PROCEEDINGS OF
THE ROYAL SOCIETY B
BIOLOGICAL SCIENCES

Land sparing to make space for species dependent on natural habitats and High Nature Value farmland

Journal:	*Proceedings B*
Manuscript ID	RSPB-2019-1483.R1
Article Type:	Research
Date Submitted by the Author:	02-Aug-2019
Complete List of Authors:	Feniuk, Claire; University of Cambridge, Zoology Department Balmford, Andrew; University of Cambridge, Zoology Green, Rhys; University of Cambridge, Zoology Department
Subject:	Ecology < BIOLOGY, Environmental Science < BIOLOGY
Keywords:	agriculture, biodiversity, High Nature Value farming, Wildlife-friendly farming, sustainable intensification
Proceedings B category:	Global Change & Conservation

Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
This article does not present research with ethical considerations

Statement (if applicable):
CUST_IF_YES_ETHICS :No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
Data and code supporting this article are provided in the electronic supplementary material and in the following uploaded files: 2014_regional_production.csv, 2050_scenarios.csv, Bird_data.csv, Bird_dyfunction_params.csv, Sedge_data.csv, Sedge_dyfunction_params.csv, Site_information.csv, Rcode.txt and read_me.txt.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
All authors designed the study. C.F. collected the field data. C.F. and R.E.G. carried out the statistical analyses. All authors wrote the manuscript and gave final approval for publication.

Land sparing to make space for species dependent on natural habitats and High Nature Value farmland

Claire Feniuk[1,2], Andrew Balmford[1] and Rhys E. Green[1,2]

[1]Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

[2]Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DL, UK

Author for correspondence: reg29@cam.ac.uk

Empirical evidence from four continents indicates that human food demand may be best reconciled with biodiversity conservation through sparing natural habitats by boosting agricultural yields. This runs counter to the conservation paradigm of wildlife-friendly farming which is influential in Europe, where many species are dependent on low-yielding High Nature Value farmland threatened by both intensification and abandonment. In the first multi-taxon population-level test of land-sparing theory in Europe, we quantified how population densities of 175 bird and sedge species varied with farm yield across 26 1-km squares in eastern Poland. We discovered that, as in previous studies elsewhere, simple land sparing, with only natural habitats on spared land, markedly out-performed land sharing in its effect on region-wide projected population sizes. However, a novel "three-compartment" land-sparing approach, in which about one-third of spared land is assigned to very low-yield agriculture and the remainder to natural habitats, resulted in least-reduced projected future populations for more species. Implementing the three-compartment model would require significant reorganisation of current subsidy regimes, but would mean high-yield farming could release sufficient land for species dependent on both natural and High Nature Value farmland to persist.

Keywords: agriculture, biodiversity, land sharing, farm yield, High Nature Value farming, wildlife-friendly farming, sustainable intensification

1. Introduction

Recent calls to set aside up to half the Earth's surface primarily for wild nature [1] are mute on the important question of how to produce sufficient food for over 7 billion people on the remaining half [2]. Even the widely accepted Aichi Targets of the Convention on Biological

Diversity envisage protecting 17% of terrestrial ecosystems by 2020 (Target 11), while simultaneously managing areas under agriculture, aquaculture and forestry in ways that ensure biodiversity conservation (Target 7) [3]. Yet cropland and pasture already cover nearly 40% of the Earth's ice-free land surface, and population growth and rising per capita demand mean that, by some forecasts, humanity's total demand for food and other farmed products is likely to double between 2000 and 2050 [4,5]. So how might these two apparently conflicting imperatives of meeting human food needs and safeguarding biodiversity be reconciled?

The recent literature on this topic has been dominated by two contrasting alternatives. Many conservationists advocate wildlife-friendly farm practices, such as retaining or restoring hedgerows and ponds, changing the timing of sowing or harvesting and limiting the use of agrochemicals, in order to boost populations of wild species within farmed landscapes [6]. However, this land-sharing approach often lowers farm yields (production per unit area of the landscape) and hence increases the total area of farmland needed for a given level of production. Hence, others have proposed land sparing, in which maximising agricultural yields allows land not required for food production to be used to retain or restore tracts of natural habitat away from farmland [7].

Quantitative evaluations of these approaches, based upon how the population densities of individual species vary in relation to farm yield, have produced remarkably consistent findings [8]. Detailed studies on four continents and involving 1599 species of birds, butterflies, dung beetles, trees, daisies and grasses indicate that most species are sufficiently sensitive to agricultural disturbance that they would have their largest total region-wide populations (on farmed and unfarmed land combined) if high-yield farming was adopted and linked to the conservation of natural habitats on spared land [9–15]. All studies that reach contrasting conclusions have not considered yields, have not examined natural habitats or high-yield landscapes, or have used only crude metrics of biodiversity such as species richness [8,16,17].

No study has yet explored the impacts on region-wide population sizes of land sharing, sparing and intermediate approaches for a wide range of individual species in Europe. However, a pioneering study of butterflies in England [18] assessed the potential effects of varying the areas of conventional farming, organic farming and nature reserves on the region-wide population of all species combined, whilst maintaining agricultural production constant. The study concluded that the total butterfly population would be largest with exclusively conventional farming, when combined with nature reserves, at the currently observed lower yields of organic compared with conventional farming. Only if the yield of organic farming was to exceed 87% of that of conventional farming would this conclusion change. This study did not assess region-wide populations of individual species, as we do here. The dearth of European studies to do this is significant, because the European biota might plausibly be expected to be relatively rich in species tolerant of farming, which would make land sparing less likely to result in the largest population size for the majority of species, because of selection pressures imposed by successive episodes of rapid vegetation change driven by glacial cycles [19], followed by thousands of years of agriculture and forest exploitation. A large proportion of European species, particularly those of high conservation concern, appear to be largely or wholly dependent on areas of extensive agricultural management (e.g. [20–22]). Often described as 'High Nature Value farmland' (HNVf) [23–25], these low-yielding farm systems are declining in extent across the continent as a result of abandonment and intensification [26]. In response (and echoing the Aichi Targets), many of those promoting biodiversity conservation in Europe call for both increased protection of natural habitats and more wildlife-friendly management of farmland [27,28]. Yet how can both these objectives be achieved without increasing the environmental impact elsewhere of Europe's already substantial food imports?

