




Biodiversity and pollination benefits trade off against profit in an intensive farming system

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Agricultural expansion and intensification have boosted global food production but have come at the cost of environmental degradation and biodiversity loss. Biodiversity-friendly farming that boosts ecosystem services, such as pollination and natural pest control, is widely being advocated to maintain and improve agricultural productivity while safeguarding biodiversity. A vast body of evidence showing the agronomic benefits of enhanced ecosystem service delivery represent important incentives to adopt practices enhancing biodiversity. However, the costs of biodiversity-friendly management are rarely taken into account and may represent a major barrier impeding uptake by farmers. Whether and how biodiversity conservation, ecosystem service delivery, and farm profit can go hand in hand is unknown. Here, we quantify the ecological, agronomic, and net economic benefits of biodiversity-friendly farming in an intensive grassland–sunflower system in Southwest France. We found that reducing land-use intensity on agricultural grasslands drastically enhances flower availability and wild bee diversity, including rare species. Biodiversity-friendly management on grasslands furthermore resulted in an up to 17% higher revenue on neighboring sunflower fields through positive effects on pollination service delivery. However, the opportunity costs of reduced grassland forage yields consistently exceeded the economic benefits of enhanced sunflower pollination. Our results highlight that profitability is often a key constraint hampering adoption of biodiversity-based farming and uptake critically depends on society's willingness to pay for associated delivery of public goods such as biodiversity.

agroecology | ecosystem services | biodiversity-friendly farming | land-use intensity | wild bees

Agricultural expansion and intensification have boosted global food production but have come at the cost of environmental degradation and biodiversity loss (1, 2). Intensive agriculture not only drives loss of intrinsic values of biodiversity [i.e., decline of rare species (3, 4)] but also causes declines in functional biodiversity and ecosystem services that support agricultural production itself (5, 6). Ecosystem service benefits are increasingly being used as arguments for why biodiversity should be enhanced on farmland (7, 8). Biodiversity underpins ecosystem functioning and delivery of ecosystem services such as pollination and natural pest control (9, 10). Evidence is rapidly accumulating that more diverse agricultural landscapes support higher biodiversity which, in turn, is linked to higher crop production (11) and lower dependency on agrochemicals (12). More diverse farming systems furthermore enhance soil quality (13), improve nutrient cycling (14), and reduce soil erosion (15). Although these benefits represent straightforward incentives for farmers to invest in biodiversity management and lower pressures on wildlife, the uptake of biodiversity-enhancing practices by the agricultural sector remains low (16), presumably because of the scarcity of evidence of their economic profitability (8). The few studies that have to date examined cost–benefit trade-offs provide contrasting evidence, suggesting that farmers may profit economically (17, 18), break-even (19), or lose money (20) from biodiversity management. However, both the benefits and costs of biodiversity management to enhance ecosystem service delivery depend on the level of management effort (e.g., degree of habitat enhancement or land-use intensity reduction), which is rarely taken into account (8) (but see ref. 19). Moreover, different conservation objectives may require different levels of biodiversity management effort. For example, enhancing rare or threatened species generally needs a larger degree of habitat improvement (21) than promoting common species that provide the bulk of ecosystem service delivery (22). Whether rare species conservation, ecosystem service delivery, and economic benefits can go hand in hand remains unknown.

Biodiversity and delivery of ecosystem services are influenced by land use in the wider landscape, for instance because ecosystem service–providing species often need multiple habitats to complete their life cycle (23). Kremen and Merenlender (24) therefore argue

Significance

Making agriculture more sustainable and environmentally friendly is one of the main routes to address the current global biodiversity crisis. Many studies have shown that enhancing biodiversity can boost agricultural production through the ecosystem services provided by wild species, but very little is known about the economic profitability of integrating biodiversity-friendly management into farming systems. Here, we show that reducing land-use intensity on agricultural grasslands benefits bee diversity and pollination service delivery, and produces up to 17% higher revenue on neighboring sunflower fields. However, the costs of reduced grassland forage yields consistently exceeded the economic benefits of enhanced pollination. Our results therefore suggest that the transition to biodiversity-friendly farming may require additional public or private financial incentives.

