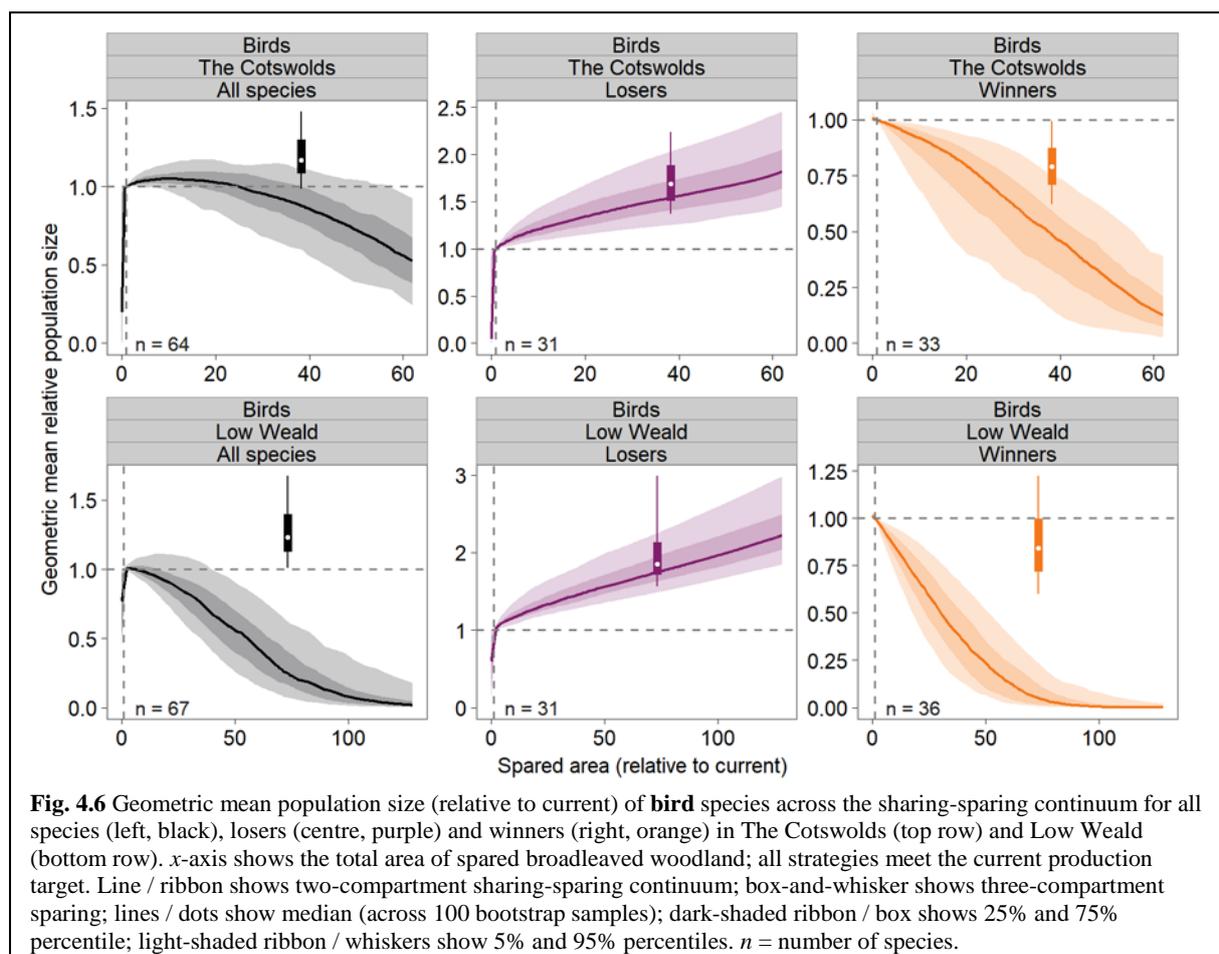
Fig. 4.6 Geometric mean population size (relative to current) of **bird** species across the sharing-sparing continuum for all species (left, black), losers (centre, purple) and winners (right, orange) in The Cotswolds (top row) and Low Weald (bottom row). *x*-axis shows the total area of spared broadleaved woodland; all strategies meet the current production target. Line / ribbon shows two-compartment sharing-sparing continuum; box-and-whisker shows three-compartment sparing; lines / dots show median (across 100 bootstrap samples); dark-shaded ribbon / box shows 25% and 75% percentile; light-shaded ribbon / whiskers show 5% and 95% percentiles. *n* = number of species.

resulted in declines in relative population size averaged across all species (**Fig 4.6**,
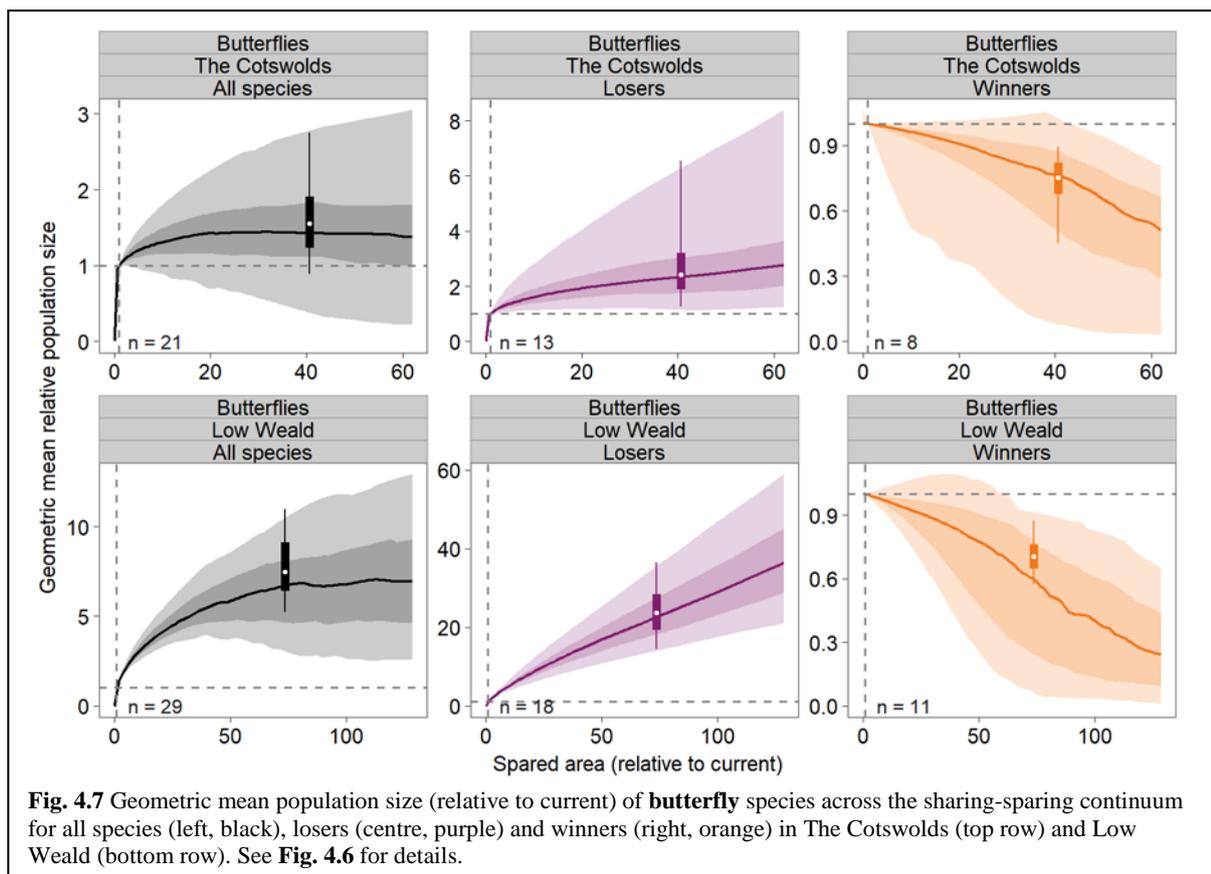
Fig. 4.7 Geometric mean population size (relative to current) of **butterfly** species across the sharing-sparing continuum for all species (left, black), losers (centre, purple) and winners (right, orange) in The Cotswolds (top row) and Low Weald (bottom row). See **Fig. 4.6** for details.

proportion of losers achieving maximum population size under sparing (**Fig. 4.5**).

Across all species, three-compartment sparing was consistently high-performing across the full range of production targets (**Figs 4.8**, **4.9**, left panel, purple line), though intermediate (blue ribbon) strategies were sometimes better at low production targets.

For loser species, land sparing maximised geometric mean relative population size across all regions, taxa and production targets. Land sharing was consistently the worst strategy for losers, and three-compartment sparing was often almost as a good as land sparing (**Figs 4.8**, **4.9**, central panel). For winner species the best strategy varied depending on the production target, though the general pattern was consistent across regions and taxa; land sharing maximised geometric mean relative population size at production targets less than or equal to current, whilst three-compartment sparing outperformed land

sharing at higher production targets (**Figs 4.8**, **4.9**, right panel).

