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An increase in food production in Europe could dramatically affect farmland biodiversity

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Conversion of semi-natural habitats, such as field margins, fallows, hedgerows, grassland, woodlots and forests, to agricultural land could increase agricultural production and help meet rising global food demand. Yet, the extent to which such habitat loss would impact biodiversity and wild species is unknown. Here we survey species richness for four taxa (vascular plants, earthworms, spiders, wild bees) and agricultural yield across a range of arable, grassland, mixed, horticulture, permanent crop, for organic and non-organic agricultural land on 169 farms across 10 European regions. We find that semi-natural habitats currently constitute 23% of land area with 49% of species unique to these habitats. We estimate that conversion of semi-natural land that achieves a 10% increase in agricultural production will have the greatest impact on biodiversity in arable systems and the least impact in grassland systems, with organic practices having better species retention than non-organic practices. Our findings will help inform sustainable agricultural development.

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Global food needs are expected to increase drastically by 2050 if current trends continue, especially in population growth and increased consumption of meat and dairy products[1–3]. Worldwide crop yield increases are unlikely to meet the projected demand for food[4–6], and the gap[7] may be further exacerbated by climate change[8,9]. A possible strategy to meet the production shortfall will be further expansion of productive agricultural land[5,10,11] which—combined with the competition for land to produce energy and develop infrastructures—will further jeopardize natural and semi-natural areas worldwide and in Europe[12,13].

In Europe, farmland covers 47% of the EU-28 area[14] and has historically supported high levels of biodiversity[15]. While large wilderness areas are prioritized to conserve biodiversity globally, conservation effort in the comparatively small scale mosaic-type European landscapes requires consideration of farmland[16,17] and associated semi-natural habitats such as field margins, fallows, hedgerows, low-input grassland, woodlots and traditional agroforestry. Whilst simplification of the agricultural landscape has halted in recent decades[18], partly due to agri-environmental policies, the question now arises, what production gain and biodiversity loss would be, if the pressure on the land would increase again and (part of) the remaining semi-natural habitats were converted to agricultural fields. To tackle the question we first investigated the set of species that are unique to European semi-natural habitats and that would disappear in case of conversion to production fields, and related that loss to the production gained by the conversion[19], also in case of conversion being to organically or conventionally managed fields. Organic farming is often proposed as a solution to feed a growing population while simultaneously minimizing the global environmental impact of agriculture[5,20–22] and supporting biodiversity[23–25]. Since organic systems in Europe usually show lower yields (20–40%; but see[26,27]) they require more land to produce the same amount of food. This raises the second question: what would a comparative loss of species in organic and non-organic systems, and on a difference farming systems (grassland vs arable vs horticulture etc.) be in case overall agricultural production should increase by 10%?

We evaluated the current productivity on farmland and the species richness of key taxonomic and functional taxa for agroecosystems on both production areas and semi-natural habitats in ten agricultural regions across Europe, from boreal to Mediterranean (Fig. 1a, Supplementary Table 1). Regions comprised various agricultural land uses from arable to grassland, mixed, horticulture and permanent crops. In each region, we randomly selected 12–20 farms from sets of 30–40 farms that had accepted to participate, approximately half certified organic. We surveyed four taxa (vascular plants, earthworms, spiders, wild bees) that represent key ecosystem functions for agriculture (contributing to soil fertility, biological pest control and pollination), different habitat compartments (soil and aboveground structures) and mobility in 910 semi-natural habitats and 492 production fields, using hierarchical preferential sampling and standardized protocols (Methods, Supplementary Table 2). Habitats were categorized as either semi-natural habitats or production fields according to criteria based on Raunkiær plant life forms[28] and management evidence[29] (Methods). Farmers provided data on yields. In each case study region, the recorded species were grouped as (i) unique to semi-natural habitats, (ii) unique to production fields or (iii) shared by both habitat categories. The use of unique species enabled the evaluation of biodiversity loss if habitats should be converted into other land use categories.

Results

High proportion of species unique to semi-natural habitats. Summed over the four taxa, 49% (±3%) of all species on average across regions were unique to semi-natural habitats, which was significantly more ($n = 40$, $P\chi^2_1 < 0.001$) than the 26% (±3%) unique to production fields (Fig. 1b) compared for the same sample coverage per region[30] (Methods, per taxa separately in Supplementary Table 3). The remaining 25% (±4%) of the species were shared by the two habitat categories. The contribution of semi-natural habitats to farmland biodiversity is strikingly high, given the limited area of 23% (min 3% – max 71%) of farmland they covered per region. Remarkably, on arable, horticultural and wine producing farms (AT, FR, NL, DE, IT), the 3–10% semi-natural habitats hosted 40–60% of the unique species. Considered separately, plant, spider and wild bee species showed similar patterns (Supplementary Fig. 1). Across the four taxa and summed over the regions, the differences between organic and non-organic systems for unique species in both semi-natural habitats and production fields, and shared species, were mainly non-significant (Supplementary Table 4), which is not surprising since the two farming systems of the study were overall very similar and not significantly different with respect to main land characteristics (Supplementary Table 5). However, the less intensive management of the organic farms led to a significantly lower yield than in the non-organic ones (Supplementary Table 6).