Here we address these gaps in knowledge by quantifying how local population densities of large numbers of bird and sedge species vary with increasing farm yield across a gradient of land-use intensity in eastern Poland. We then explore the relative benefits of land sharing and land sparing through the simple "two-compartment" model of Green et al. [7], which assigns land either to farmland, all of which is farmed at the same yield, or to zero-yielding natural habitats. However, in a European context, a more sophisticated framework in which high-yield farming spares land both for natural habitats and low-yielding HNVf might identify scenarios that result in higher projected region-wide populations for more species than the two-compartment land sparing approach. We therefore use the same data to assess outcomes from three-compartment land sparing, in which a third compartment comprises HNVf. Our results suggest this latter approach offers a promising solution to simultaneously meeting food demand and the conservation needs both of wild species which depend upon natural habitats and those currently dependent on extensively-managed farmland.

2. Materials and methods

(a) Study region and survey sites

The study was conducted in a 14,000 km^2 area of the Polesian lowlands in the Lubelskie region of eastern Poland. The expected vegetation of the region in the absence of human influence would be mixed deciduous/coniferous forest, with floodplain grassland, fen mires, peat bogs and other wetland habitats in river valleys. Current non-urban land comprises permanent arable land (40%), mosaics of mixed arable/grassland agriculture (16%), grassland (13%, including meadows, pastures and some natural floodplains, forest (16%, both natural and managed), and wetlands (2%, marshes and peatbogs). We chose 26 1-km square study sites to cover a gradient of agricultural use. Nine squares in protected areas comprised only natural habitats and had no agricultural yield (four with mixed/deciduous forests, which were not old-growth, and five with floodplains and fen mires). The remaining 17 study squares included farmed land and were chosen to span a range from low-yielding through to high-yielding agricultural land. These farmed squares were located on both 'forest' soils (n = 8 sites) of the same type as for the zero-yield forest squares and on floodplain soils (n = 9) like those of the wetland sites. Study squares were selected to be surrounded by a 1-km buffer with similar land cover to minimise the influence of neighbouring land uses. We did this to facilitate the simulation of region-wide population sizes of species under the assumption that land uses would be assigned to large contiguous tracts of land. See electronic supplementary material for further details.

(b) Agricultural yields

We estimated the mean annual food energy yield in GJ ha^{-1} yr^{-1} for each study square from the extents of natural vegetation and each type of cropland and pasture within it and the annual yield of agricultural produce of each land-cover type, in terms of mass per unit area. Yields were obtained from a combination of interviews with farmers, data submitted by local agricultural advisors and regional agricultural statistics published by the local government. Product-specific edible proportions of harvested crop and energy values taken from the literature were used to convert the results to food energy. The yield averaged over the whole study square was then obtained as the sum of products of land type-specific areas and yields. See electronic supplementary material and [29] for further details.

(c) Species' population densities

We used data from surveys conducted in spring/summer 2013 and 2014 in each study square to estimate the population densities, averaged over the whole square, of 125 breeding bird species and 50 sedge species. See electronic supplementary material for details of field survey methods and density estimation.

(d) Density-yield functions

We used regression methods to fit smooth parametric functions to the relationship, for each species, between its observed population density in a survey square and the agricultural yield of the whole square. The family of functions used allows the relationship of density to yield to be monotonic increasing or decreasing, or sigmoid, or to be hump-shaped or U-shaped with symmetrical or asymmetrical form and one peak or trough. This set of functions has been found in previous studies [8,9] to approximate the observed form of the survey data reasonably well, whilst having a small number of fitted parameters. The dependent variable for birds was the count of the focal species observed on transects in each site. We conducted non-linear Poisson regression with a logarithmic link function and with the logarithm of the total effective area surveyed in the square as an offset term. This makes the fitted regression equivalent to a model of density in relation to yield. The dependent variable for sedges was the mean proportion of the area within quadrats surveyed in the square which was covered by a given species. We fitted the same types of function as for birds, but used non-linear least squares regression because the data were not counts. We allowed for possible differences between the two soil types by fitting density-yield functions by regression in which parameters were assumed either to be the same as, or to differ between, soil types and then applying a model section procedure to choose an appropriate model for each species (see electronic supplementary material). To simulate outcomes of a three-compartment land sparing scenario (see Methods section (f) below), we used the mean, across a set of species, of the yield at which the population density was greatest. To obtain these values, we examined each species' fitted density-yield curves.

(e) Simulation of region-wide species' population sizes for land-sharing and two-compartment land-sparing land-use scenarios

We followed the approach of previous studies [7,9] by simulating the region-wide population size of each bird and sedge species, on farmed and unfarmed land combined, under simplified hypothetical land-use scenarios. At one extreme, our land-sharing scenario assumed that the entire region was farmed at the 'lowest permissible' yield, which is the minimum just sufficient to meet a level of regional production, as specified in each of the range of region-wide food energy production level scenarios we considered (see below), if the entire region is farmed [7]. At the other extreme, our two-compartment land-sparing scenario assumed that part of the region, whose extent was determined by the specified level of region-wide food energy production, was farmed at the highest attainable yield and all other land not required to achieve that production was covered by natural habitats. Following previous studies [9], we took the highest attainable yield to be 1.25 times the maximum yield observed in our study squares. This multiplier of the highest observed yield is arbitrary, but a value greater than 1 is justified because our sample of farmed squares was small and the true maximum attainable yield would therefore be underestimated by the observed maximum. It has been shown for other datasets that changing the assumed multiplier makes little difference to the conclusions drawn, as was also found to be the case here, Appendix 4 of ref. 29]. We assumed that natural habitats would comprise forests and wetlands in the present-day proportion of forest and wetland soils (75% forest, 25% wetland). Region-wide populations were calculated from simulated areas of land with different yields and yield-specific population densities obtained from the fitted density-yield functions. We also simulated region-wide population sizes of every species under intermediate-yield scenarios in which land was farmed at a range of yields between the lowest permissible and the highest attainable, in intervals of 1 GJ ha^{-1} yr^{-1}. For each simulation, we assumed that all land not required to achieve a specified level of food energy production was covered by natural habitats.