The benefits of scrub
For birds in Low Weald (the only taxon and region for which density estimates were available for scrub), scenarios which included a combination of scrub and woodland on spared land resulted in higher geometric mean relative population size than strategies with only woodland or only scrub (**Fig. 4.10**). Across all species, the optimal proportion of scrub on spared land was approximately 0.3, under a three-compartment sparing strategy (**Fig. 4.10b**). Changing the proportion of scrub had little effect on the response of geometric mean relative population size across the sharing-sparing continuum; three-compartment sparing remained the best strategy on average across all species (**Fig. 4.10a**).
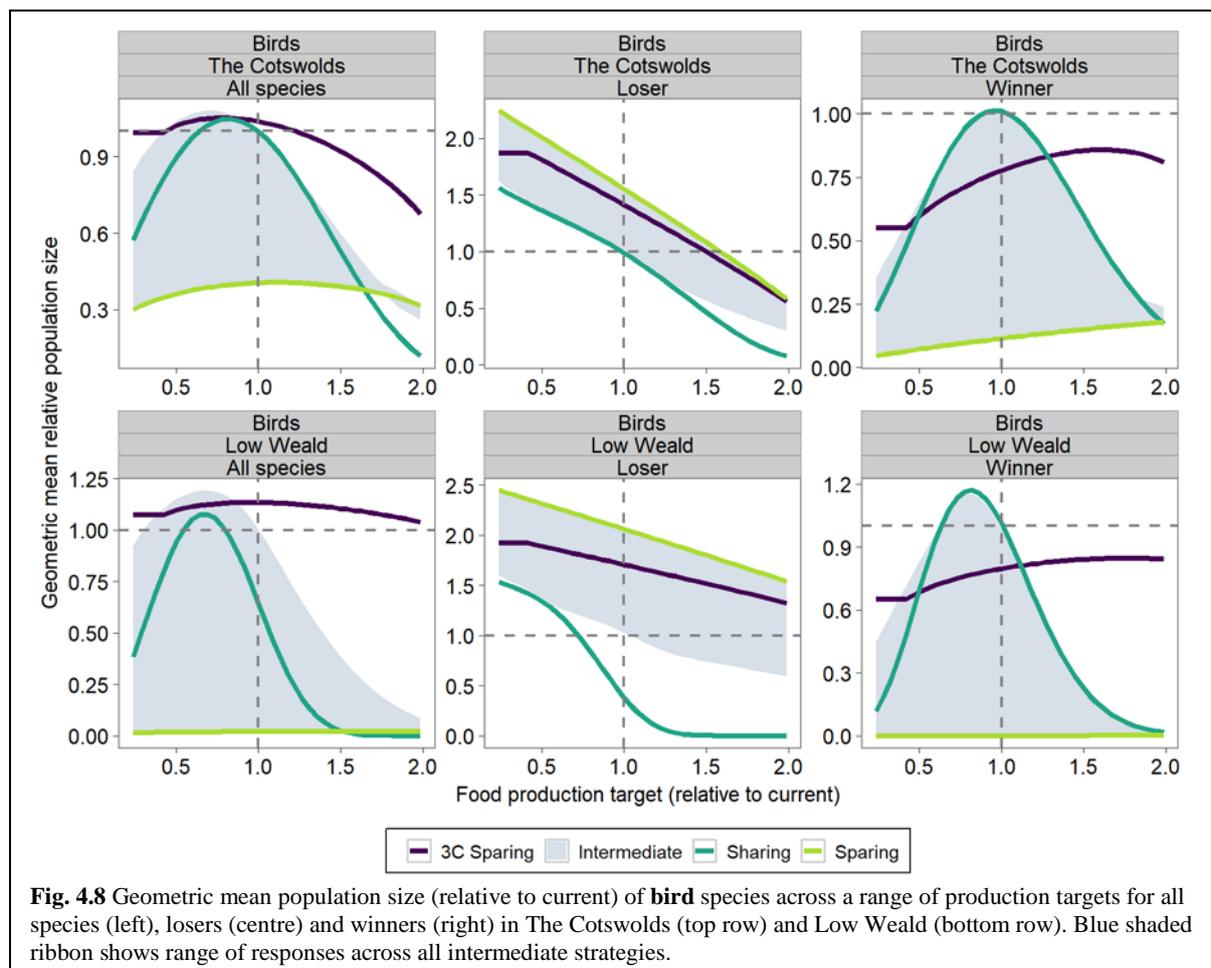
Fig. 4.8 Geometric mean population size (relative to current) of **bird** species across a range of production targets for all species (left), losers (centre) and winners (right) in The Cotswolds (top row) and Low Weald (bottom row). Blue shaded ribbon shows range of responses across all intermediate strategies.

Discussion

The aim of this module was to evaluate the sharing-sparing framework for birds and butterflies in two new regions, in order to understand the generality of our previous findings (Finch *et al.* 2019). Whilst we find some important differences between regions and taxa, our overall conclusion – that three-compartment sparing comes closest to reconciling the trade-off between food production and the conservation of both winners and loser species – is strongly supported in all cases (**Table 4.1**).

Some common threads have emerged across this and our previous work, including:

1. Most 'loser' species (i.e. farmland-avoiders) achieved maximum population size under land sparing, and land sparing maximised geometric mean relative population size of loser species across almost all production targets;

2. Most 'winner' species (i.e. farmland-adapters) achieved maximum population size under land sharing, and land sharing maximised geometric mean relative population size of winner species across most production targets (except in Salisbury Plain where an intermediate strategy was best);

3. Extreme land sharing resulted in declines in geometric mean relative population size across all taxa and regions, except for winner species and/or at low production targets;

4. Land sparing maximised the population size of an increasingly high proportion of species as the production target increases;

5. Strategies which promote multiple (semi-)natural habitat types on spared land outperformed those which promote only one habitat type;

Fig. 4.9 Geometric mean population size (relative to current) of **butterfly** species across a range of production targets for all species (left), losers (centre) and winners (right) in The Cotswolds (top row) and Low Weald (bottom row). Blue shaded ribbon shows range of responses across all intermediate strategies.

Fig. 4.10a Geometric mean population size (relative to current) of **bird** species across the sharing-sparing continuum for all species in Low Weald. *x*-axis shows the total area of spared land, which is a combination of broadleaved woodland and scrub; colour-scale denotes ratio of woodland to scrub on spared land (dark green = less scrub, pale green = more scrub). Triangle shows three-compartment sparing; all strategies meet the current production target. **b** shows geometric mean relative population size for three-compartment sparing with different proportions of scrub on spared land.

Table 4.1 Summary table. **a** shows average composition of farmed 1-km squares in 2015. Numbers in parentheses show **b** yield relative to mean yield, **c** spared area (i.e. spared semi-natural habitat) relative to current spared area, **d** % of species classed as winners/losers (bold font indicates the dominant of the two), and **e** % of species achieving maximum population size under sharing, sparing or an intermediate strategy (bold font indicates the most 'popular' strategy). In **f**, 'Best strategy' is defined as that which maximised all-species geometric mean relative population size at current production. 2C = two-compartment, 3C = three-compartment.

	The Fens	*Salisbury Plain*		*The Cotswolds*		*Low Weald*
a						
% arable	86%	57%		51%		22%
% improved grassland	11%	34%		34%		54%
% woodland (broadleaf + coniferous)	0.6% + <0.1%	2% + 0.2%		10% + 1%		15% + 1%
b						
Mean yield (GJ ha^{-1})	52 (1.0)	26 (1.0)		16 (1.0)		10 (1.0)
Maximum yield (GJ ha^{-1})	108 (2.1)	45 (1.7)		36 (2.3)		34 (3.4)
Minimum yield (GJ ha^{-1})	50 (1.0)	19 (0.7)		16 (1.0)		10 (1.0)
Low-yield farmland yield (GJ ha^{-1})	24 (0.5)	32 (1.2)		11 (0.7)		9 (0.9)
c						
Current spared area	4% (1.0)	26% (1.0)		0.9% (1.0)		0.6% (1.0)
Maximum spared area (extreme sparing)	54% (13.5)	58% (2.2)		55% (61.0)		71% (118.3)
Spared area under 3C sparing[1]	31% (7.8)	44% (1.7)		41% (45.6)		33% (55)
	Birds	*Birds*	*Birds*	*Butterflies*	*Birds*	*Butterflies*
d						
Winners	39 (39%)	**50 (60%)**	**33 (52%)**	8 (38%)	**36 (54%)**	11 (38%)
Losers	**62 (61%)**	33 (40%)	31 (48%)	**13 (62%)**	31 (46%)	**18 (62%)**
e						
Sharing	32 (32%)	18 (21%)	**34 (53%)**	**11 (52%)**	**33 (49%)**	10 (34%)
Intermediate	9 (9%)	**35 (42%)**	10 (16%)	2 (10%)	6 (9%)	4 (14%)
Sparing	**60 (59 %)**	31 (37%)	20 (31%)	8 (38%)	28 (42%)	**15 (52%)**
f						
Best 2C strategy	*Sparing*	*Intermediate sparing*	*Intermediate sparing*	*Intermediate sparing*	*Intermediate sparing*	*Sparing*
Best overall strategy	*3C sparing*	*Intermediate sparing*[2]	*3C sparing*	*3C sparing*	*3C sparing*	*3C sparing*

[1] Under three-compartment sparing, the area of low-yield farmland is equal to the spared area, and is <u>not</u> included in the figure reported here.

[2] The best intermediate strategy in Salisbury Plain had farmland yield of 31.5 GJ ha^{-1} (1.2 relative to current mean) and 39% spared area (1.2 relative to current). This strategy delivered an all-species geometric mean relative population size of 2.22, compared to 2.09 under three-compartment sparing.

6. Three-compartment sparing maximised (or nearly maximised) the geometric mean relative population size of all species across all taxa, regions and production targets, and outperformed extreme sparing and extreme sharing.

The inconsistencies are as follows:

1. Among bird species, loser species outnumbered winner species in The Fens, but not in The Cotswolds, Low Weald or (in particular) Salisbury Plain;
2. In The Cotswolds and Low Weald, loser species outnumbered winner species among butterfly species but not among birds;
3. In The Cotswolds, many loser species achieved maximum population size under land sharing (though most still did best under land sparing), whereas in all other regions land sparing was overwhelmingly the most popular strategy among loser species;
4. In Salisbury Plain, most winners achieved maximum population size under intermediate sparing, whereas in all other regions, most winners achieved maximum population size under land sharing.

1: Why are a high proportion of bird species classified as winners in The Cotswolds and Low Weald (and Salisbury Plain)?

In The Fens, and in all other parts of the world where the density-yield curve approach has been used to compare land sharing and land sparing, a majority of species were classified as losers from agriculture (Phalan *et al.* 2011; Hulme *et al.* 2013; Kamp *et al.* 2015; Dotta *et al.* 2016; Williams *et al.* 2017). These species are predicted to have smaller populations under all production scenarios (i.e. all positions across the sharing-sparing continuum) than in a hypothetical pre-agricultural baseline where all land is 'spared' as natural or seminatural habitat. That a majority of species are losers from agriculture should be unsurprising, because agriculture has been absent for most of their evolutionary history, and farming involves the appropriation of primary productivity which could otherwise form the base of a natural food web.

Why, then, are a majority of bird species classified as winners from agriculture in The Cotswolds, Low Weald and (especially) Salisbury Plain (**Table 4.1d**)? First, we should acknowledge that our understanding of the pre-agricultural landscapes of southern Britain is limited, and thus our estimates of pre-agricultural regional population sizes are uncertain. It's unlikely that lowland Britain was uniformly wooded; instead, a mosaic of open and wooded habitats seems most congruent with the available palaeoecological evidence (Allen 2017; Alexander *et al.* 2018). Due to the lack of such environments in present-day Britain, we're limited in our ability to estimate pre-agricultural regional population sizes.

Even assuming a baseline of relatively closed woodland in The Cotswolds and Low Weald, these regions contain only a handful of 1-km squares dominated by woodland, none of which were surveyed by the BBS. The maximum woodland cover of any BBS square was 64% in The Cotswolds and 52% in Low Weald. Our mixture modelling approach attempted to assign bird records into woodland and non-woodland habitats based on the area of woodland within each transect section. It's impossible, however, to extrapolate these densities to larger (i.e. ≥100 ha) patches of unfarmed habitat, because few such patches exist and none have been surveyed. Although larger woodlands typically contain more breeding bird species (Whytock *et al.* 2018), some species are likely to achieve higher densities in small patches with a higher edge:core ratio (e.g. Robin *Erithacus rubecula*, Dunnock *Prunella modularis*, Wren *Troglodytes troglodytes*) and others in larger patches (e.g. Marsh Tit *Poecile palustris*, Great Spotted Woodpecker *Dendrocopos major*, Dolman *et al.* 2007), so it's unclear how the inclusion of data from larger woodland patches might influence our results. Comparing our

estimated woodland densities with woodland densities estimated using census data from RSPB reserves (Lamb *et al.* 2019) – representing larger patches of woodland managed primarily for conservation – suggests that we have under-estimated woodland densities of some species (**Fig. 4.11**). If so, we may have mis-classified some loser species as winners, and so might be underestimating the value of land sparing for these species.