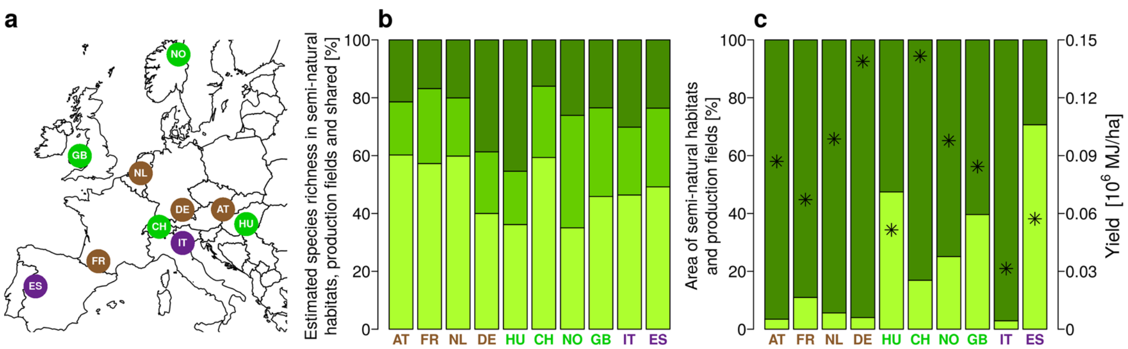

Fig. 1 Importance of semi-natural habitats for biodiversity in ten European farmland regions. a Location of the study regions with dominant type of agricultural land use (brown: arable crops, mixed systems and horticulture, bright green: grassland, violet: permanent crops). **b** Proportions of summed vascular plant, earthworm, spider and bee species unique to semi-natural habitats (light green bars), shared by the semi-natural habitats and production fields (medium green bars) and unique to production fields (dark green bars) per region (per taxa separately in Supplementary Fig. 1). **c** Percentage of farm area occupied by semi-natural habitats (light green bars) and production fields (dark green bars) per region, and average yield (stars) over fields of sampled farms in the ten study regions.

Moderate production gain and dramatic species loss by conversion of semi-natural habitats. In the context of land take for food production, the conversion of semi-natural habitats to production fields would increase the production and the species richness unique to production fields due to the area gained, but species unique to semi-natural habitats would be lost. To quantify the trade-off between food production and biodiversity conservation, we modelled the impact of a progressing conversion of semi-natural habitats to production fields from sample-size based extrapolations of unique species occurring there[31] (Methods). Potential production gain was calculated by multiplying the average yield over the various crops by the area of converted land. Yields were expressed in mega joules (MJ) per hectare (ha) of harvestable energy. They varied considerably within and between case study regions, as a function of the geographic location and the farm type (Fig. 1c). Average yield per region ranged from 31 461 MJ ha^{-1} (IT) to 141 577 MJ ha^{-1} (CH). Productivity (evaluated as MJ per hectare, Fig. 1c) was not related to the share of semi-natural habitats (Spearman's rho = 0.095, ns) suggesting that farms with large semi-natural habitat area could also perform well regarding production. To investigate the pattern of species loss and production gain, we calculated and plotted the accumulation curves of species unique to semi-natural habitats backward, and added the corresponding gained species unique to production fields and species shared (Methods, Supplementary Fig. 2). The pattern of species richness decline (all taxa combined) with accumulative conversion was similar across regions (Fig. 2), and organic and non-organic systems (Supplementary Fig. 3). The concave downward curves (slope increased with larger area of semi-natural habitats converted) indicate a low impact of converting few semi-natural habitats; this suggests high similarity of species compositions among them. Even, species richness increased slightly in FR and DE first due to the overcompensation of species unique to production fields compared to species unique to semi-natural habitats. This was particularly true for organic systems in FR, DE, NO and ES (Supplementary Fig. 3). This indicates the buffering role of organic farming in case of semi-natural habitat loss. However, when more than half of the semi-natural habitats were converted, species loss increased dramatically on organic farms as well.

In all study regions, the impact of converting 50% of the semi-natural area on species richness estimates was low and partly compensated by an increase of species numbers on the larger available production area (Table 1 and Supplementary Table 7). However, converting 90% of the semi-natural area (assuming that 10% are unconvertible due to geomorphological constraints and poor soil quality) resulted in a net species loss of 24% (±3) on average across regions and 37% (±3) in the worst-case situation (accounting of uncertainty of species loss modelling, Methods). While the biodiversity loss in percentage of the total species richness was similar across regions, the production gain varied remarkably. Arable and horticultural systems (AT, DE, FR and NL) would gain only 6% (±2) in production but would lose 26% (±7, worst case: 38% ± 6) of their species if 90% of the semi-natural habitats were converted to production fields. Grassland dominated regions would gain 47% (±14) in production due to conversion of the currently large available semi-natural area (CH, HU, NO and GB) and biodiversity loss would amount to 21% (±5, worst case: 36% ± 6) of their species. Amongst permanent crops, an intensification of low productive olive groves in Spain (ES) would increase production by 217% (but note that the bulk of semi-natural habitats in Spain are extensively managed olive groves, for which production was not accounted for, this means that the increased production is overestimated; Methods). The intensification of Spanish olive groves would induce a 27% (worst case: 37%) species loss. Vineyard farms in Italy (IT) would gain 3% production but would lose 22% (worst case: 41%) of the species.