The authors declare no competing interest.

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that the solution lies in managing entire landscapes to work for both biodiversity and people. For example, by growing multiple crops in close proximity, provision of key resources is spread over time which allows more species of pollinators or natural enemies to coexist, which in turn could result in an increase in the services they provide (25). On the one hand, this could reduce the costly necessity to create new habitats specifically tailored for delivery of ecosystem services, such as wildflower strips or hedges (26). On the other hand, it would increase the importance of managing for optimal synergies among fields rather than managing for maximum yield on a single field. Reducing management intensity to boost biodiversity on a field in one crop could enhance total farm profits if it disproportionately enhances yield in another crop.

To test the overall impact of managing for ecosystem services, here, we quantify the ecological, agronomic, and net economic benefits of enhancing biodiversity in grasslands adjacent to sunflower crop fields in Southwest France. We focus on pollination as a key ecosystem service supporting the production of insect-pollinated crops, and bees as the main group of pollinators visiting sunflower (27). Reported declines of wild bees (28, 29) have raised concern among policymakers and the general public and have increased interest in bee conservation (30). In Europe, grasslands constitute the most important bee habitat as they can provide both floral resources and nesting sites to wild bees (3). We ask whether conjoint, integrated management of grassland and

sunflower fields for provisioning and regulating ecosystem services can be more profitable than maximizing production at the individual fields, and whether this also benefits intrinsic biodiversity values, rare bee species in particular. To this end, we selected 21 pairs of sunflower fields and adjacent grasslands in the Long-Term Socio-ecological Research site “Zone Atelier Plaine & Val de Sèvre” (31) (Fig. 1), with the grasslands covering a gradient in harvesting frequency, a measure of grassland land-use intensity (32). Grasslands included permanent grasslands (>5 y old), temporary grasslands (≤5 y old) sown with grass species, and temporary grasslands sown with mixtures of grass and legume species (SI Appendix, Table S1), and were located in landscapes with approximately 80% arable land and 10% grassland (SI Appendix, Table S2). We surveyed flowering plant species and bees in the grasslands, and bees in the sunflower fields, and assessed the contribution of insect pollination to sunflower crop yield using pollinator exclusion treatments. Information on the management of sunflower fields and grasslands was collected by means of farmer interviews allowing to calculate their associated costs and income.

Results

Biodiversity and Pollination Benefits. To assess ecosystem service benefits to sunflower yield, we used linear mixed models (LMMs) and an information theoretic approach. We found that,