In The Cotswolds and Low Weald, bird species classified as losers from agriculture included woodland specialists (with concave decreasing density-yield curves) such as Blackcap *Sylvia atricapilla*, Chiffchaff *Phylloscopus collybita*, Coal Tit *Periparus ater*, Treecreeper *Certhia familiaris*, Great Spotted Woodpecker and Marsh Tit, as well as generalists (with convex decreasing density-yield curves) such as Blackbird *Turdus merula*, Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, Chaffinch *Fringilla coelebs*, Robin and Wren. Aside from the methodological issues described above, that such species are in a minority must partly reflect the (pre-)historic loss of other woodland species from these regions. Bird species including Wood Warbler *Phylloscopus sibilatrix*, Lesser Spotted Woodpecker *Dryobates minor*, Hawfinch *Coccothraustes coccothraustes*, Nightingale *Luscinia megarhynchos* and Willow Tit *Poecile montanus* have all suffered severe declines in range and/or abundance throughout at least the last half-century (Balmer *et al.* 2013), and were absent from one or both of The Cotswolds and Low Weald. Other birds of broadleaf woodland lost entirely from Britain as breeding species include Wryneck *Jynx torquilla* (Monk 1963) and possibly Collared Flycatcher *Ficedula albicollis* and White-backed Woodpecker *Dendrocopus leucotus* (Tomiałojć 2000).

Some woodland birds were, surprisingly, classified as winners from agriculture, including Redstart *Phoenicurus phoenicurus* (both regions), Nightingale (Low Weald), and Spotted Flycatcher *Muscicapa striata*

and Willow Tit (The Cotswolds), suggesting that these species benefit from the heterogeneity and habitat complementarity characteristic of low–medium yield farmland. Whether these species are truly 'winners' probably depends on the extent to which natural disturbance processes in pre-agricultural Britain delivered the heterogeneity and ecotones promoted by farmland today. We suspect that some of these species (e.g. Redstart, Nightingale and Willow Tit) are simply very scarce in our study regions; they're absent from most woodlands, so our mixture models estimate low average densities, resulting in hump-shaped density-yield curves driven by the few farmed squares which include some suitable woodland or scrub habitat.

On the face of it, the dominance of loser species in The Fens compared to our other regions is surprising; of all our study regions this is the most intensely farmed, with almost no remaining natural or semi-natural habitat (**Table 4.1a**). Extinction filters (Balmford 1996) are likely to be well advanced here. However, the few spared areas in The Fens are relatively large and support many species in high abundance, with wetland birds having colonised new habitat 'islands' with apparent ease (e.g. Stanbury & UK Crane Working Group 2011). In our other study regions, although woodland cover is much higher than in The Fens, these habitat patches are small, fragmented, and not managed primarily for wildlife, so unlikely to support many true woodland specialists. Such differences in land-use history likely go some way to explaining differences between our study regions (von Wehrden *et al.* 2014). It's also possible that, compared to the wetlands promoted under land sparing in The Fens, woodland (and chalk grassland in Salisbury Plain) simply supports fewer species, especially when woodland fragments are small and relatively uniform in structure. The total avian species pool is substantially larger in The Fens than in the other three
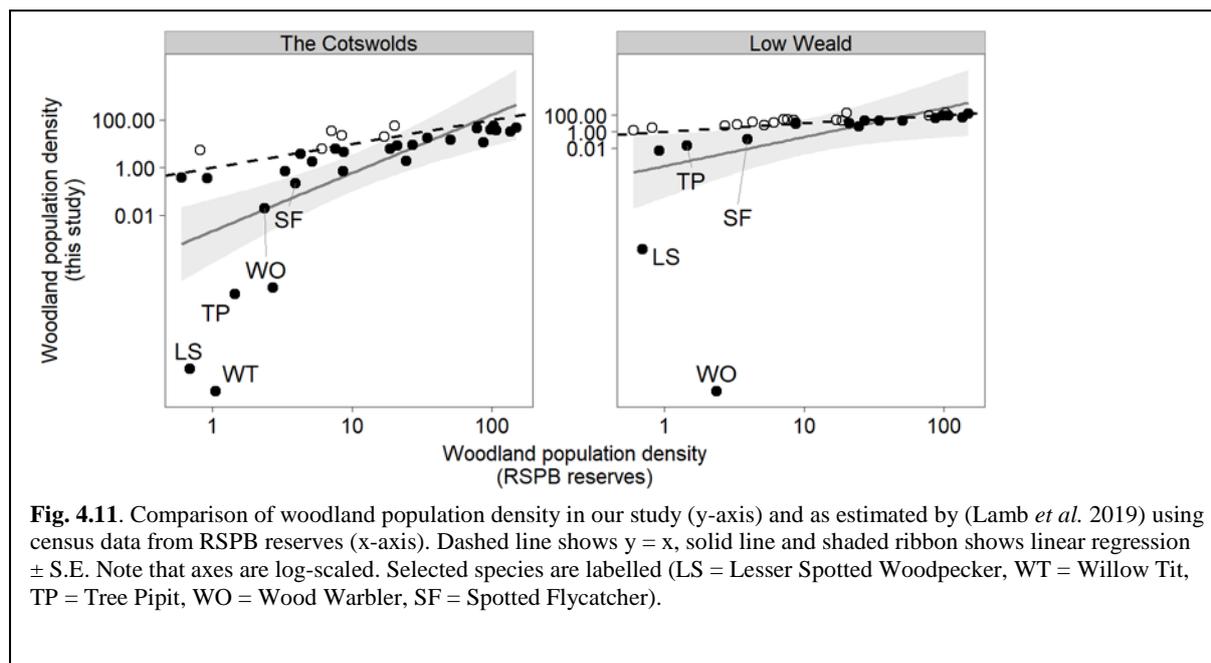
Fig. 4.11. Comparison of woodland population density in our study (y-axis) and as estimated by (Lamb *et al.* 2019) using census data from RSPB reserves (x-axis). Dashed line shows y = x, solid line and shaded ribbon shows linear regression ± S.E. Note that axes are log-scaled. Selected species are labelled (LS = Lesser Spotted Woodpecker, WT = Willow Tit, TP = Tree Pipit, WO = Wood Warbler, SF = Spotted Flycatcher).

regions, with most unique species being wetland specialists.

The Fens is also much further along the 'production target' gradient than any other study region. As illustrated in **Fig. 4.5**, the proportion of species classified as losers increases as the production target increases, reflecting the fact that the minimum feasible yield under land sharing increases at higher production targets (**Table 4.1b**).

The high proportion of winner species in Salisbury Plain probably reflects a combination of (i) potentially downwards-biased estimates of woodland population density, (ii) chalk grassland supporting high densities of relatively few species, and (iii) low–intermediate yield farmland supporting high densities of relatively many species. Here, compared to chalk downland, farmland promotes a mosaic of arable land, grassland, small woodlands, and hedgerows. The light soils in this region are often associated with spring tillage, over-winter stubbles, intact seed banks, etc. Salisbury Plain (together with The Cotswolds) has also been highly targeted by environmental stewardship schemes for farmland bird conservation; some of these schemes might increase bird density without a detectable yield penalty (at least as estimated here).

2: Why do loser species dominate among butterflies, but winners among birds?

In The Cotswolds and Low Weald, density-yield curves were fitted for both birds and butterflies, allowing within-region comparison between the two taxa groups. The main difference between birds and butterflies, consistent across both regions, was that losers made up a majority of species among butterflies but not birds (**Table 4.1d**). This result echoes conclusions from other studies of land sharing and sparing, where a higher proportion of species are classified as winners among bird species compared to plant and invertebrate taxa (Phalan *et al.* 2011; Williams *et al.* 2017).

This implies that birds are generally less sensitive than other taxa to agricultural land-use, which perhaps goes some way to explaining the fact that, globally, contemporary extinction rates are lower among birds (132 extinctions per million-species-years) than mammals (243 extinctions per million-species-years) (Pimm *et al.* 2014), and that relatively few bird species are considered threatened (c.

Fig. 4.12. Land-use profiles across the yield gradient in our four study regions. Points show, for each farmed 1-km square, proportional area of Arable & horticulture, Improved grassland and Woodland (broadleaf + coniferous) as a function of that square's energetic yield. Lines show 5-df GAM smooth. Solid vertical line shows minimum feasible yield under land sharing; dashed vertical line shows yield of low-yield farmland. Note different x-axes.

14%), compared to mammals (25%), selected dicotyledonous plants (35%) and amphibians (40%; IUCN 2019). The mechanism driving birds' increased resilience to disturbance is unclear, but their higher mobility could facilitate their persistence in fragmented landscapes (Sauvajot *et al.* 1998), where 'interstitial' habitats can be utilised for resources at different points throughout the day / season.

An alternative explanation is that birds are *more* sensitive to land-use change than butterflies (perhaps because of larger minimum habitat area requirements), and that many loser species have been lost from the regional avian species pool, but not from the butterfly species pool.

3: Why do a relatively high proportion of loser species do best under land sharing in The Cotswolds?

In The Fens, Salisbury Plain and Low Weald, the vast majority of loser species achieved maximum population size under land sparing (i.e. with concave decreasing density-yield curve, reaching maximum density in natural habitat, and showing a

steep decline in density as yield increases). In The Cotswolds, however, this majority was substantially reduced, with more than a third of loser species achieving maximum population size under land sharing (i.e. with convex decreasing density-yield curve, reaching maximum density in natural habitat, but showing only a gradual decline in density as yield increases).

This pattern was consistent across birds and butterflies, and must be driven by relatively low densities in spared habitat, and/or relatively high densities in low–medium yield farmland. One potential explanation is that low–medium yield farmland in The Cotswolds contains more woodland compared to our other regions, allowing the persistence of woodland generalists. However, whilst the total area of broadleaf woodland across farmed squares is substantially higher in The Cotswolds (10%) than in either The Fens (0.6%) or Salisbury Plain (2%), Low Weald has more woodland cover still (15%; **Table 4.1**). The Cotswolds and Low Weald have very similar land-use profiles across the yield gradient, suggesting that "low–medium

Fig. 4.13. Comparison of woodland population density in The Cotswolds (x-axis) and Low Weald (y-axis). Dashed line shows y = x, solid line and shaded ribbon shows linear regression ± S.E. JD = Jackdaw, RO = Rook, GO = Goldfinch, BC = Blackcap, CH = Chaffinch, WR = Wren, GT = Great Tit, B. = Blackbird, R. = Robin, WP = Woodpigeon, BT = Blue Tit.
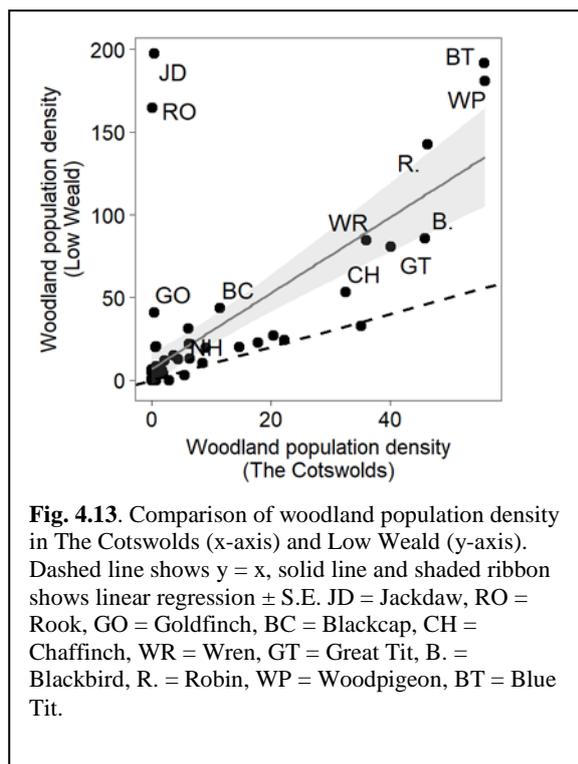
yield farmland" describes land with a similar land-use composition in each region (**Fig. 4.12**).