On average, non-organic farms were 15.4% more productive than organic farms (Supplementary Table 6, Supplementary Data). On the other hand, organic farms, on average across regions, retained 1.8% (±11.2) and 5.9% (±7.1) more species of the four taxa combined than non-organic farms, when 50% and 90% of the semi-natural habitats were converted to productive

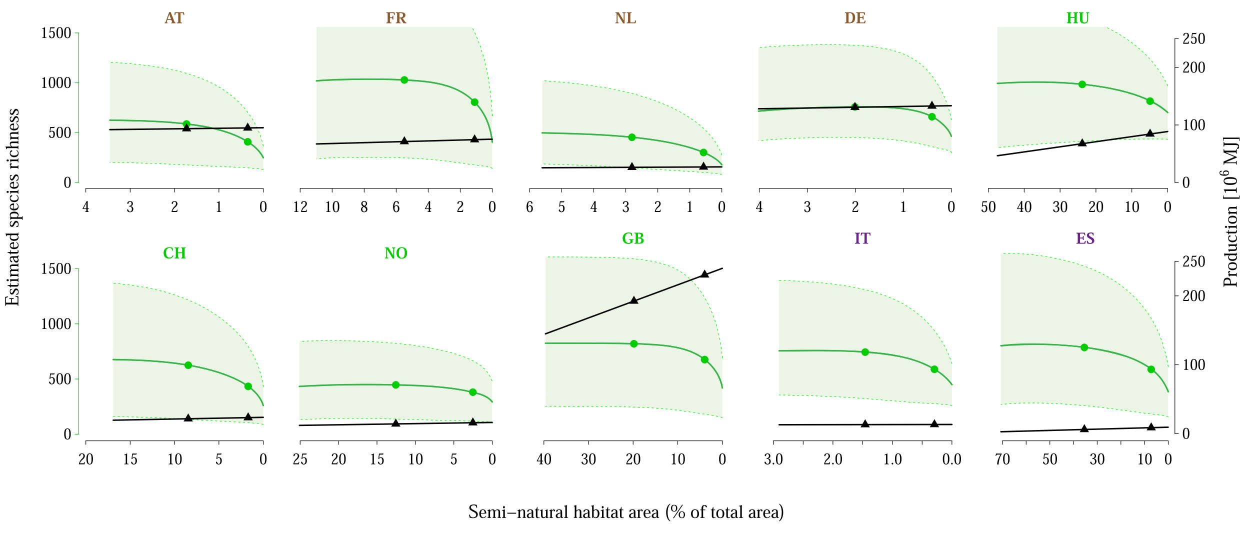

Fig. 2 Estimated species richness and production for gradual conversion of semi-natural habitats to production fields in ten European farmland regions (brown: arable crops, mixed systems and horticulture, bright green: grassland, violet: permanent crops). The effect of the conversion of semi-natural habitats (percentage of the total farm area) on species richness (green lines, sum of vascular plant, earthworm, spider and wild bee species) is estimated with backward sample-size-based extrapolations[31] of species unique to semi-natural habitats and addition of species unique to production fields and species shared (Methods). Confidence intervals (95%) are the sum over the confidence intervals of the four species groups. Effect on production (black lines) is calculated by multiplying the converted semi-natural area by the overall yield of the region. Effects of a 50% and 90% conversion of the semi-natural area are indicated for species richness (green dots) and production (black triangles) (Supplementary Table 7).

Table 1 Average estimated species richness loss, gain and net change, and production gain by conversion of semi-natural habitats to production fields across ten European farmland regions.