We performed these simulations for a wide range of region-wide food energy production levels from 1 to 99 GJ ha^{-1} yr^{-1}, averaged over the study region. The highest production level we considered is that which would result from farming the whole region at the highest attainable yield. However, we focussed on the annual regional production for 2014, based on current land use, and two illustrative production scenarios for 2050: (i) 'Business as Usual', which assumed that total regional food energy production continues to increase in line with 2005-2014 trends, resulting in a 72.5% increase in by 2050, and (ii) 'Lower Bound', which assumed that combined demand from the agricultural sector, comprising consumption, exports and biofuel production, was capped at 2014 levels and that edible food waste was reduced by half, resulting in a 17.5% decrease in required production by 2050 compared with 2014. For each simulation, we classified every species according to whether its region-wide population was highest for land sharing, land sparing, or when land was farmed at an intermediate yield. Further details of simulations are given in the electronic supplementary material.

(f) Simulation of three-compartment land sparing

We modified the land-sparing scenarios described above by assuming that land spared from farming by producing food at the highest attainable yield was divided between natural habitat and extremely low-yielding farmland, extensively managed to benefit wild species as HNVf. We took as the food energy yield of the HNVf compartment the mean yield of our nine farmed study sites for which site-level yield was below the lowest permissible for the Lower Bound production scenario (8 GJ ha^{-1} yr^{-1}). This choice was also guided by the yields at which many species of birds and sedges showed a peak in their population density (see Results (b)). We then used the density-yield functions to estimate the expected density of each species on HNVf with this yield. We conservatively assumed that HNVf makes no contribution to total region-wide food production, as this allows for management of the third compartment to be focused on conservation rather than agricultural outcomes. We also needed to define the proportion of spared land comprising HNVf, rather than natural habitats. We did this by varying the proportion of spared land comprising HNVf iteratively to find the value which maximised the geometric mean, across all bird and sedge species, of the ratio of total region-wide population under three-compartment sparing to the estimated total regional population with land use as it was in 2014. This was done for each production level. For each region-wide production level, we then counted the number of species for which the total regional population was highest with farming at the lowest permissible yield (land sharing), the highest attainable yield with all spared land assigned to natural habitat (two-compartment land sparing), or the highest attainable yield where spared land is divided between natural habitat and HNVf (three-compartment land sparing).

(g) Region-wide species' populations in 2050 relative to those in 2014

To assess the overall consequences of these alternative land-use scenarios we calculated the ratio of each species' region-wide population to its regional population estimated from 2014 patterns of land use for each focal 2050 production scenario. We then took the geometric mean of these ratios across species. We also counted the numbers of species in the following categories of projected 2014 – 2050 population change: 'severe decline' (>50% decline); 'decline' (up to 50%); 'increase' (up to 100% increase) and 'major increase' (>100% increase).

3. Results

(a) Region-wide population outcomes for the land-sharing and two-compartment land-sparing scenarios

When spared land was assumed to support only natural habitats, most species of birds had their highest projected region-wide populations (on farmed and unfarmed land combined) when farming was at the highest attainable yield (figure 1). This result held at all levels of region-wide food energy production we considered, and the ratio of the number of species potentially benefitting from land sparing to those benefitting from land sharing increased as the assumed production level increased. A similar pattern was seen for sedges, but the proportion of species potentially benefitting from land sparing was higher for sedges than for birds at all production levels. For both taxa, there was a minority of species for which the total population was highest with farming at a yield intermediate between the lowest permissible and highest attainable yields, but this proportion decreased rapidly as the assumed production level increased.

(b) Yield at which maximum population density occurred

Species which have a 'humped' density-yield function, with a peak in their population density in farmed landscapes at a yield between zero and the maximum attainable yield, potentially have their highest region-wide population size in two-compartment scenarios with farming at a yield intermediate between the lowest permissible and highest attainable yields. However, whether farming at the optimal yield is permissible depends upon the assumed region-wide production level [7]. We therefore compared the yield at which the peak population density of each species occurred with the lowest permissible yields for the 2014, Lower Bound and Business as Usual production scenarios. For 42% of bird species and 54% of sedges, the peak population density occurred in natural habitats with no agricultural yield (figure 2). The maximum population density of only a few birds (10%) and sedges (2%) occurred at the highest attainable yield. Hence, many species of birds (48%) and sedges (44%) had peak population densities at yields greater than zero, but less than the highest attainable yield. These species were those with highest region-wide populations at intermediate yields when total region-wide food energy production was very low (purple shading in figure 1). However, most of the species with these intermediate peak yields (90% for birds and 86% for sedges) had their maximum population density on land whose yield was below the minimum permissible yield, even for our lowest-demand production scenario for 2050 (Lower Bound: the dotted line on figure 2). Hence, few of the species with humped density-yield functions can benefit from intermediate-yield farming in the two-compartment scenarios, because their optimal yields are mostly well below the minimum levels required for current and projected food demand to be met. However, some of these species might benefit from an alternative form of land sparing in which high-yield farming spares land both for natural habitats and HNVf because their peak densities occur at yields that are, on average, similar to the 8 GJ ha^{-1} yr^{-1} we used in three-compartment simulations (arrow on figure 2). This possibility is explored in the next sections.