Alternatively, densities in spared woodland could be lower in The Cotswolds than in Low Weald. We found support for this for bird species (paired t-test; t = 3.49, df = 67, p < 0.001; **Fig 4.13**) but not for butterflies (t = 1.16, df = 26, p = 0.25). This could be driven by differences in the species composition or structure between the woods in the two regions, perhaps driven by soil type or history of management, though we did not test these hypotheses.

4: Why do most winner species achieve maximum population size under intermediate strategy in Salisbury Plain, but land sharing in all other regions?

In Salisbury Plain, many winner species showed hump-shaped density-yield curves, reaching peak density in intermediate yielding (i.e. mixed) farmland. Geometric mean relative population size thus declined under both land sparing and land sharing, reaching its maximum under intermediate sparing. This fact explains (i) why the trade-off between winner and loser species is relaxed in Salisbury Plain (because

intermediate sparing, the best strategy for `winners, is almost as good as the best strategy for losers), and (ii) why three-compartment sparing is essentially redundant in Salisbury Plain (because the yield of farmland under intermediate sparing is the same as 'low-yield farmland' under three-compartment sparing). In contrast, for all other regions and taxa, a large majority of winner species achieved maximum population size under land sharing, resulting in a stark trade-off between the response of winner and loser species across the sharing-sparing continuum.

The preference of many winner species for intermediate-yielding farmland in Salisbury Plain can probably be interpreted as a preference for mixed farmland, with neither too much nor too little arable land. The biodiversity benefits of heterogeneity within agricultural landscapes are well described (e.g. Benton, Vickery & Wilson 2003), with arable land and grassland providing complementary foraging and/or nesting resources (Robinson, Wilson & Crick 2001). In Salisbury Plain, the optimal intermediate strategy had a yield of 31.5 GJ ha^{-1}, implying farmed 1-km squares containing 50–75% arable and 10–40% improved grassland (**Fig. 4.12**). These levels of arable cover were unfeasibly low in The Fens except at reduced productions targets (at which a greater proportion of winner species achieved maximum population size under an intermediate strategy). In The Cotswolds and Low Weald, however, yields under land sharing (under which most winners achieved maximum population size) imply a grassland-dominated farmed landscape. It's unclear why the optimal yield for winner species is more arable-dominated in Salisbury Plain than in The Cotswolds or Low Weald, though it's possible that the light rendzina soils in Salisbury Plain support a richer variety and/or abundance of weeds and insects. Microclimate, management history, and the presence of small patches of semi-natural chalk grassland within the farmed landscape may also be important.

Conclusion

Despite the variations described above, the overwhelming high-level conclusion – across all regions, taxa, and production targets – is that three-compartment sparing comes close to reconciling the trade-off between food production and the conservation of both winner and loser species. Although there were some cases where three-compartment sparing was outperformed by other strategies (e.g. at low production targets, and in Salisbury Plain), it always performed close to the best strategy. Importantly, support for three-compartment sparing increased at higher production targets.

We suggest that three-compartment sparing represents a consistently reliable approach through which a region can deliver food production at the same time as conserving both farmland-avoiders (losers) and farmland-adapters (winners).

Finally, for the avoidance of confusion, three-compartment sparing is *not* intermediate between land sharing and land sparing, because it involves high-yield (that is, maximum yield) farming. Instead, we see it as a land-sparing strategy which incorporates some 'shared' low-yield farmland (see **Fig. 1.1**).

Section 5: Discussion

Our firm conclusion is that three-compartment sparing (**Fig. 5.1**) can best reconcile the conflict between food production and conservation whilst delivering additional environmental benefits such as reducing global warming potential and diffuse pollution. Whilst there are inevitable trade-offs between these environmental outcomes, multiple-win strategies are possible, and three-compartment sparing appears to represent a reliable approach across regions.

This finding corroborates existing research suggesting that environmental outcomes are likely to be maximised by producing more food from farmland in order to leverage the protection or restoration of land for conservation (Balmford, Green & Phalan 2015; Williams *et al.* 2018). We add to this research by showing that in lowland England – for biodiversity outcomes in particular – conservation land should include some low-yield farmland in addition to semi/natural habitat, depending on the relative importance afforded to winners compared to losers.

Three-compartment sparing in practice

The exact properties of a three-compartment sparing strategy will vary between regions according to conservation priorities. There are four key questions to address:

1. *How much land should be devoted to low-yield farmland versus spared semi-/natural habitat?*
   Any increase in the area of land managed largely for conservation is likely to have positive outcomes for local biodiversity. Our 'default' three-compartment scenario assumes equal areas of low-yield farmland and spared habitat. Whilst this definition is arbitrary, it performed well, almost always resulting in a higher geometric mean relative population size compared to other strategies along the two-compartment sharing-sparing

continuum. We did not attempt to optimise the area of low-yield farmland relative to spared habitat in Low Weald or The Cotswolds, but for bird conservation in The Fens the optimal area of the third compartment was approximately 4/5th the area of spared habitat (i.e. close to 50:50; see **Section 3**). In Salisbury Plain, the optimal area of the third compartment was much lower, because the optimal yield of the main farmland compartment was less than the maximum (i.e. intermediate sparing; see **Table 4.1**).

2. *What kind(s) of semi/natural habitat should be promoted on spared land?*
   Spared land provides semi/natural areas for the conservation of farmland-avoiders (loser species) and is also important for the delivery of ecosystem services such as carbon sequestration and nutrient capture. The types of habitat promoted on spared land will be constrained by geographical factors such as soil, topography, hydrology and climate. Still, management decisions can modify spared habitats, in particular through the removal of biomass by grazing or through mechanical means to maintain early–mid successional habitats such as scrub, heath or semi-natural grassland. Our results suggest that promoting multiple habitat types on spared land (woodland & scrub in Low Weald, fen & wet grassland in The Fens, chalk grassland & woodland in Salisbury Plain) will deliver maximum conservation benefits, by supporting species with different habitat requirements.
   When deciding which spared habitats to promote in a region, we should consider not only the composition and conservation status of species within the region, but also the relative importance of the region in supporting those species. Salisbury Plain, for example, is internationally important for its chalk grassland plant and animal communities. The value of different
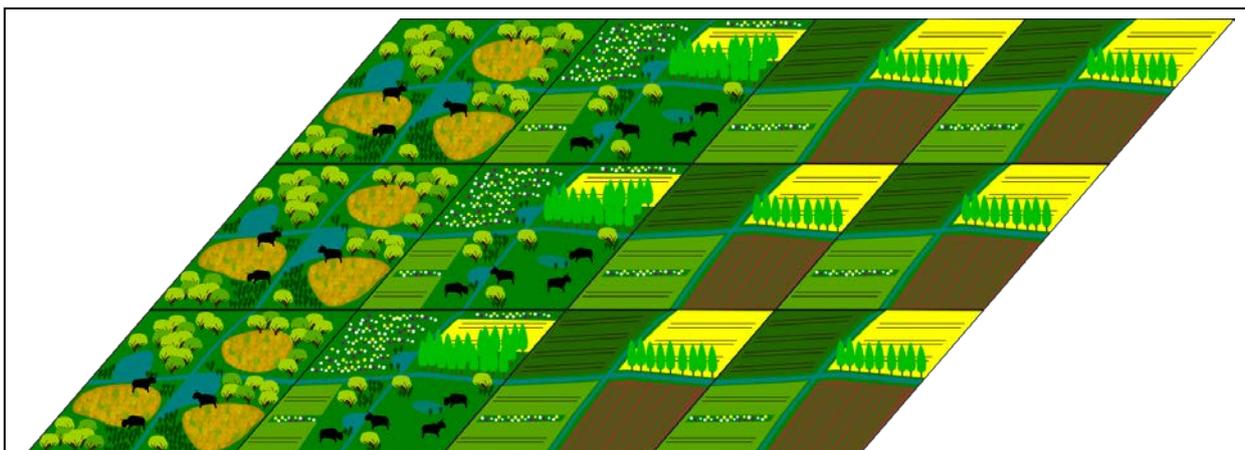
Fig 5.1 Illustration of region managed under three-compartment sparing. The region is made up of 12 'landscapes', each 100 ha in size. Three landscapes are spared as (semi-)natural habitat, represented here by fen (first column). Three landscapes are managed as low-yield, wildlife-friendly farmland, represented by mixed farmland (second column). Six landscapes are managed as high-yield farmland, represented by arable farmland (third and fourth columns).

habitats for delivering ecosystem services (and local demand for these services) should also be considered.

3. *What kind(s) of farming systems should be promoted as low-yield farmland?*
Low-yield farmland supports agricultural-adapters (winner species) which are absent from (or reach low densities in) both spared habitat and high-yield farmland. We defined low-yield farmland as land with the region-specific median yield at which species with hump-shaped density-yield curves reach peak density. This corresponds roughly to mixed farmland (arable-dominated in The Fens & Salisbury Plain, grassland-dominated in The Cotswolds and Low Weald; see **Fig. 4.12**), though the exact characteristics of low-yield farmland will depend on regional conservation priorities, which may be best delivered through the promotion of multiple types of low-yield farmland within a region. Grassland-or arable- dominated systems may be more or less suitable in different regions depending on conservation priorities, but a key element across low-yield farmland should be a reduction in management intensity (e.g. few or no chemical inputs, low stocking density, low harvest frequency).
Low-yield farming would probably deliver most gains if arranged to provide

buffers around or stepping-stones between spared semi/natural areas, (thus contributing to joined-up ecological networks; Lawton *et al.* 2010).
Finally, we acknowledge the semantic grey area between, for example, spared semi-natural grassland managed by conservation grazing and low-yield pastoral farming, though both systems are clearly distinct from high-yield farming.

4. *How should high-yield farmland be managed?*
Because land managed or spared largely for conservation is low- or zero-yielding, a substantial area of higher-yield farmland is necessary to meet any realistic regional food production requirement. Our results suggest that the environmental costs – at least those considered here – of managing this farmland at the maximum yield are outweighed by the benefits arising from minimising the area of farmland (and so maximising the area of spared semi/natural habitat and low-yield farmland).
We defined high-yield farmland as land with the region-specific maximum observed yield, reflecting the prime purpose of this land: maximising food production. This definition is crude though; more precisely, we should be interested in maximising food production

over the *long term*. High-yield farming must be sustainable and resilient. This implies that natural capital – soil structure and fertility, freshwater, and 'fossil' resources in particular – should not be used faster than it can renew itself. Functional biodiversity such as pollinators and natural enemies should also be maintained, to the extent that the costs of their conservation are compensated for by (long-term) agronomic benefits.

Providing resources for functional species could result in co-benefits to other non-beneficial farmland species, and some well-designed & strategically-implemented wildlife-friendly practices may be worth promoting within high-yield farmland (Pywell *et al.* 2015). Such efforts should aim to bend the density-yield curve upwards, by delivering more biodiversity at a given yield.