	Group	Loss of species unique to semi-natural habitats (%)	Gain of species unique to production fields (%)	Species net change (%)	Production gain (%)
Average situation					
(I) 90% SNH converted	All regions	47.6 ± 3	24.1 ± 3.5	−23.6 ± 3.3	43.2 ± 21.1
	arable	48.8 ± 4.9	23.2 ± 6.3	−25.7 ± 7.1	5.9 ± 1.8
	grassland	44.8 ± 6.1	23.9 ± 6.5	−20.9 ± 5.2	47.2 ± 14.2
	permanent	50.9 ± 4.9	26.4 ± 7.3	−24.6 ± 2.3	109.8 ± 107.1
(II) 50% SNH converted	All regions	24.8 ± 2.6	23.1 ± 3.1	−1.7 ± 1.5	24 ± 11.7
	arable	24.7 ± 4.4	22.7 ± 6	−2 ± 3.4	3.3 ± 1
	grassland	23.5 ± 4.7	22.1 ± 5.2	−1.4 ± 2.2	26.2 ± 7.9
	permanent	27.5 ± 6.7	25.8 ± 7	−1.7 ± 0.2	61 ± 59.5
(III) 10% more production	All regions	44.2 ± 9.4	23 ± 3.1	−21.2 ± 8.4	7.7 ± 1
	arable	65.5 ± 14	23.2 ± 6.3	−42.3 ± 12.6	5.9 ± 1.4
	grassland	22 ± 3.3	21.4 ± 4.2	−0.6 ± 2.3	10 ± 0
	permanent	45.6 ± 29	25.6 ± 8.2	−20 ± 20.8	6.5 ± 3.5
Best case situation					
(I) 90% SNH converted	All regions	51.7 ± 3.8	42.3 ± 5.1	−9.4 ± 4.7	43.2 ± 21.1
	arable	51.1 ± 5.9	41.7 ± 10	−9.4 ± 10.6	5.9 ± 1.8
	grassland	50.3 ± 7.2	39.9 ± 8.5	−10.3 ± 6	47.2 ± 14.2
	permanent	55.6 ± 10.3	48.3 ± 9.4	−7.4 ± 0.9	109.8 ± 107.1
(II) 50% SNH converted	All regions	32 ± 3.5	39.7 ± 4.5	7.7 ± 1.9	24 ± 11.7
	arable	32.2 ± 6.8	39.7 ± 9.3	7.6 ± 3.5	3.3 ± 1
	grassland	29.5 ± 4.4	36.3 ± 6.3	6.7 ± 3.6	26.2 ± 7.9
	permanent	36.6 ± 11.1	46.5 ± 8.6	9.9 ± 2.5	61 ± 59.5
(III) 10% more production	All regions	49.7 ± 13.8	38.8 ± 4.8	−10.9 ± 11.5	7.7 ± 1
	arable	79.3 ± 20.7	41 ± 10.6	−38.3 ± 18.2	5.9 ± 1.4
	grassland	17.8 ± 3.1	34.3 ± 3.6	16.6 ± 2.9	10 ± 0
	permanent	54.5 ± 45.5	43.3 ± 14.8	−11.1 ± 30.7	6.5 ± 3.5
Worst case situation					
(I) 90% SNH converted	All regions	−53.8 ± 3.6	16.5 ± 1.9	−37.4 ± 3.1	43.2 ± 21.1
	arable	−54 ± 5.9	16.4 ± 3.2	−37.6 ± 6.1	5.9 ± 1.8
	grassland	−52 ± 7	15.5 ± 3.1	−36.4 ± 6	47.2 ± 14.2
	permanent	−57.3 ± 7.8	18.5 ± 5.8	−38.8 ± 2	109.8 ± 107.1
(II) 50% SNH converted	All regions	−24.5 ± 2.6	16.5 ± 1.9	−8 ± 2	24 ± 11.7
	arable	−23.9 ± 4	16.4 ± 3.2	−7.5 ± 2.8	3.3 ± 1
	grassland	−24.1 ± 4.8	15.5 ± 3.1	−8.6 ± 3.4	26.2 ± 7.9
	permanent	−26.4 ± 7.7	18.5 ± 5.8	−7.8 ± 1.8	61 ± 59.5
(III) 10% more production	All regions	−57.4 ± 11.6	16.5 ± 1.9	−40.9 ± 10.8	7.7 ± 1
	arable	−82.6 ± 17.4	16.4 ± 3.2	−66.2 ± 15.7	5.9 ± 1.4
	grassland	−29.2 ± 2	15.5 ± 3.1	−13.7 ± 2.6	10 ± 0
	permanent	−63.5 ± 36.5	18.5 ± 5.8	−45 ± 30.7	6.5 ± 3.5

Percent and standard error are shown. Details per region are in Supplementary Table 7. Results are presented for three situations (see Methods): (1) Average situation: richness of unique species estimated from rarefaction and extrapolation curves; (2) Best case situation: species change estimated from the lower bound of the confidence interval (CI) of the expected species richness unique to semi-natural habitats, the upper bound of the CI of the expected species richness unique to production fields, and the lower bound of the CI of the expected shared species richness; (3) Worst case situation: species richness estimated from the upper bound of the confidence interval (CI) of the expected species richness unique to semi-natural habitats, the lower bound of the CI of the expected species richness unique to production fields, and shared species assumed to not be able to survive without semi-natural habitats and considered like species unique to semi-natural habitats. Three scenarios are shown: (I) 90% and (II) 50% of the area covered by semi-natural habitats are converted to production fields, (III) semi-natural habitats are converted to production fields required for a 10% production increase. Means are calculated across all regions and groups of regions, i.e. arable and horticultural (AT, FR, NL and DE), grassland (HU, CH, NO and GB) and permanent crops (IT, ES).

land, respectively. Still, the difference between both systems was not significant (Supplementary Table 8), partly due to the high variability between farms.

Contrasting impact of setting a goal of 10% production increase. The model allows to simulate whether certain production goals can be reached and what the impact on farmland species diversity would be. A report by the FAO[32] postulates a global needed supply of food increase by almost 30% by 2030 and around 50% by 2050 to equal the rise in global demand. Here, we show the impact of a 10% increase in production in the regions studied, which corresponds to the level that about half of them could not reach, although they convert the entire semi-natural area to production fields.