(c) Population outcomes for land-sharing, two-compartment land-sparing and three-compartment land-sparing scenarios

Across all region-wide production levels, more bird and sedge species had their largest region-wide population under two-compartment land sparing than under three-compartment land sparing or land sharing (figure 3). However, a substantial minority of species had their highest modelled total population size under three-compartment sparing, and this proportion increased as total region-wide production level increased. Based on the geometric mean across all species of their regional population size relative to 2014, the optimal proportion of spared land assigned to HNVf under the three-compartment scenario was 35% for the Lower Bound scenario and 33% for the Business as Usual scenario.

(d) Changes in population size from 2014 to 2050 for land-sharing, two-compartment land-sparing and three-compartment land-sparing scenarios

Declines in region-wide population size by 2050 were projected for most species of birds and sedges under the land-sharing scenario, with the proportion of species declining being somewhat lower under the reduced-demand Lower Bound production scenario than with Business as Usual demand (figure 4). Both two-compartment and three-compartment land sparing resulted in a smaller proportion of species with declines than land sharing. The proportion of species simulated to decline by more than half (darkest shading on fig. 4) was lower for three-compartment than two-compartment land sparing both for birds and sedges, and for both projected 2050 production levels. Species with peak density on low-yielding farmland were more likely than other species to undergo future population declines but, as for species in general, the proportion this subgroup of species simulated to decline by more than half was lower for three-compartment than two-compartment land sparing.

4. Discussion

Our analysis indicates that high-yield farming, linked to land sparing for natural habitats alone, would result in larger region-wide population size for more species of birds and sedges in eastern Poland than land sharing or farming at intermediate yields. This is the first quantitative comparison to be conducted in Europe of the expected consequences of land sharing and land sparing for species-specific population sizes of large sets of species. Our study concerns just two of the many groups of species present in the study region and we cannot assume that our conclusions apply to its entire biota. We chose birds and sedges because they have large numbers of species that are relatively easy to identify and survey. However, our findings might be broadly representative of those for a wider range of taxa because they are similar to those for trees, grasses and dung beetles studied elsewhere and to results for birds studied in six other regions [8]. Despite the long period of ecological disturbance caused by glacial cycles in the Pleistocene, followed by millennia of extensive agriculture, our findings for Poland from the two-compartment land-sparing scenario resemble those obtained in comparable studies elsewhere, in regions with different patterns of past environmental change [8]. It does not appear that a large proportion of species potentially favoured by land sparing is a result confined to regions in which tropical or subtropical forest is the predominant natural habitat [30]. Although this outcome has been observed for regions with natural vegetation comprising tropical or subtropical forest (Ghana [9], Uganda [10], India [9]), Mexico [11]), there are also similar results for the pampas grasslands of Brazil and Uruguay [12], temperate grassland/steppe in Kazakhstan [13], and now from the present study in a mixed temperate forest region of Europe.

A limitation of our study is that our scenarios consider only the effects on species' projected population sizes of changes in the extent of the different types of land use we surveyed. The configuration and size of tracts of land use will also affect densities and hence population sizes. For example, a study of birds and dung beetles in Colombia found that many species were more abundant on low-intensity pastureland close to natural forests than distant from them [31], so that having a given total area of forest distributed in smaller patches would increase the mean densities of these species on farmland. Despite this, a land-sparing strategy, in which the area of farmland was minimised by maximising the proportion of the farmland area that was grazed, still resulted in the majority of species from both taxa achieving the highest population size. Effects of configuration opposite to this are expected where population densities within natural habitat are lower near farmland (i.e. there are negative edge effects). In that case, distributing natural habitat in tracts of the largest possible size would lead to the largest region-wide population size. Empirical data on the magnitude of edge effects in natural habitat are insufficient to measure their effects in any existing study of land sparing and land sharing, but simulations using a plausible range of edge effect magnitudes indicate that the benefits of sparing over sharing would not be reversed unless edge effects were large and patches of natural habitat were small [32].

Species vary markedly in their projected response to land sparing and land sharing in terms of projected region-wide population size [7–9]. The species expected to benefit most from land sparing are those restricted to natural habitats and those with monotonic convex density-yield relationships. Species with monotonic concave density-yield relationships are favoured by land sharing [7]. However, our study in Poland highlights a proportion of species with density-yield relationships that are more complex than these simple forms. In particular, we found a substantial proportion of species with a hump-shaped relationship between population density and yield. Which farming strategy is associated with the greatest region-wide population size of these species depends upon the yield at which their densities peak and, for those that peak below the lowest permissible yield, the shape of their density-yield function beyond this [7]. In Poland we found that most species with hump-shaped functions had peak density at yields well below the lowest permissible yield, even if future demand was assumed to be lower than the current level. To address the conservation needs of these species we therefore developed a three-compartment land-sparing formulation in which high-yield farming spares land not just for natural habitats, but also for HNV low-yield farmland. Three-compartment land sparing (with roughly one-third of the spared land assigned to HNVf) avoided large population reductions, compared with 2014, for more species than did two-compartment sparing. These results were based on a simple method for selecting the yield and area of the HNVf compartment. Further refinements of the three-compartment model might improve its performance further by optimising the HNVf yield in a more rigorous way. Past region-wide population sizes, in the era before agricultural disturbance began, are highly uncertain for the species most likely to benefit from three-compartment land sparing. Some of these species may have been absent, or much rarer than they are today because of lower levels of habitat disturbance. However, it is also possible that they were associated with disturbed habitats created and maintained by large wild herbivores that are now extinct or have much diminished populations [33].