Sustainable agriculture also implies reducing the negative externalities (e.g. greenhouse gas emissions, nutrient run-off, pesticide drift) imposed on other systems. It should be born in mind, however, that any reduction in food production will demand a larger area of farmland to meet a given food production target, reducing the potential area of spared semi/natural areas which can play an important role in mitigating many of agriculture's environmental costs. As we show in **Section 2** (see also Balmford *et al.* 2018), the environmental costs associated with delivering a particular quantity of food can often be minimised by high-yield (i.e. land-efficient) farming, provided this is combined with habitat restoration. What magnitude of land sparing might be possible? A recent assessment of technically plausible potential yields suggested an upper limit of 1.3% growth per annum, averaged across major UK crop and livestock commodities (Lamb *et al.* 2016b). Even with projected increases in demand for domestic production, these yield gains could be sufficient to spare 5,043,000 hectares of land by 2050 across the UK (Lamb *et al.* 2019).

Underpinning these four questions is the issue of scale. Specifically, how large should units of spared land and low-yield farmland be (i.e. grain size), and over how large a region should three-compartment sparing be planned (i.e. extent)?

Grain size will depend partly on the ecology of target species (e.g. home range size, minimum habitat area) as well as practical considerations relating to the scale at which land-management decisions are made. Our scenarios assume a grain size of 1 km^2, though this was largely determined by the scale at which national bird and butterfly monitoring surveys are conducted. We suggest a lower bound of 0.5–1 km^2 for establishing spared areas, though larger areas are preferred, as these are likely to support larger, more robust populations, be more physically and biologically diverse and be less sensitive to negative edge effects (Lawton *et al.* 2010). In this context, it's worth noting that the median area of SSSIs in England is just 0.26 km^2, whilst lowland calcareous grassland, reedbed and broadleaved woodland have mean patch sizes of 0.11, 0.44 and 0.10 km^2, respectively (Lawton *et al.* 2010).

Sparing land at larger scales presents a considerable practical challenge given that the mean land holding size across English farms is 0.87 km^2 (Defra 2019). Restoring habitats patches > 1 km^2 in size is therefore impossible within the average land holding, so will require coordination amongst adjacent land holdings.

In terms of extent, we suggest that English National Character Areas (NCAs) provide a reasonable scale (c. 500 km^2) at which to implement three-compartment sparing strategies. Sparing land within NCAs is likely to ensure that the full suite of habitats and species is represented, and should facilitate a reasonably equitable distribution of semi/natural areas.

Policy suggestions

We suggest the following policy mechanisms for implementing a three-compartment land sparing strategy in practice.

1. *Mechanisms to support sustainable yield growth*
    Maximising long-term food production (i.e. sustainable intensification; Dicks *et al.* 2019) may require land managers to make decisions which don't make economic sense in the short-term. Access to knowledge and technology may also limit their ability to achieve high sustainable yields. At a higher level, declining investment in agricultural research and development, as well as regulations which currently limit yield-boosting technologies could be reconsidered.

2. *Mechanisms to incentivise large-scale conservation on private land*
    In contrast to current agri-environment schemes, which typically involve perhaps 5–15% of land being managed for biodiversity and ecosystem services, land sparing implies much larger areas of land – potentially entire land holdings – being restored to unfarmed habitat or managed as low-yield wildlife-friendly farming. Such land is unlikely to deliver sufficient marketable goods to turn a profit, so – given that most land in the UK is privately owned – mechanisms such as the Environmental Land Management Scheme (ELMS) could incentivise land managers to deliver conservation and ecosystem services at scale and over the long-term (Hanley *et al.* 2012).
    In addition, land sparing may require land belonging to multiple adjacent land-owners to managed for conservation, perhaps through Farm Clusters or agglomeration bonuses linked to ELMS contracts (e.g. Parkhurst *et al.* 2002).

3. *Mechanisms to link yield growth to habitat restoration*

Our results are only valid to the extent that high-yield farming results in land sparing. In fact, evidence for 'passive' land sparing is relatively weak (Ewers *et al.* 2009). Instead, policies are needed to explicitly link one to the other, or at least to ensure that both occur simultaneously (Phalan *et al.* 2016). Our results show that environmental outcomes are typically improved at lower food production targets. Underlying these supply-side mechanisms should be efforts to limit growth in demand for food and agricultural land. As the global human population grows in size and wealth, efforts to reduce inefficiencies in the food system – primarily through reductions in avoidable food waste and the consumption of animal products – will be important to curb growing global demand (Van Zanten *et al.* 2018; World Resources Institute 2018). Competition between food and biofuels should also be avoided (Cooper *et al.* 2018; World Resources Institute 2018).

Future conservation science needs

Associated with these policy requirements are several outstanding conservation science needs.

1. *National-scale prioritisation exercise*
    As described above, defining the properties of a real-world three-compartment land sparing strategy – in particular the nature of spared land and low-yield farmland, and the relative area devoted to each – will require an evidence-based assessment of regional conservation priorities.
    Regional land-use plans – perhaps forming part of the development of the Nature Recovery Network, or Local Natural Capital Plans – should identify priorities and targets for land sparing, accounting for the potential distribution of habitats, the wider importance of habitats and their associated species, and the relative agricultural potential of each region. These plans should also consider spatial variation in ecosystem service demand (e.g. flood attenuation) and

supply potential (e.g. carbon sequestration).

There is also a need for robust decision support tools to optimise the spatial placement of habitat restoration (especially for outcomes such as diffuse pollution, for which spatial placement of semi/natural areas appears crucial).

2. *Social and economic levers*

There is a large social science gap, particularly in relation to the delivery of conservation management at scale on private land. Large land holdings may present an initial opportunity to study the socio-economic levers which might deliver land sparing, but ultimately we need to better understand how to encourage coordination among adjacent land holdings.

3. *Low-cost conservation in high-yield farmland*

High-yield farmland will likely make up a large proportion of land in most regions, so efforts to bend the density-yield curve upwards will be important for halting the decline of some common and widespread species. It's important, however, that such conservation efforts avoid displacing agricultural production elsewhere. This may involve describing density-yield relationships for alternative forms of potentially wildlife-friendly systems.

When considering the food production costs of farmland conservation interventions, we should ideally quantify yields over the long-term.

Caveats and limitations

The following caveats apply to the findings of this report, and present additional science needs.

1. *Edge effects and connectivity*

When predicting the population size of breeding bird species, we did not account for edge effects, connectivity, or landscape factors. Such effects might involve small or isolated spared areas supporting lower densities than large or well-connected ones (Hinsley *et al.* 1995); spared areas adjacent to high-yield farmland supporting lower densities than spared areas adjacent to low-yield farmland (Habel *et al.* 2019); and farmland adjacent to spared areas supporting higher densities than farmland far away from spared areas (Gilroy *et al.* 2014).

The magnitude of these effects is challenging to quantify in practice, but simulation-based exercises using data from Ghana and India suggest that our approach is relatively robust (Lamb *et al.* 2016a; Balmford *et al.* 2019).

2. *Temporal dynamics*

When predicting the population size of breeding bird species, we ignored two potentially important temporal aspects. First, some populations are increasing and others are decreasing, so population densities estimated using contemporary survey data may not reflect future population densities at sites of the same yield. Extinction debts, for example, mean that it may take decades for the effects of habitat loss to manifest (Semper-Pascual *et al.* 2018). Second, we ignore the time taken for restored areas to achieve the same population densities as current spared areas.

3. *Limited regions and taxa*

The research described in this report provides, we think, convincing evidence that three-compartment sparing represents a reliable conservation approach across lowland England. Whilst this conclusion is quite intuitive, it would be worth testing elsewhere such as in regions dominated by pastoral farming, or with sandy acidic soil where heathland is the primary seminatural habitat.

Applying our model to an upland system would also be valuable, though this brings additional challenges in the form of: inter-linked farming systems, with livestock often overwintered in the

lowlands; limited remaining natural vegetation; and non-agricultural economic activities such as shooting and forestry.

In addition to birds and butterflies, density-yield curves for plant taxa as well as pollinating insects would be valuable and policy-relevant.

4. *Limited existing field data*

As described in **Section 4**, it's possible that we under-estimated bird population density in spared (woodland) habitat in Low Weald and The Cotswolds. The same is likely true in Salisbury Plain. Large patches of well-managed woodland are rare in these regions, and are poorly monitored by the national Breeding Bird Survey. Our selection of these regions as case studies was based largely on good availability of BBS data, so uncertain density estimates for spared land is likely to be an even bigger problem in other regions. Replicating our analytical approach elsewhere in England would thus require additional field data collection, in particular for the estimation of population density in spared habitat. Additionally, we were unable to collect field data to validate our estimates of agricultural yield. Although our desk-based method appears to be reassuringly robust in The Fens and Salisbury Plain (Finch *et al.* 2019), it's unclear how well it performs in grassland-dominated regions such as Low Weald. Our method does not distinguish between improved grassland under different management regimes. This is likely to add noise (rather than bias) to our yield estimates, but we recommend further effort is made to validate desk-based estimates of yields in pastoral systems.

5. *Costs of high-yield farming*

In **Section 2** we showed that land sparing can reduce regional global warming potential and nutrient export. High-yield farming is, of course, associated with additional costs which we were unable to measure, including reductions in soil quality and quantity, pollution by pesticides, anti-biotic use and animal welfare. Nor did we account for the impact of high-yield farming on functional biodiversity such as pollinating insects and natural enemies, which may be important for long-term resilience of yields.

6. *Yield currency*

We primarily refer to 'yield' in energetic terms, converting agricultural production into human-edible energy. We have previously expressed yield as edible protein, with no material change to our conclusions (Finch *et al.* 2019). Still, a balance of various macro- and micro-nutrients is important for adequate human nutrition, and quantifying food production in a currency which better reflects human nutritional requirements would better align our research with concerns relating to human health and malnutrition.

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Appendix 1: Supplementary Information for Section 2

A. Methods: land-use change algorithm

At their foundation, our scenarios involved changing the land-use of 25 m^2 units of land within 1-km squares. Specifically, our scenarios involved the conversion of spared 1-km squares to or from farmland (resulting in a wholesale change in land-use from farmland to natural or seminatural habitat), as well as the replacement within farmed 1-km squares of arable 25 m^2 units of land with non-arable ones, and vice versa (thus increasing or reducing agricultural production).

In order to update the 50-m land-use raster to reflect these land-use changes (as is required for calculating land-use change for the purposes of estimating GWP, and as an input file for the NDR model) we used a simple algorithm, as follows:

1. First, we calculated the number of 25 m^2 units of each land-use to add or remove from each 1-km square, with the sum of additions and removals necessarily equalling 0 m^2 (e.g. remove 5 units of arable; add 3 units of improved grassland; add 2 units of broadleaved woodland).

2. Next, we calculated the number of 25 m^2 units of each 'from' land-use to convert to each 'to' land-use (e.g. 3 units of arable to improved grassland; 2 units of arable to broadleaved woodland).

3. In cases where there were multiple 'to' and from 'land-uses' (e.g. 40 arable units and 60 improved grassland units to 94 chalk grassland units and 6 broadleaved woodland units), we apportioned each unit of 'to' land-use to a unit of 'from' land-use, according to the proportional area of each 'from' land-use (i.e. $94 \times \frac{40}{40+60} = 38$ arable to chalk grassland;

$94 \times \frac{60}{40+60} = 56$ improved grassland to chalk grassland; $6 \times \frac{40}{40+60} = 2$ arable to broadleaved woodland; $6 \times \frac{60}{40+60} = 4$ improved grassland to broadleaved woodland).