The conversion to achieve the 10% production increase target has a very different impact depending on the type of land use. In arable systems, the required conversion would result in a dramatic species loss of 66% (±16) in a worst case situation (accounting for the variability in the data as specified in Methods; average situation: 42% ± 13%) and considering a total conversion that could only be achieved in arable farmland with heavy investment in machinery. In that scenario, three of the four regions (AT, NL, DE) could not even reach 10% more production, because the share of semi-natural habitats is already so low, that not enough land can be converted (Table 1). Similarly, the vineyard region (IT) could not achieve the production goal and would lose up to 76% (average situation: 41%) of the species. In contrast, grassland dominated regions and olive groves would be able to produce 10% more than the current production while biodiversity would be less affected than for the arable systems (worst case situation: −14% ± 3 and −14%, average situation: −0.6% ± 2 and +0.8, respectively).

The organic farming sector is growing due to increased consumer demand. Yet, organic per hectare yield was significantly

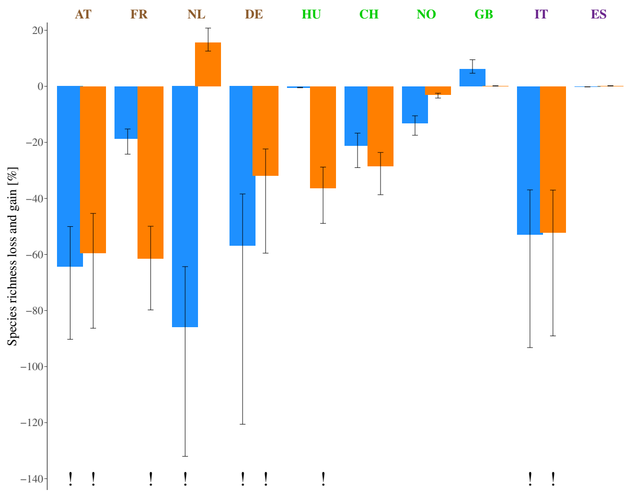

Fig. 3 Comparative change in species richness (sum of vascular plant, earthworm, spider and bee species) by aiming at a 10% production increase in organic and non-organic systems of ten European farmland regions (brown: arable crops, mixed systems, and horticulture, bright green: grassland, violet: permanent crops). Net loss and gain of species (sum of vascular plant, earthworm, spider and bee species) by conversion of semi-natural habitats to production fields to achieve 10% more production than the non-organic level for non-organic systems (blue bars) and for organic systems (orange bars). Exclamation marks indicate a total conversion of semi-natural habitats without reaching 10% production increase. Species loss and gain are derived from sample size based extrapolation (Methods). Confidence intervals (95%) are the sum over the confidence intervals of the four species groups.

(15.4%, Supplementary Table 6) lower than non-organic on average across the study regions, which is in the lower range compared to previous studies[26,27] ($n = 876$ fields, $P\chi^2_1 < 0.001$). In case of 10% more harvestable energy needed, non-organic and organic systems showed contrasting effects of the conversion of semi-natural habitats to production fields, non-organic systems losing more species (Fig. 3). Six non-organic and five organic systems, not paired in regions, out of 20 could successfully produce 10% more harvestable energy than today's non-organic farms by converting semi-natural habitats to production fields, and would lose 8% and 3% of species on average, respectively (Supplementary Table 9). These are notably the grassland systems in CH, NO, GB and the olive farms in ES. In those systems, the differences in management and yield between organic and non-organic farming is smaller than in arable farming and in vineyards, both of which tend to be more intensively managed. Also, the share of semi-natural habitats is higher in grassland than in arable systems, so that a conversion has less drastic consequences. Four non-organic and five organic systems could not achieve 10% more production despite conversion of the entire available semi-natural area, and would at the same time lose all species unique to semi-natural habitats, namely on average 65% and 48% of their species, respectively. The significant species gains in organic systems in NL and in non-organic systems in GB are due to the comparatively higher share of unique species in production fields in the two regions.

Discussion

The key results from our large-scale study pertain to the confirmed essential contribution of semi-natural habitats to farmland biodiversity across all Europe, and a considerable species loss for a limited production gain in many farming systems if semi-natural habitats are converted to production fields. They indicate that in half of the study regions—arable-dominated, horticultural and wine production—half of the wild species are restricted to semi-natural habitats that make up only 10% or less of the farms. The conversion of those small remnant semi-natural areas would not markedly increase production but impair species richness. By contrast, in grassland-dominated regions with large semi-natural areas, conversion would only marginally decrease species richness and substantially increase production. However, the assumption of achieving the same yield on such converted areas than on existing productive fields is probably overly optimistic as most of those grasslands would already have been intensified if soil and topographical conditions were favorable. Organic farms had higher species richness than non-organic farms in both semi-natural and production fields likely due to synergetic effects between both types of habitats. This allows organic systems to suffer lower losses in the event of a 10% increase in harvestable energy needed.