Our results suggest that, in eastern Poland, and possibly elsewhere in Europe, species conservation objectives would be enhanced if the area required for production-focused agriculture was minimised through high-yield farming to make space both for natural habitats and for HNVf landscapes managed to benefit species which currently depend upon them. If this was achievable, there would be a legitimate role for public policy, and private individuals and organisations who wish to promote biodiversity conservation, to support high-yielding agricultural systems for conservation reasons, even if their direct value for biodiversity is low. However, governmental and non-governmental conservation agencies usually do not attribute any conservation advantages to high-yield farming. This is perhaps not surprising, given that the promotion of high-yield farming on its own will not contribute much to conservation unless it is combined with incentives to spare land elsewhere for conservation [34,35] – in our case both through retaining or restoring natural habitats and maintaining or recreating areas of HNVf managed largely for those species that appear dependent on low-yield farm landscapes. In addition, the overall sustainability of high-yield farming needs to be improved by identifying and promoting farming systems that have low levels of negative externalities per unit of agricultural product [36]. Encouragement of high-yield farming could involve a range of measures, including investment in research and development, support for innovation, agricultural advice, and grants or loans for capital investments including beneficial technology and upgrades to farm infrastructure [35]. Delivering effective land sparing at low environmental cost will require both restructuring of existing incentive schemes so that support for yield increases on farmland is conditional on enhancement of conservation on other land, and a strong regulatory underpinning to ensure that producers use farming methods that limit negative environmental externalities.

The European Union already has effective policies to protect remaining areas of intact natural habitat (e.g. the Natura 2000 network, and the Birds and Habitats Directives [37]) and there are potential mechanisms to restore natural habitat in areas where it has been damaged or lost (e.g. through EU LIFE+ funding). Private nature conservation organisations in Europe also expend their own resources for the protection and restoration of natural habitats, as well as deploying their technical expertise to make effective use of the EU funding. The potential for land sparing to allow restoration of natural habitats is substantial.

In our study area in eastern Poland, we found that two-compartment land sparing at the current region-wide agricultural production level would approximately double the area available for natural habitats compared with 2014. The area that would need to be restored to natural habitat under two-compartment land sparing with the Lower Bound 2050 production level would be even larger (3.4 times the 2014 extent of natural habitat). However, the restoration of natural forest and wetland habitats on abandoned farmland takes time and has financial costs. There can also be hydrological constraints that limit the realisable extent of wetland restoration, but spatially-explicit land-use modelling indicates that the modelled levels of restoration in our study are feasible [29]. Our estimates for region-wide species population outcomes assume that population densities in existing natural habitats have been realised on restored spared land, but in practice this will only be the case after a time lag.

In terms of conserving species whose density peaks under low-yielding agriculture, we suggest that existing agri-environment policies could be improved by explicitly targeting low-yielding HNVf practices. Areas of high uptake of agri-environment funding do not currently coincide with existing areas of HNVf in Europe [22] and many HNVf systems continue to face major economic challenges, suggesting improved targeting and higher payment rates may be necessary for them to persist. Alongside low-yield farming, this support could encourage extensive, conservation-focused management to maintain species dependent on occasional habitat disturbance. Such an approach is already used in many semi-natural protected areas within Europe, supported by agri-environment schemes, EU LIFE+ funding and resources contributed by private individuals and conservation organisations.

Because these alternative uses all compete for land, it is vital that policies for the protection of natural and semi-natural habitats are coupled with the promotion of sustainable high-yield farming, and with the effective implementation of demand-side measures to reduce edible food waste and meat consumption, and to limit demand for crop-based biofuels. Without such efforts to reduce the land required for food production, significant increases in the area managed primarily for nature could only be achieved by Europe displacing its environmental footprint by importing more of its food from elsewhere.

In broadest terms, our results indicate that if the ambitious levels of habitat protection called for in the Aichi Targets and even more so by Half Earth advocates are to be achieved they will require a parallel, linked commitment to promoting sustainable high-yield farming. We suggest that humanity cannot afford the space that nature needs unless this is done. In Europe, there appears to be a strong case for areas primarily focused on conservation to include extensively managed habitats aimed at benefiting species dependent on periodic habitat disturbance, now produced by human activities, and for European policies addressing agriculture and conservation to be revised to better deliver both traditional conservation and biodiversity-focused HNVf. This will in turn require explicit policy linkages between high-yield farming and the sparing of land for conservation. The development of effective policy mechanisms for achieving such coupling is in its infancy, but we think this in partly because conservation efforts often fail to recognise the pivotal role which high-yield farming can play in making room for nature.

Data accessibility

Data and code supporting this article are provided in the electronic supplementary material and in the following uploaded files: 2014_regional_production.csv, 2050_scenarios.csv, Bird_data.csv, Bird_dyfunction_params.csv, Sedge_data.csv, Sedge_dyfunction_params.csv, Site_information.csv, Rcode.txt and read_me.txt.

Authors' contributions

All authors designed the study. C.F. collected the field data. C.F. and R.E.G. carried out the statistical analyses. All authors wrote the manuscript and gave final approval for publication.

Competing interests

We declare we have no competing interests.

Funding

This work was supported by a NERC CASE studentship to C.F.

Acknowledgements

We are very grateful to Paul Donald, Anthony Lamb, Ben Phalan and David Williams for advice and comments. The support and guidance of Jarosław Krogulec at Ogólnopolskie Towarzystwo Ochrony Ptaków (OTOP) was essential to the project. Bernadetta Wołcuk, Grzegorz Siwek, Jarosław Sczuwarski and Wojciech Zgłobicki provided invaluable help and advice. Kate Willott helped us to prepare the manuscript.

.References

[1] Wilson EO. 2016. *Half-Earth: our planet's fight for life.* London: Liveright Publishing.

[2] Balmford A, Green RE. 2017 How to spare half a planet. *Nature* **552,** 175.