4. We then converted 'from' land-use pixels to 'to' land-use pixels, starting with a randomly selected 'from' land-use pixel (e.g. arable) immediately adjacent to a 'to' land-use pixel (e.g. improved grassland). Thus, new improved grassland was created next to existing improved grassland.

5. If no 'from' land-use pixels were immediately adjacent to any 'to' land-use pixels, we first converted a randomly selected 'from' land-use pixel adjacent to any other land-use. Thus, new improved grassland was seeded on the edge of arable land.

6. If no 'from' land-use pixels were adjacent to any different land-use (i.e. if the 1-km square was 100% covered by 'from' land-use) we first converted any randomly selected 'from' land-use pixel. Thus, new improved grassland was seeded anywhere within arable land.

7. We iterated this process until all 'from' 25 m^2 units had been converted to 'to' units.

B. Methods: emissions factors

In order to quantify total global warming potential (GWP) of each scenario, we used *Tier 1* emissions factors and methodologies from IPCC (2006) and IPCC (2013) for the three main greenhouse gases (CO_2, CH_4 and N_2O). We converted each gas to CO_2 equivalent (GWP_{100}) according to their radiative forcing over 100 years (CH_4 = 25·CO_2; N_2O = 298·CO_2, after Forster *et al.* (2007)). UK-specific *Tier 2* emissions factors were used for lowland peatland habitats in the UK (Evans *et al.* 2016) and for forest carbon accumulation rates (Forestry Commission 2018). For all other greenhouse gas fluxes for which IPCC *Tier 1* emissions factors did not exist (e.g. for semi-natural habitats) we used regionally appropriate peer-reviewed emissions factors, as detailed in the text.

Agricultural inputs

For improved agricultural land-uses (arable crops and improved grassland), we derived land-use-specific nitrogen application rates (kg N per ha per year, England & Wales, 2013) from the 2013 British Survey of Fertiliser Practice (Defra 2014). These national average values were multiplied by the ratio between the regional and national average arable and grassland application rates (East region for The Fens: ×1.04 on arable, ×0.84 on grass; Wessex region for Salisbury Plain: ×0.87 on arable, ×0.84 on grass). We used the Farm Business Survey to estimate the region-specific proportion of Nitrogen applied as farmyard manure (0.01 in The Fens; 0.23 in Salisbury Plain). We then used the emissions factors (kg CO_2 equiv. per kg of total, synthetic or organic N) in **Table A1** to quantify the emissions associated with nitrogen inputs.

Preliminary analysis suggested that emissions from pesticide manufacture and machinery use would be small relative to other sources, so we ignored these emissions sources.

Livestock

For grazed land-uses (improved, calcareous and neutral grassland and fen/marsh/swamp) we estimated stocking rates of beef cattle, dairy cattle and sheep as described in **Table A2**. We used the emissions factors in **Table A3** to estimate the emissions associated with enteric fermentation and manure management, assuming daily nitrogen excretion rates of 0.198, 0.202 and 0.041 kg N per head for beef, dairy and sheep, respectively (assuming respective body masses of 600, 420 and 48.5 kg; IPCC 2006). We assumed that sheep were outside year-round, dairy cattle (on improved grassland in Salisbury Plain only) were outside for 164 days a year, and beef cattle were outside for 240 days a year on improved grassland, 200 days a year on neutral grassland and fen/marsh/swamp, and year-round on calcareous grassland (**Table A2**). For the portion of the year spent outside, we treated excreted (organic) N as in **Table A1**.

Woodland

According to the Forestry Commission's Biomass Carbon Lookup Table (2018), and following Lamb *et al.* (2016b), we used the emissions factors in **Table A4** to estimate mean annual sequestration from woodland, annualised over a 200-year growing cycle (with a 0% discount rate).

Soil

On non-peat soil (skirt soil in The Fens and all soils in Salisbury Plain) we assumed that all soil carbon was at equilibrium, and estimated the annualised change in soil carbon over 50 years following land-use change (between arable, grassland and woodland) using the equation:

$$\frac{C_0 - \left(C_f - \left(C_f - C_0 \right) \times e^{t/\frac{k}{\log(0.01)}} \right)}{t}$$

Where C_0 and C_f are the soil carbon densities of the previous and new land-use (120, 146 and 150 t C per ha for arable, grassland and woodland, respectively), t is the time period (50 years) and k is a time

constant (200 when $C_f > C_0$ and 100 when $C_f < C_0$) (Lamb *et al.* 2016b).

On organic soil (and wet skirt soil) in The Fens, we used the land-use specific emissions factors in **Table A5** for drained and wet soil representing CH_4, CO_2 and N_2O fluxes from land, CH_4 flux from ditches, and losses of dissolved organic carbon (DOC). For drained soil, emissions factors were available from IPCC (2013) for arable, grassland and woodland, and from Evans *et*

al. (2016) for arable and grassland. For wet soil, emissions factors were available from IPCC (2013) for fen, and from Evans *et al.* (2016) for fen and neutral (extensive) grassland. Where emissions factors were available from both IPCC (2013) and from Evans *et al.* (2016), we used each separately and tested the sensitivity of our results. For newly re-wetted soils we applied a methane spike of 25 t CO_2 *equiv.* per ha (representing 2.5 t CO_2 *equiv.* per ha per year for 10 years) (Lamb *et al.* 2016b).

Table A1 Emissions associated with nitrogen inputs

Source	Emissions Factor	Min	Max	Units	Reference
Direct N_2O emissions	9.4	2.81	28.10	kg CO_2 equiv. per kg total N	IPCC 2006 Chapter 11
N_2O volatilisation	0.9	0.06	14.05	kg CO_2 equiv. per kg synthetic N	IPCC 2006 Chapter 11
N_2O volatilisation	1.9	0.09	23.41	kg CO_2 equiv. per kg organic N	IPCC 2006 Chapter 11
N_2O run-off	2.1	0.06	14.05	kg CO_2 equiv. per kg total N	IPCC 2006 Chapter 11
Synthetic N manufacture[1]	5.6	2.8	8.4	kg CO_2 equiv. per kg synthetic N	Yara

[1] No uncertainty given, so we assume ± 50%

Table A2 Livestock stocking density and pasture days

Region	Land-use	Animal	Head per ha per year	Pasture days per year	Reference
The Fens	Improved grassland	Beef cattle	1.05	240	Stocking density from FBS[1], pasture days from UKGHI[2]
		Sheep	0.85	365	Stocking density from FBS[1]
	Neutral grassland	Beef cattle	1.01	200	Landowner survey
	Fen/marsh/swamp	Beef cattle	0.3	200	Landowner survey
Salisbury Plain	Improved grassland	Beef cattle	0.903	240	Stocking density from FBS[1], pasture days from UKGHI[2]
		Dairy cattle	0.449	164	Stocking density from FBS[1], pasture days from UKGHI[2]
		Sheep	0.413	365	Stocking density from FBS[1]
	Calcareous grassland	Beef cattle	0.1	365	Landowner survey
		Sheep	0.2	365	Landowner survey

[1] Farm Business Survey (Duchy College Rural Business 2017)
[2] Annex to (DECC 2013) UK Greenhouse Gas Inventory, 1990 to 2011; Annual Report for Submission under the Framework Convention on Climate Change

Table A3 Emissions associated with livestock production

Source	Animal	Emissions Factor	Min	Max	Units	Reference
CH$_4$ (enteric fermentation)[1]	Beef cattle	1425	712.5	2137.5	kg CO$_2$ equiv. per head per year	IPPC 2006, Chapter 10
	Dairy cattle	2925	1462.5	4387.5		
	Sheep	200	100	300		
CH$_4$ (manure)[1]	Beef cattle	150	75	225	kg CO$_2$ equiv. per head per year	IPPC 2006, Chapter 10
	Dairy cattle	525	262.5	787.5		
	Sheep	4.8	2.4	7.2		
N$_2$O (winter manure)	Cattle	4.7	0.0	9.4	kg CO$_2$ equiv. per kg N excreted indoors	IPPC 2006, Chapter 10

[1] No uncertainty given, so we assume ± 50%

Table A4 Carbon emissions from forestry (t CO$_2$ equiv. per ha per year), representing the mean annual sequestration over a 200-year growing cycle, assuming no thinning. Min and max represent ± 2 yield classes

Species (yield class)	Region	Land-use	Emissions Factor	Min	Max	Reference
Beech (8)	Salisbury Plain	Broadleaf woodland	–7.8	–6.5	–9.0	
Douglas Fir (14)	Salisbury Plain	Coniferous woodland	–6.6	–5.9	–7.2	Forestry Commission
Sycamore/Ash/Birch (6)	The Fens	Broadleaf woodland (dry)	–4.0	–3.1	–5.0	
Willow/Birch (4)	The Fens	Broadleaf woodland (wet)	–3.1	–2.3 [1]	–4.0	

[1] No yield class 2, so we assumed the difference between yield classes 4 and 2 was equal to the difference between yield classes 4 and 6.

Table A5 Emissions factors for drained and wet organic soils (kg CO_2 equiv. per ha)

Source	Land-use	Emissions Factor	Min	Max	Sum × 0.001	Reference
CH_4 ditch[1]	Arable	29125	8375	49875	43.7	IPCC 2013
CH_4 land		0	−70.0	70		
CO_2 land		28966.7	23833.3	34466.7		
DOC		1136.7	696.7	1686.7		
N_2O land		12175.4	7679.9	16858.3		
CH_4 ditch[1]	Arable[3]	85.0	0.0	170.0	38.7	Evans *et al.* 2016
CH_4 land		−70.0	-100.0	−40.0		
CO_2 land		26335.0	24860.0	27810.0		
DOC		216.0	198.0	234.0		
N_2O land[2]		12175.4	7679.9	16858.3		
CH_4 ditch[1]	Fen[4]	0	0	0	9.9	IPCC 2013
CH_4 land		7200	0	28533.3		
CO_2 land		1833.3	−2603.3	6270		
DOC		880	513.3	1320		
N_2O land		0	0	0		
CH_4 ditch[1]	Fen[5]	590.0	295.0	885.0	−2.8	Evans *et al.* 2016
CH_4 land		2180.0	1090.0	3270.0		
CO_2 land		−5130.0	−2565.0	−7695.0		
DOC		135.0	67.5	202.5		
N_2O land[2]		0	0	0		
CH_4 ditch[1]	Grassland[6]	13175	7125	19225	17.5	IPCC 2013
CH_4 land		975	−72.5	2025		
CO_2 land		13200	6600	19800		
DOC		1136.7	696.7	1686.7		
N_2O land		1498.5	524.5	2528.7		
CH_4 ditch[1]	Grassland[7]	200.0	100.0	300.0	18.0	Evans *et al.* 2016
CH_4 land		−50.0	−25.0	−75.0		
CO_2 land		15870.0	7935.0	23805.0		
DOC		648.0	324.0	972.0		
N_2O land[2]		1498.5	524.5	2528.7		
CH_4 ditch[1]	Woodland	5425	1025	9825	13.6	IPCC 2013
CH_4 land		62.5	−15.0	142.5		
CO_2 land		9533.3	7333.3	12100		
DOC		1136.7	696.7	1686.7		
N_2O land		2622.4	−533.8	5713.1		
CH_4 ditch[1]	Neutral grassland[8]	1000.0	500.0	1500.0	12.7	Evans *et al.* 2016
CH_4 land		-60.0	-30.0	-90.0		
CO_2 land		10930.0	5465.0	16395.0		
DOC		306.0	153.0	459.0		
N_2O land[2]		1498.5	524.48	2528.7		

[1] Figures are expressed per ha of ditch, which we assume make up 5% of land area

[2] N_2O emissions from IPCC 2013 wetlands supplement

[3] Mean of sites EF-DA and EF-SA

[4] "Shallow-drained, nutrient-rich" as defined by IPCC

[5] Site EF-LN ± 50%

[6] "Nutrient rich" as defined by IPCC

[7] Site SL-IG ± 50%

[8] Site SL-EG ± 50%

C. Methods: yield growth

To evaluate a land-sparing upper limit, we increased the per hectare yields of agricultural land-uses, extending our extreme sparing scenarios to allow even more habitat restoration.