There are four major limitations to this analysis. First, we are aware that results may be affected by the specific regions, taxa considered and the data from only one year. Still, our models allow a first approximation of quantifying the trade-off between increased agricultural production and biodiversity loss for Europe. Application to biomes elsewhere with very large natural or semi-natural areas would be critical as biodiversity might be difficult to estimate with the conventional methods used here. The second limitation is that it assumes that production fields reclaimed from semi-natural habitats would have similar productivity as the already existing farmland. Yet, their productivity is likely to be lower due to constraints related to local soil conditions and topography. Therefore, the modelled yield increases are probably overestimated. The third limitation relates to the use of species richness as proxy for biodiversity. The conservation value of the species unique to semi-natural habitats is likely to be higher than the conservation value of species that are unique to farmland, which are mostly more common and widespread species. Therefore, the biodiversity loss in terms of conservation would probably be more severe than reflected by species numbers alone. The fourth limitation is that our model cannot account for the associated loss of ecosystem services provided by wild species (e.g. pollination and pest control), which would impair crop yields.

Despite those limitations, the analysis allows to approximate the detrimental consequences for farmland biodiversity in Europe of converting semi-natural habitats to farmland, in arable regions in particular. Potential increase of harvestable MJ energy production exists in grassland regions that would little impair biodiversity if kept reasonable, but this could hardly be in form of typical arable products such as cereals due to unfavorable topography, climate and soil conditions. Thus, although the harvestable MJ energy production may be balanced between regions, production types and modes can only be marginally transferred. The analysis supports the necessity to develop alternative solutions for sustainable food production in the future, by combining up-to-date technologies[2], agro-ecological approaches and best practices that minimize land use and preserve semi-natural land and biodiversity[33]. Because the potential for production increase is limited, a sustainable European food system will also need to reduce food waste and require diets of the European population to adapt[1,34,35].

Methods

Study regions and farms. Ten European regions from boreal to Mediterranean were selected (Supplementary Table 1). They represented major agricultural land uses such as arable crops including horticulture, mixed farming, grassland and perennial crops (vineyards and olives). Within each region, a pool of ~20–40 farms was selected from which 12–20 farms were randomly selected (169 in total) that belonged to the same farm type, produced under homogeneous climatic and environmental circumstances and fulfilled specific criteria regarding their main production branch. In case the selected farms were not willing to participate, we asked other farms from the pool till the sufficient number has been reached. The selected organic farms had all been certified for at least five years. Farmers were asked if they were willing to participate in the study. If they refused, additional random sampling was conducted. In the region NL, 11 organic farms agreed to participate but only three non-organic farms, whereas seven organic farms and 11 non-organic farms were available in the region HU. During the study, one non-organic farmer in the region CH ceased participation.

Habitat maps and farm interviews. The complete area of all selected farms was mapped, using the BioHab method[36]. Excluded from the farm area were woody and aquatic habitats larger than 800 m^2 and summer pastures. Within the farm area, areal and linear habitats were recorded. For an areal habitat, the minimal mapping unit was 400 m^2 with a width of at least 5 m. More narrow habitats, between 0.5 and 5 m wide and at least 30 m long, were mapped as linear habitats. Habitats were distinguished in habitat types according to Raunkiær life forms, environmental conditions and management evidence[28]. Further, a farmland class was assigned to each habitat that described whether the habitat was managed for agricultural production or other objectives such as e.g. nature conservation. In face-to-face interviews following a standardized questionnaire, farmers provided detailed information on field management and yield.

Categorization as production fields and semi-natural habitats. Based on the habitat maps and available information about management intensity, we categorized all habitats as either semi-natural habitats or production fields. In agricultural landscapes, these two categories are often not clearly distinguishable. There is a gradient from more intensively managed production fields to less intensively used semi-natural habitats. In addition, a categorization at the local scale can be different from an approach at a European scale ([29] and see p. 45 of[37]). Here, we applied the same criteria for all ten study regions.

In all cases, we categorized as production fields: arable crops, intensively managed grasslands (following main plant species observed, management evidence and objectives, with fertilization and/or two or more cuts a year), horticultural crops, and vineyards.

We categorized as semi-natural habitats: linear habitats, habitats that were managed for nature conservation objectives, habitats where mainly geophytes, helophytes or hydrophytes were growing, grasslands with woody vegetation (shrubs and/or trees), and extensively managed grasslands (no fertilization, no or one cut a year).

Species sampling. Vascular plant, earthworm, spider and bee species were sampled in all different habitat types of a farm. One plot per habitat type was randomly selected per farm for species sampling. This resulted in 1402 selected habitat plots on 169 farms (Supplementary Table 2). In the selected habitats, species were sampled during one growing season, using standardized protocols[19,38]. Plant species were identified in squares of 10 × 10 m in areal habitats and in rectangular strips of 1 × 10 m in linear habitats. Earthworms were collected at three random locations of 30 × 30 cm per habitat. First, a solution of allyl isothiocyanate (AITC) was poured out to extract earthworms from the soil. Afterwards, a 20-cm-deep soil core from the same location was hand sorted to find additional specimens. Identification took place in the lab. Spiders were sampled on three dates at five random locations per habitat within a circle of 0.1 m^2. Using a modified vacuum shredder, spiders were taken from the soil surface, transferred to a cool box, frozen, or put in ethanol, sorted and identified in the lab. Bees (wild bees and bumble bees) were sampled on three dates, during dry, sunny and warm weather conditions. They were captured with an entomological aerial net along a 100 m long and 2 m wide transect, transferred to a killing jar and identified in the lab.