[3] Secretariat of the Convention on Biological Diversity. 2010 COP-10 Decision X/2. https://www.cbd.int/decision/cop/?id=12268

[4] Tilman D, Balzer C, Hill J, Befort BL. 2011 Global food demand and the sustainable intensification of agriculture. *PNAS* **108,** 20260–20264. (doi: 10.1073/pnas.1116437108)

[5] Hunter MC, Smith RG, Schipanski ME, Atwood LW, Mortensen DA. 2017 Agriculture in 2050: recalibrating targets for sustainable intensification. *BioScience* **67,** 386–391. (doi: 10.1093/biosci/bix010)

[6] Pywell RF, Heard MS, Bradbury RB, Hinsley S, Nowakowski M, Walker KJ, Bullock JM. 2012 Wildlife-friendly farming benefits rare birds, bees and plants. *Biol. Lett.* **8,** 772–775. (doi: 10.1098/rsbl.2012.0367)

[7] Green R, Cornell S, Scharlemann J, Balmford A. 2005 Farming and the fate of wild nature. *Science* **307,** 550–555. (doi: 10.1126/science.1106049)

[8] Balmford A, Green R, Phalan B. 2015 Land for food and land for nature? *Daedalus* **144,** 57–75. (doi: 10.1162/DAED_a_00354)

[9] Phalan B, Onial M, Balmford A, Green RE. 2011 Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* **333,** 1289–1291. (doi: 10.1126/science.1208742)

[10] Hulme MF et al. 2013 Conserving the birds of Uganda's banana-coffee arc: land sparing and land sharing compared. *PLoS ONE* **8,** e54597. (doi: 10.1371/journal.pone.0054597)

[11] Williams DR, Alvarado F, Green RE, Manica A, Phalan B, Balmford A. 2017 Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatán, Mexico. *Glob. Change Biol.* **23,** 5260–5272. (doi: 10.1111/gcb.13791)

[12] Dotta G, Phalan B, Silva TW, Green R, Balmford A. 2016 Assessing strategies to reconcile agriculture and bird conservation in the temperate grasslands of South America: grasslands conservation and agriculture. *Conserv. Biol*. **30,** 618–627. (doi: 10.1111/cobi.12635)

[13] Kamp J, Urazaliev R, Balmford A, Donald PF, Green RE, Lamb AJ, Phalan B. 2015 Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches. *J. Appl. Ecol.* **52,** 1578–1587. (doi: 10.1111/1365-2664.12527)

[14] Onial M. 2011 Responses of biodiversity to agricultural intensification: a study in the upper Gangetic Plain, India. University of Cambridge: PhD thesis.

[15] Dotta G. 2013 Agricultural production and biodiversity conservation in the grasslands of Brazil and Uruguay. University of Cambridge: PhD thesis.

[16] Kremen C. 2015 Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Ann. N. Y. Acad. Sci.* **1355,** 52–76. (doi: 10.1111/nyas.12845)

[17] Luskin MS, Lee JSH, Edwards DP, Gibson L, Potts MD. 2017 Study context shapes recommendations of land-sparing and sharing; a quantitative review. *Glob. Food Sec.* **16,** 29–35. (doi: 10.1016/j.gfs.2017.08.002)

[18]

[19] Allen JRM, Hickler T, Singarayer JS, Sykes MT, Valdes PJ, Huntley B. 2010 Last glacial vegetation of northern Eurasia. *Quat. Sci. Rev.* **29,** 2604–2618. (doi: 10.1016/j.quascirev.2010.05.031)

[20] Tscharntke T, Klein A, Kruess A, Steffan-Dewenter I, Thies C. 2005 Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecol. Lett.* **8,** 857–874. (doi: 10.1111/j.1461-0248.2005.00782.x)

[21] Bignal EM, McCracken DI. 1996 Low-intensity farming systems in the conservation of the countryside. *J. Appl. Ecol.* **33,** 413–424.

[22] Halada L, Evans D, Romão C, Petersen J-E. 2011 Which habitats of European importance depend on agricultural practices? *Biodivers. Conserv.* **20,** 2365–2378. (doi: 10.1007/s10531-011-9989-z)

[23] Baldock D, Beaufoy G, Bennett G, Clark J. 1993 *Nature conservation and new directions in the Common Agricultural Policy*. London: Institute for European Environmental Policy.

[24] Keenleyside C, Beaufoy G, Tucker G, Jones G. 2014 *High Nature Value farming throughout EU-27 and its financial support under the CAP.* Report Prepared for DG Environment, Contract No ENV B.1/ETU/2012/0035. London: Institute for European Environmental Policy. (doi: 10.2779/91086)

[25] Bignal EM, McCracken DI. 2000 The nature conservation value of European traditional farming systems. *Environ. Rev.* **8,** 149–171. (doi: 10.1139/er-8-3-149)

[26] Henle K et al. 2008 Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe – a review. *Agric. Ecosyst. Environ.* **124,** 60–71. (doi: 10.1016/j.agee.2007.09.005)

[27] Lawton JH et al. 2010 *Making space for nature: a review of England's wildlife sites and ecological networks.* Report to Defra.

[28] RSPB. 2011 *High Nature Value farming, how diversity in Europe's farm systems delivers for biodiversity.* Sandy, UK: RSPB.

[29] Feniuk C 2015 Reconciling Food Production and Biodiversity Conservation in Europe. University of Cambridge: PhD thesis.

[30] Godfray HCJ. 2011 Food and biodiversity. *Science* **333,** 1231–1232. (doi: 10.1126/science.1211815)

[31] Gilroy JJ, Edwards FA, Medina Uribe CA, Haugaasen T, Edwards DP 2014 Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. J. Appl. Ecol. **51,** 1337–1346. (doi: 10.1111/1365-2664.12284)

[32] Lamb A, Balmford A, Green RE, Phalan B 2016 To what extent could edge effects and habitat fragmentation diminish the potential benefits of land sparing? Biological Conservation **195,** 264-271. (doi.org/10.1016/j.biocon.2016.01.006)

[33] Vera FWM 2000 Grazing Ecology and Forest History. CABI, Wallingford.