Lamb *et al.* (2016b) report upper-bound estimates of crop yield increases and livestock feed-conversion efficiency improvements, based on an expert-led assessment of the technical potential of the UK agriculture sector. In addition to extreme sparing with no yield growth, we explore 5 scenarios of yield growth, reflecting improvements over 50 years equivalent to 10, 20, 30, 40 and 50% of the upper bound annual growth rates suggested by Lamb *et al.* (2016b). Our upper limit is therefore conservative. For example, Lamb *et al.* (2016b) report an upper bound of 1.016% for cereal yield annual growth, resulting in a 118% increase over 50 years; our most extreme scenarios assumed a 59% increase in cereal yields over 50 years.

Birds

We assumed that a given increase in the average yield of a 1-km square would have an equivalent effect on bird density whether arising due to land-use change (i.e. more arable) or yield growth. We therefore used density-yield curves as described in the main text to estimate bird population density (and thus regional population size) of each species, according to the average yield of each 1-km square.

Global warming potential

For arable land-uses, we increased nitrogen application rates in proportion to the per hectare yield increase, assuming that a 59% in yield would require an equivalent increase in fertiliser application.

For improved grassland we assumed an equivalent increase in stocking density, resulting in a proportional increase in the emissions associated with manure management and enteric fermentation.

Nutrient export

For arable land-uses, we increased nitrogen and phosphorus loading values in proportion to the per hectare yield increase, assuming that a 59% in yield would require an equivalent increase in fertiliser application.

D. Results: GWP uncertainty

In The Fens, two sources of emissions factor estimates were available for greenhouse gas fluxes associated with drained and wet organic soils. The results reported in the main text used emissions factors from Evans *et al.* (2016), reflecting UK-specific estimates of emissions factors for lowland peat. Emissions factors from IPCC (2013) were slightly higher (i.e. higher emissions from arable on drained organic soil, and net emissions rather than net sequestration on wet fen), resulting in higher total net GWP across the sharing-sparing continuum (**Fig. A1**). For some scenarios (e.g. *Least cost* extreme sparing) GWP was lower than under

Business as Usual when Evans *et al.* (2016) emissions factors, but higher than *Business as Usual* when using IPCC (2013) emissions factors. Otherwise, our conclusions are essentially unchanged: *Deep peat* extreme sparing is overwhelmingly the best strategy for minimising GWP (even when, as IPCC (2013) assumes, wet fen is a net emitter of greenhouse gases).

Using the upper or lower bound estimates of each emissions factor, as opposed to the point estimate, made relatively little difference to the predicted change in GWP across the sharing-sparing continuum (**Fig. A2**)
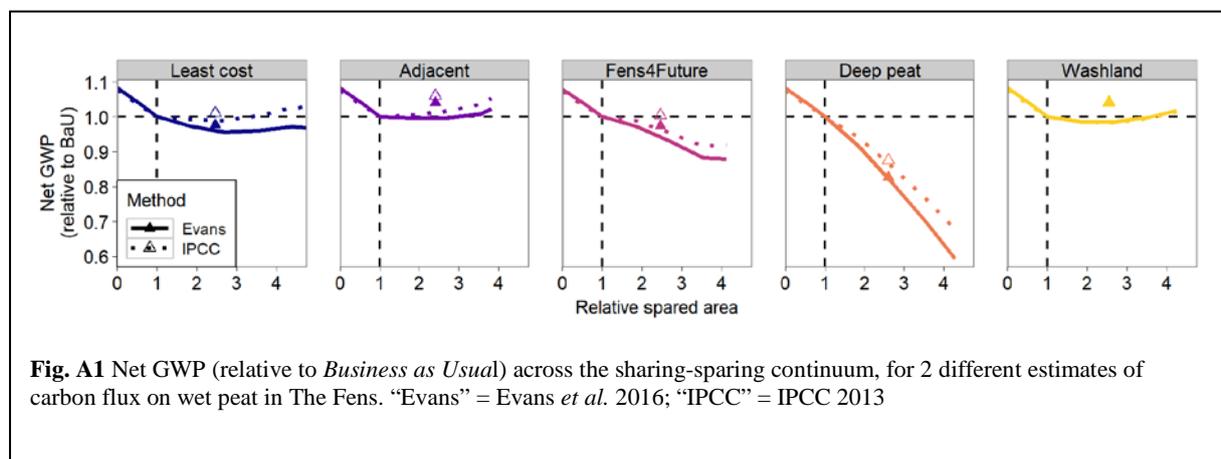
Fig. A1 Net GWP (relative to *Business as Usual*) across the sharing-sparing continuum, for 2 different estimates of carbon flux on wet peat in The Fens. "Evans" = Evans *et al.* 2016; "IPCC" = IPCC 2013
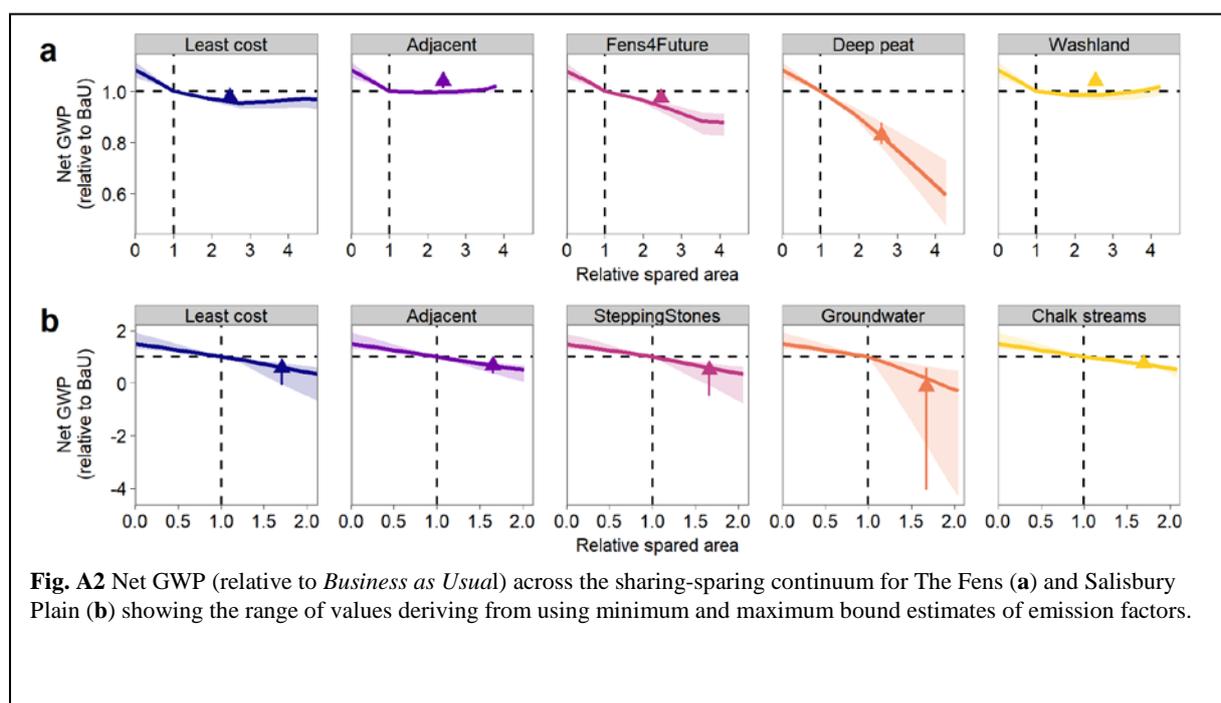
Fig. A2 Net GWP (relative to *Business as Usual*) across the sharing-sparing continuum for The Fens (**a**) and Salisbury Plain (**b**) showing the range of values deriving from using minimum and maximum bound estimates of emission factors.

E. Results: production target

At increased production targets, higher mean farmland yields are required to deliver regional production for a given area of spared land.

Bird population size

Geometric mean relative population size was maximised at $P = 0.75$ for both winner and loser species in The Fens, but only for loser species in Salisbury Plain (**Fig. A3**). In Salisbury Plain, winner species achieved maximum geometric mean relative population size under land sharing at $P = 1.25$. At higher production targets, the optimum strategy for winner species (and all species on average) shifted towards extreme land sparing. Maximum geometric mean relative population size across all species

was, therefore, rather insensitive to P in Salisbury Plain.

GWP

In both regions, net GWP (relative to *Business as Usual*) was minimised at $P = 0.75$, especially in The Fens (**Fig. A4**). At lower production targets in The Fens, increasingly extreme land sparing eventually resulted in an upwards trajectory in GWP, after all drained peat has been wetted and the benefits of habitat restoration for carbon sequestration diminish.