Grouping of species data. Species data were pooled per taxa, habitat and region, and three sub-communities were formed with species (1) exclusively found in semi-natural habitats, i.e. unique to semi-natural habitats, (2) exclusively found in production fields, i.e. unique to production fields, and (3) found in both habitat categories i.e. shared by production fields and semi-natural habitats. For calculations of effects over all four taxa, species richness was the sum of the individual taxa species richnesses.

Estimating species richness. Species richness was estimated using coverage- and sample-size-based rarefaction and extrapolation curves[31,39,40]. Rarefaction and extrapolation, including confidence intervals (bootstrap method) and sampling coverage, were calculated in R 3.4.0[41] using package iNEXT[42]. Detailed information is provided below for each topic.

Estimating richness of unique species to compare semi-natural habitats and production fields. To legitimately compare the richness of species unique to semi-natural habitats and to production fields, we used the coverage-based method, i.e. we standardized the samples by their completeness[30]. The point of comparison was determined by the so-called 'base coverage' identified by the following procedure[31]: (1) select the maximum sample coverage at reference sample size (number of sampling units) of the sub-communities under comparison, (2) select the minimum sample coverage at twice the reference sample size of the sub-communities under comparison, (3) identify the maximum of the results from step (1) and step (2) as 'base coverage'. The species richness estimates were then read off from the species sample-size-based rarefaction and extrapolation curves at the 'base coverage' for each sub-community being compared. If zero or exactly one species was unique to a sub-community at the reference sample size, no sample coverage could be calculated. In this case, we set the species richness at 0 or 1, respectively. The species richness estimate of the other sub-community under comparison was then read off at twice the reference sample size on the curve.

The 'base coverage' was individually defined for each region and each taxonomic group since the mixed effects models used to analyze the data took into account the variation among regions and taxonomic groups.

Differences in species richness unique to semi-natural habitats and production fields. The difference between the species richness unique to semi-natural habitats and unique to production fields was tested with mixed effects models using package lme4 (Version 1.1-12) in R[43]. The data were $(S_{ij} | \beta, b, x) \sim \text{Poisson}(\mu_{ij})$ from $i = 1, \ldots, 10$ regions. The model is:

$$\ln\left(\mu_{ij}\right) = \beta_0 + \beta_1 x_{1i} + b_{1i} \quad (1)$$

$$b_1 \sim N(0, \sigma 2)$$

where β_0 is a fixed intercept, β_1 a fixed effect sub-community x_{1ij} (species unique to semi-natural habitats versus species unique to production fields), b_{1i} are random intercepts for region i. Random effects are normally distributed with mean 0 and variance σ^2. The significance of term β_1 was calculated by log-likelihood ratio tests with one degree of freedom. For the models over all four taxa, an additional random intercept was included, i.e. b_{2j} with mean 0 and variance σ^2 for $j = 1, \ldots, 4$ taxa (Fig. 1b).

Differences in species richness between organic and non-organic systems. The comparison between organic and non-organic systems of species unique to semi-natural habitats and to production fields, and of species shared by the two habitat categories, relied on coverage-based extrapolation as described above. Differences between management systems were tested for significance using mixed-effects models with management system $\beta_1\ x_{1ij}$ as fixed effect in (1).

Estimating species loss due to conversion of semi-natural habitats to production fields. To predict the species loss due to conversion of semi-natural habitats to production fields, we relied on sample-size-based extrapolations[31] with species incidence frequencies. We estimated the richness of the species pool for the total number of mapped habitats including the extrapolated species richness unique to semi-natural habitats and unique to production fields, and the observed richness of shared species for each of the four taxa. This species pool provided the basis for the calculation of the species loss or gain (Table 1 and Supplementary Table 7). To model the species richness decrease for any amount of semi-natural habitats converted to production fields, we calculated and drew backward the curve composed of the accumulation curve for species unique to semi-natural habitats, to which the estimated total species richness unique to production fields (constant) and the corresponding gain of species unique to production fields (increases with increasing area of production fields as semi-natural habitats are converted), and the richness of observed shared species (constant) were added. This is the species decrease curve (Supplementary Fig. 2). If started at the observed species richness, this curve corresponds exactly to a species richness curve calculated by a cumulative random removal of semi-natural habitats one by one from the pool of all habitats. The four taxa decrease curves were added for the curve in Fig. 2. Confidence intervals (CI, 95%) shown in Figs. 2 and 3 are calculated by bootstrapping within the calculation of the species accumulation curves (iNEXT[42]), upper and lower bounds of the 95% CI of the four taxa being added. From the species decrease curve, we read off the predicted species richness for a conversion of 50% and 90% of the semi-natural habitats, and a conversion required to increase production by 10%.