[34] Ewers RM, Scharlemann JPW, Balmford AP, Green RE 2009 Do increases in agricultural yield spare land for nature? *Global Change Biology* **15,** 1716-1726. (/doi/full/10.1111/j.1365-2486.2009.01849.x)

[35] Phalan B, Green RE, Dicks LV, Dotta G, Feniuk C, Lamb A, Strassburg BBN, Williams DR, zu Ermgassen EKHJ, Balmford A. 2016 How can higher-yield farming help to spare nature? *Science* **351,** 450–451. (doi: 10.1126/science.aad0055)

[36] Balmford A et al. 2018 The environmental costs and benefits of high-yield farming. *Nat. Sustain.* **1,** 477–485. (doi: 10.1038/s41893-018-0138-5)

[37] Sanderson FJ, Pople RG, Ieronymidou C, Burfield IJ, Gregory RD, Willis SG, Howard C, Stephens PA, Beresford AE, Donald PF. 2016 Assessing the performance of EU nature legislation in protecting target bird species in an era of climate change. *Conserv. Lett.* **9,** 172–180. (doi: 10.1111/conl.12196)

LEGENDS TO FIGURES

Figure 1. Proportion of species of birds and sedges expected under the two-compartment scenario to have their highest region-wide population size when land is farmed at the highest attainable yield and remaining land is all under natural habitat (land sparing - red), when the entire region is farmed at the lowest permissible yield (land sharing - blue) and at intermediate yields in the permissible range (purple). Results are shown for a range of values of region-wide food production, expressed as an annual yield averaged over the whole region. The vertical lines indicate region-wide mean yield in 2014 (solid line), and under the Lower Bound (dotted line) and Business as Usual (dashed line) scenarios for agricultural production in 2050.

Figure 2. Frequency distributions of the estimated yield at which the peak population density occurred for species of birds and sedges. Species with highest density in natural habitats (white bar) and on farmland with the highest attainable yield (black bar) are shown on the left and right respectively. Numbers of species with maximum densities at yields between these extremes are shown by grey bars for bins of 5 GJ ha^{-1} yr^{-1}. Vertical lines indicate the minimum permissible yield under land sharing to achieve the regional production of 2014 (solid line), and under the Lower Bound (dotted line) and Business as Usual (dashed line) scenarios for agricultural production in 2050. The arrows show the yield assumed for High Nature Value farmland for the purpose of the three-compartment scenario.

Figure 3. Proportion of species of birds and sedges projected to have their highest total population size when all land is farmed at the lowest permissible yield (land sharing - blue), when land is farmed at the highest attainable yield and spared land is used only for natural habitat (2C-Sparing - red), and under a three-compartment model in which some spared land has natural habitat and some supports HNVf (3C-Sparing, orange). Vertical lines indicate the minimum permissible yield under Land Sharing to achieve the regional production of 2014 (solid line), and under the Lower Bound (dotted line) and Business as Usual (dashed line) scenarios for agricultural production in 2050.

Figure 4. Proportions of bird and sedge species projected to undergo decreases or increases in region-wide population size of various magnitudes between 2014 and 2050 under contrasting land-use strategies. Shaded segments within each horizontal bar represent the proportion of species undergoing a severe decline (>50% decline: black); a decline' (up to 50% decline: grey); an increase (up to 100% increase: grey hatching) and a major increase (>100% increase: black hatching). The horizontal extent of each set of shaded bars sums to 100% of species, with the division between decreasing and increasing species placed at the

vertical thick line. Vertical lines show divisions representing 25% of species. Results are presented for farming at the lowest permissible yield (Sh = land sharing), farming at the highest attainable yield with only natural habitats on spared land (2C Sp = two-compartment land sparing) and farming at the highest attainable yield with both natural habitat and HNVf on spared land (3C Sp = three-compartment land sparing). Two region-wide agricultural production levels for 2050 are compared: Business as Usual and Lower Bound. Results are shown separately for all species and for those species with peak population density at a yield greater than zero but less than the lowest permissible yield under the Lower Bound 2050 production scenario.

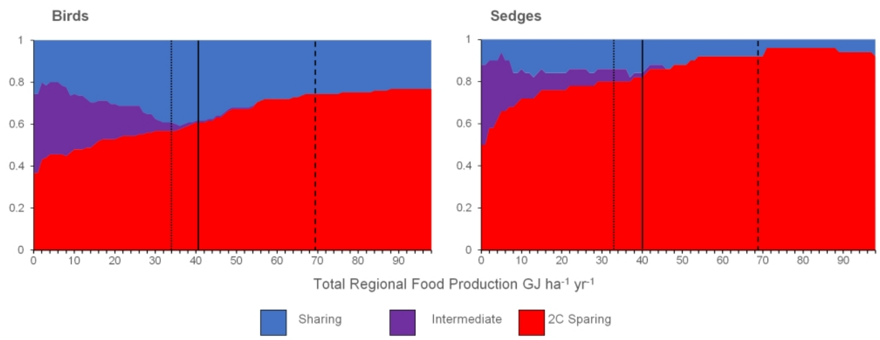

Figure 1. Proportion of species of birds and sedges expected under the two-compartment scenario to have their highest region-wide population size when land is farmed at the highest attainable yield and remaining land is all under natural habitat (land sparing - red), when the entire region is farmed at the lowest permissible yield (land sharing - blue) and at intermediate yields in the permissible range (purple). Results are shown for a range of values of region-wide food production, expressed as an annual yield averaged over the whole region. The vertical lines indicate region-wide mean yield in 2014 (solid line), and under the Lower Bound (dotted line) and Business as Usual (dashed line) scenarios for agricultural production in 2050.