Nutrient export

In both regions, both N and P export were minimised at $P = 0.75$ (**Fig. A5**, **Fig. A6**). Differences in N and P export between different production targets were much greater than differences across the sharing-sparing continuum.
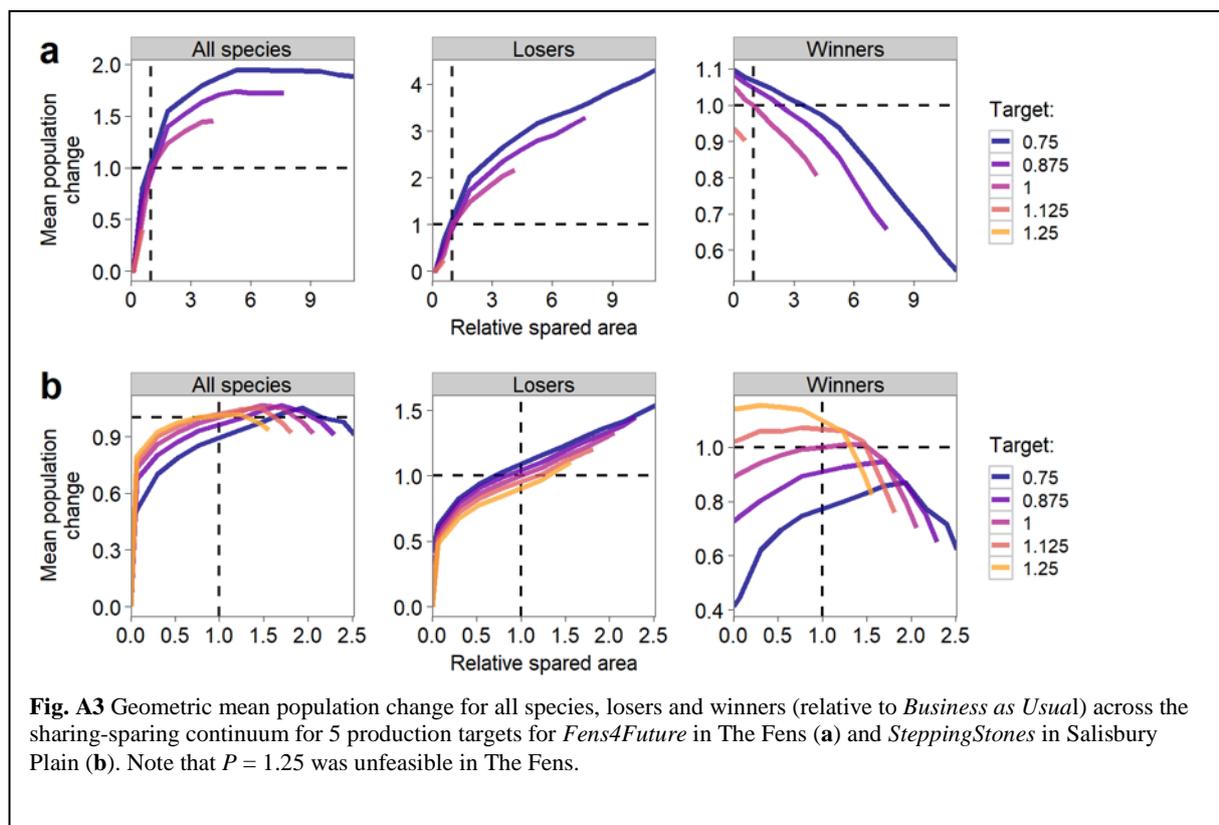
Fig. A3 Geometric mean population change for all species, losers and winners (relative to *Business as Usual*) across the sharing-sparing continuum for 5 production targets for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Note that $P = 1.25$ was unfeasible in The Fens.
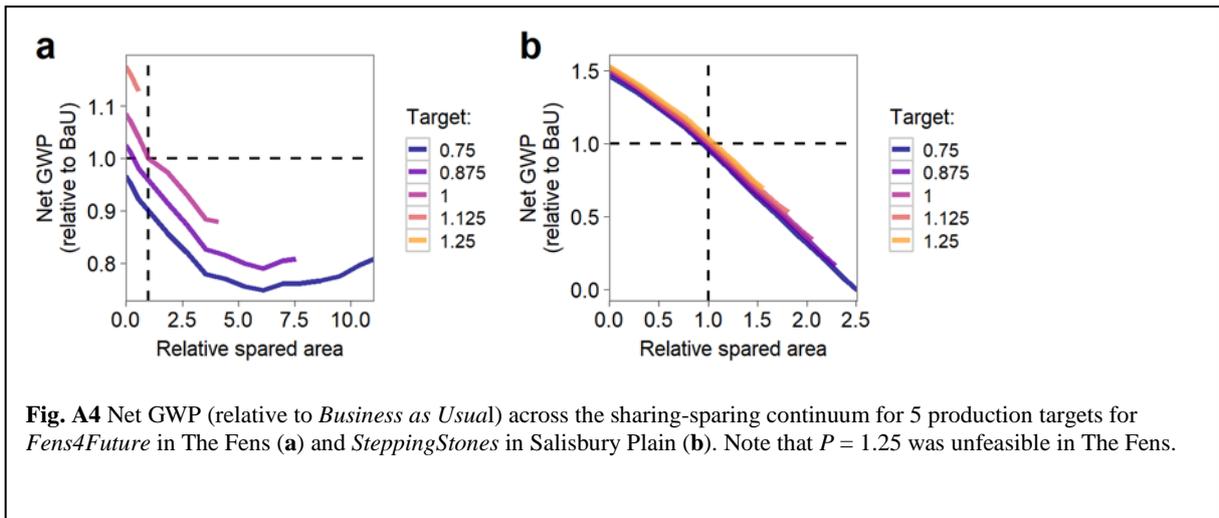
Fig. A4 Net GWP (relative to *Business as Usual*) across the sharing-sparing continuum for 5 production targets for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Note that $P = 1.25$ was unfeasible in The Fens.
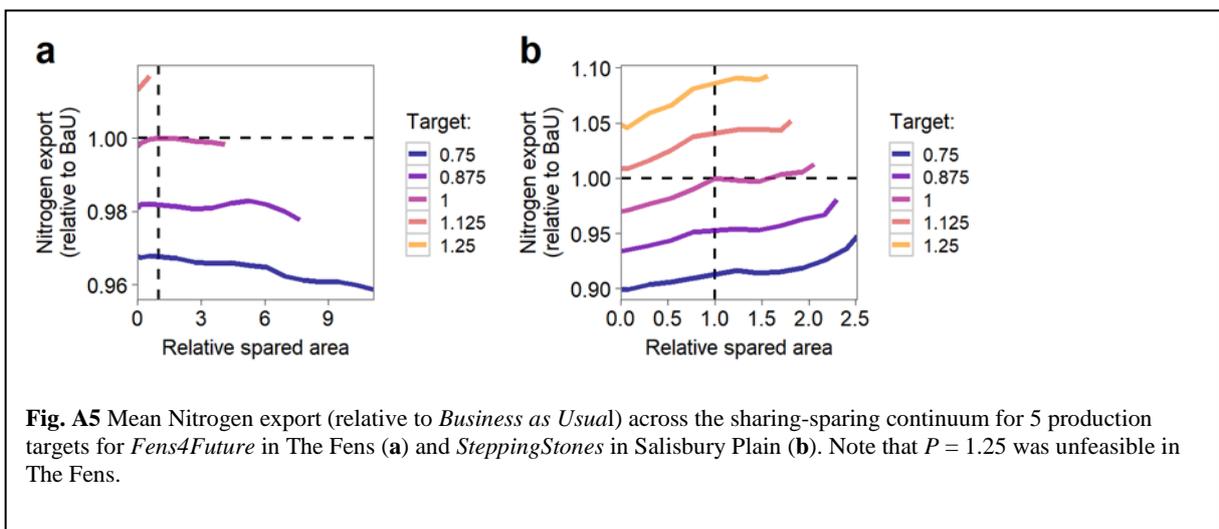
Fig. A5 Mean Nitrogen export (relative to *Business as Usual*) across the sharing-sparing continuum for 5 production targets for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Note that $P = 1.25$ was unfeasible in The Fens.
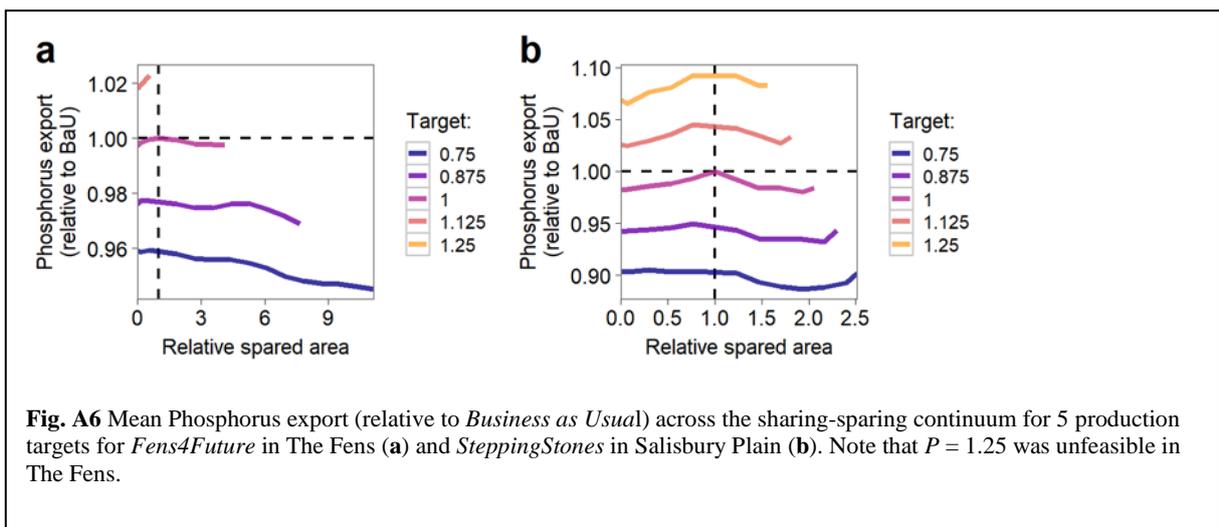
Fig. A6 Mean Phosphorus export (relative to *Business as Usual*) across the sharing-sparing continuum for 5 production targets for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Note that $P = 1.25$ was unfeasible in The Fens.

F. Results: yield growth

Further extending the sharing-sparing continuum by increasing the per-hectare yield of agricultural land-uses resulted in a substantial increase in the potential area of spared land.

Birds

For birds, our density-yield curve approach is 'blind' to whether variation in yield is driven by land-use change or change in per-hectare yields. Yield growth scenarios essentially resulted in an extrapolation of the patterns described previously, with loser species seeing increasingly high geometric mean relative population size with yield growth, and winners seeing increasingly low geometric mean relative population size (**Fig. A7**).

GWP

We assumed that yield growth would be associated with a proportional increase in agricultural inputs. In both regions, these additional input-associated emissions were outweighed by the additional carbon sequestration associated with land sparing, though increasingly extreme land sparing in The Fens eventually resulted in an upwards trajectory in GWP, after all drained peat has been wetted and the benefits of habitat restoration for carbon sequestration diminish (**Fig. A8**).

Nutrient export

We assumed that yield growth would be associated with a proportional increase in fertiliser inputs. In The Fens, these additional nutrient inputs were outweighed by the additional nutrient sequestration associated with land sparing, such that increasingly extreme land sparing resulted in increasingly low N and P export (**Fig. A9**). In Salisbury Plain, N & P export both increased with increasing yield growth but declined at very high levels of yield growth, presumably due to the location of spared habitat unlocked at very high levels of land sparing (**Fig. A10**).

Fig. A7 Geometric mean population change for all species, losers and winners (relative to *Business as Usual*) across the sharing-sparing continuum for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Line shows scenarios with no yield growth, and points show extreme scenarios with yield growth increasing from 10% to 50% of the technical upper limit.

Fig. A8 Net GWP (relative to *Business as Usual*) across the sharing-sparing continuum for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Line shows scenarios with no yield growth, and points show extreme scenarios with yield growth increasing from 10% to 50% of the technical upper limit.

Fig. A9 Mean Nitrogen export (relative to *Business as Usual*) across the sharing-sparing continuum for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Line shows scenarios with no yield growth, and points show extreme scenarios with yield growth increasing from 10% to 50% of the technical upper limit.

Fig. A10 Mean Phosphorus export (relative to *Business as Usual*) across the sharing-sparing continuum for *Fens4Future* in The Fens (**a**) and *SteppingStones* in Salisbury Plain (**b**). Line shows scenarios with no yield growth, and points show extreme scenarios with yield growth increasing from 10% to 50% of the technical upper limit.