As species were sampled in 20% of all mapped habitats on average per region (min. 8%, max. 35%), extrapolated species accumulation curves used to build the species decrease curve were calculated for more than two to three times the reference sample size, which is the suggested range for reliable extrapolation of the species richness estimator[31,44]. Obviously, the confidence intervals (CI) of the species richness extrapolations here became wide (Supplementary Fig. 4). As we still wanted to show the impact of a conversion of the whole semi-natural area into production fields on the production gain in the ten regions, we used the uncertainty (upper and lower bounds of the 95% CI of the four taxa added) to define two situations in addition to the average case to predict species richness for a 50% and a 90% semi-natural habitat conversion, and a conversion required to increase production by 10%: (1) a worst case situation with the upper bound of the CI of the expected species richness unique to semi-natural habitats, the lower bound of the CI of the expected species richness unique to production fields, and shared species assumed not to be able to survive without semi-natural habitats and considered like species unique to semi-natural habitats (i.e. upper bound); and (2) a best case situation with the lower bound of the CI of the expected species richness unique to semi-natural habitats, the upper bound of the CI of the expected species richness unique to production fields, and the lower bound of the CI of the expected shared species richness.

Estimating production gain. Farmer interviews delivered an average yield per crop type per farm for the years 2008–2010 (Supplementary Data[45] shows details for organic and non-organic systems separately). Farmers indicated yield in kilograms or tons per hectare. This was transformed into energy units, i.e. mega joules per hectare (MJ ha^{-1}) using standard values[46]. From this, for each region, the average yield (MJ ha^{-1}) was calculated by first multiplying individual crop type yields by the corresponding crop type areas to obtain the production per crop type, then summing up the production of all crop types, and finally dividing this sum by the total area of the crop types. For livestock farms, the fodder production of grasslands was estimated based on the average requirements per livestock unit, accounting for the amount of feed grain, legumes, silage maize and of imported feedstuff. All yields relate to plant biomass production and do not comprise livestock products. The average yield takes into account the relative cover of the different crop types in the regions. Therefore, the conversion of the semi-natural area to production fields was region-specific. The production of certain semi-natural habitats as e.g. olive groves in Spain was not part of the production calculation. The reason is that data on production for semi-natural habitats were mainly not available and/or negligible, e.g. extensively used grassland in CH or in HU, and we decided to apply the same treatment to all the regions. Consequently, in case of olive groves in Spain the effective increase in production is overestimated. To calculate the production gain per region, the production field area added by the conversion of semi-natural habitat area was multiplied by the average yield. In practice, in many regions it may be impossible to convert semi-natural habitat to productive land due to geomorphological constraints and poor soils, and even if land were converted, yields would be much lower than these averages. The results presented here, especially the 90% scenario, are therefore over-optimistic. On the other hand, our calculations are based on the area of semi-natural habitat available for conversion on existing farms, but in some regions other sources of semi-natural land may be available for conversion, e.g. former agricultural land that has been abandoned.

Species loss and production gain for three scenarios. We calculated the change of species richness and the production gain under current day production efficiency for two scenarios: (1) a conversion of 90% of the semi-natural area into production fields. The 10% of semi-natural area remaining is considered unsuitable for agricultural use or even impossible to cultivate; (2) a conversion of 50% of the semi-natural area into production fields, and (3) a necessary conversion of the semi-natural area into production fields to achieve a 10% production increase per region.

Standardization for organic and non-organic systems. Although the overall mapped area, the number of semi-natural habitats, the number of production fields and the average habitat size did not significantly differ between the two management systems (Supplementary Table 5), we standardized the number and size of habitats to the average across both systems per region to compare the species loss and production gain at current day production efficiency in the organic and non-organic systems. The total production in organic and non-organic systems per region was calculated based on the respective yield and the average mapped area of the production fields across both systems as described in section “Estimation of production gain”. The impact on biodiversity was analyzed for the scenario that organic systems should achieve the same level of production as non-organic systems by converting semi-natural habitats to production fields. We calculated the amount of the required area to be converted into production fields and the corresponding species change.

Differences between management systems were again tested for significance using mixed-effects models with management system $\beta_1\ x_{1ij}$ as fixed effect in (1).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Species, habitat and agricultural management data that support the findings of this study are available in Lüscher et al.[19], (https://doi.org/10.1890/15-1985.1). The production data (yield) that support the findings of this study are provided as Supplementary Data 1 at Jeanneret et al.[45], (https://doi.org/10.5281/zenodo.5115742).

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Author contributions

F.H., P.J., D.B., P.D., W.F., J.K.F., R.H.G.J., M.K., G.M., M.G.P., P.P. and J.-P.S. conceived the project; M.A., D.B., K.B., A.B., J.-P.C., M.D., P.D., S.E., Z.E. W.F., T.F., J.K.F, I.R.G., P.G., T.G., P.J., G.L., G.J., R.H.G.J., M.K., A.K.-H., G.M., J.N., M.-L.O., M.G.P., J.-P.S., M.K.S., N.S., D.S., S.W. coordinated field sampling and data processing in the respective study region; P.J. and G.L. analysed the data, together with M.K.S., P.P. and F.H.; P.J. and G.L. wrote the paper with input from all the authors.

Competing interests

The authors declare no competing interests.

Additional information

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