254x190mm (300 x 300 DPI)

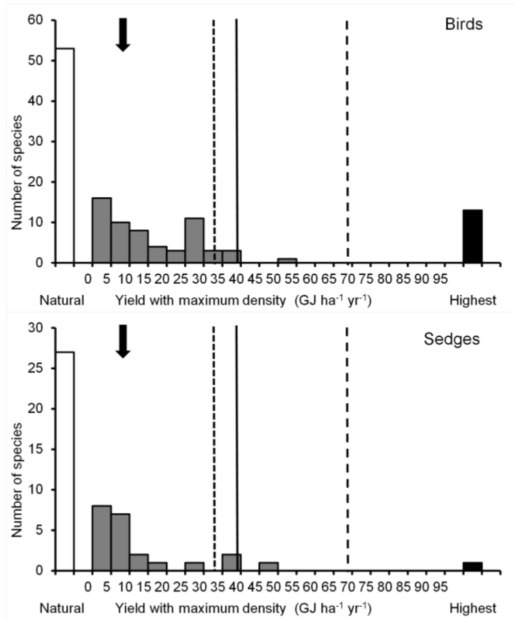

Figure 2. Frequency distributions of the estimated yield at which the peak population density occurred for species of birds and sedges. Species with highest density in natural habitats (white bar) and on farmland with the highest attainable yield (black bar) are shown on the left and right respectively. Numbers of species with maximum densities at yields between these extremes are shown by grey bars for bins of 5 GJ ha-1 yr-1. Vertical lines indicate the minimum permissible yield under land sharing to achieve the regional production of 2014 (solid line), and under the Lower Bound (dotted line) and Business as Usual (dashed line) scenarios for agricultural production in 2050. The arrows show the yield assumed for High Nature Value farmland for the purpose of the three-compartment scenario.

254x190mm (300 x 300 DPI)

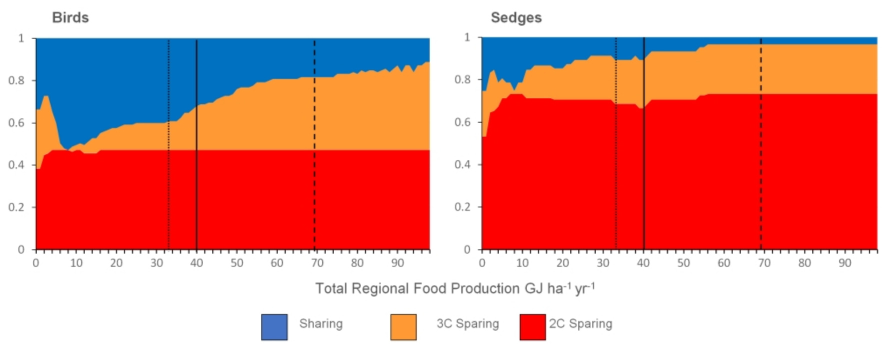

Figure 3. Proportion of species of birds and sedges projected to have their highest total population size when all land is farmed at the lowest permissible yield (land sharing - blue), when land is farmed at the highest attainable yield and spared land is used only for natural habitat (2C-Sparing - red), and under a three-compartment model in which some spared land has natural habitat and some supports HNVf (3C-Sparing, orange). Vertical lines indicate the minimum permissible yield under Land Sharing to achieve the regional production of 2014 (solid line), and under the Lower Bound (dotted line) and Business as Usual (dashed line) scenarios for agricultural production in 2050.

254x190mm (300 x 300 DPI)

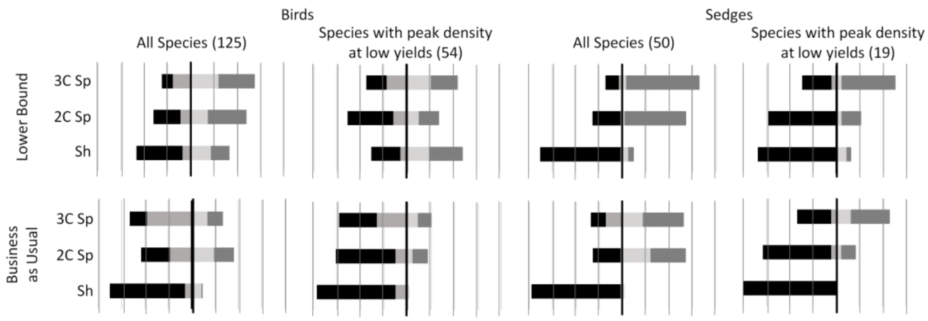

Figure 4. Proportions of bird and sedge species projected to undergo decreases or increases in region-wide population size of various magnitudes between 2014 and 2050 under contrasting land-use strategies. Shaded segments within each horizontal bar represent the proportion of species undergoing a severe decline (>50% decline: black); a decline' (up to 50% decline: grey); an increase (up to 100% increase: grey hatching) and a major increase (>100% increase: black hatching). The horizontal extent of each set of shaded bars sums to 100% of species, with the division between decreasing and increasing species placed at the vertical thick line. Vertical lines show divisions representing 25% of species. Results are presented for farming at the lowest permissible yield (Sh = land sharing), farming at the highest attainable yield with only natural habitats on spared land (2C Sp = two-compartment land sparing) and farming at the highest attainable yield with both natural habitat and HNVf on spared land (3C Sp = three-compartment land sparing). Two region-wide agricultural production levels for 2050 are compared: Business as Usual and Lower Bound. Results are shown separately for all species and for those species with peak population density at a yield greater than zero but less than the lowest permissible yield under the Lower Bound 2050 production scenario.

254x190mm (300 x 300 DPI)