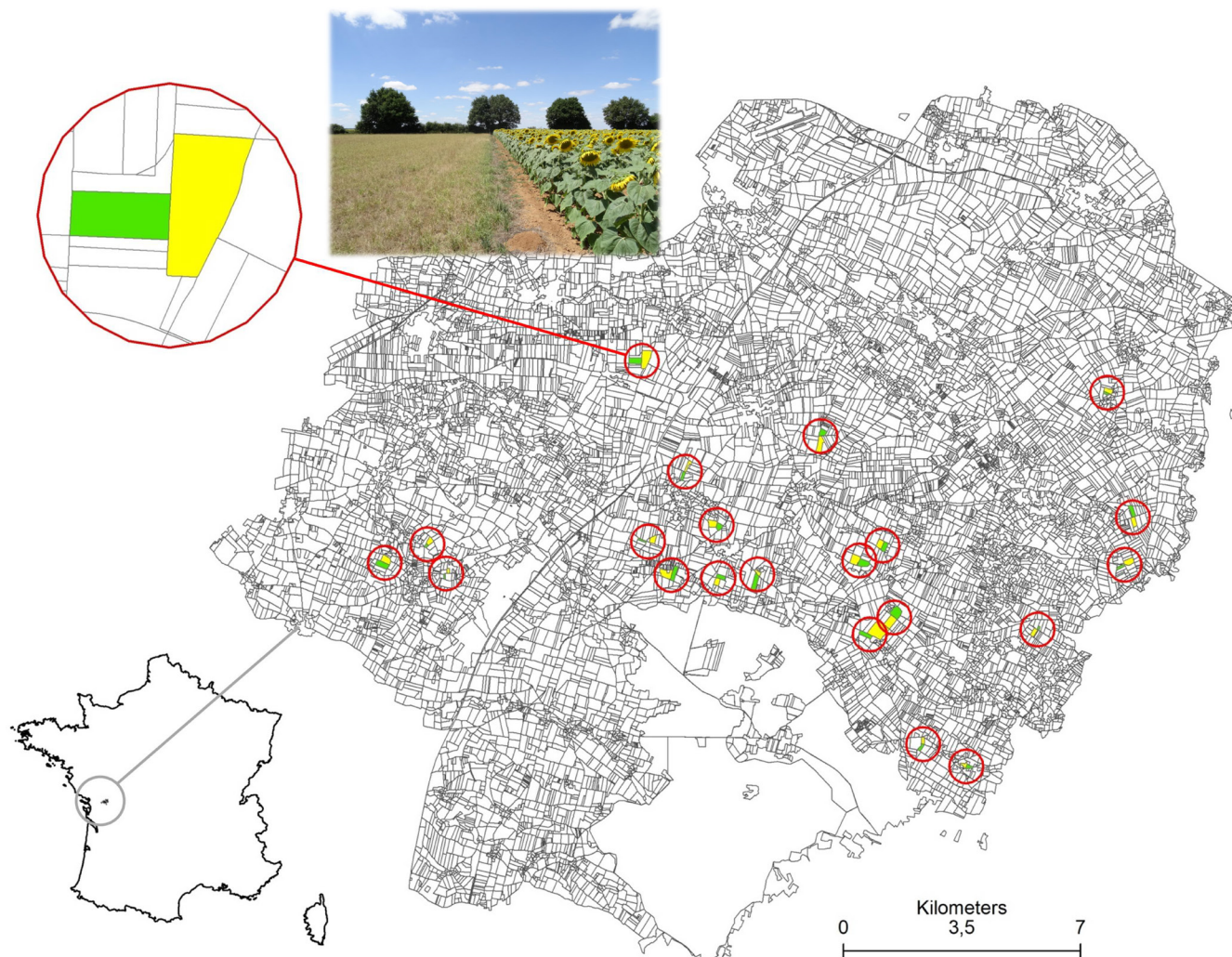


Fig. 1. Study region and experimental setup. Twenty-one pairs of grassland (green) and sunflower (yellow) fields were selected across the study region in Southwest France. Study landscapes (500 m radius around the edge between the two fields in each pair) are indicated by red circles.

on average, insect pollination enhanced sunflower yield by 7.8%, but the magnitude of the pollination effect depended on the fertilizer application rate in the sunflower fields and the species richness of wild bees visiting the sunflower fields (single best model within $\Delta AIC_c < 6$; marginal $R^2 = 0.75$; conditional $R^2 = 0.85$; *SI Appendix, Table S3*). Yield differences between open-pollinated and pollinator-excluded sunflower plants increased with increasing richness of flower-visiting wild bees, with the positive effects of increased bee richness being most pronounced at intermediate nitrogen fertilizer input (Fig. 2A and *SI Appendix, Fig. S1*). This suggests that enhancing wild pollinators could potentially (partially) replace external nitrogen input to sunflower fields under real-world field conditions, thereby corroborating the results of

previous experimental studies (33, 34). Interestingly, honeybees accounted for 93% of the total crop pollinators but were not related to pollination benefits, possibly because these managed pollinators were not limiting in any of the study sites (35).

Next, based on the information gained from the single-best LMM above, we used piecewise structural equation models (SEM) to assess how pollination service delivery in sunflower fields was related to the characteristics of the adjacent grasslands. We found that bee pollinator richness in sunflower fields was affected by the management and type of adjacent grasslands (Fig. 2B). Lower harvesting frequency in grasslands was associated with higher wild bee diversity in adjacent sunflower fields, primarily through positive effects of reduced harvests on grassland

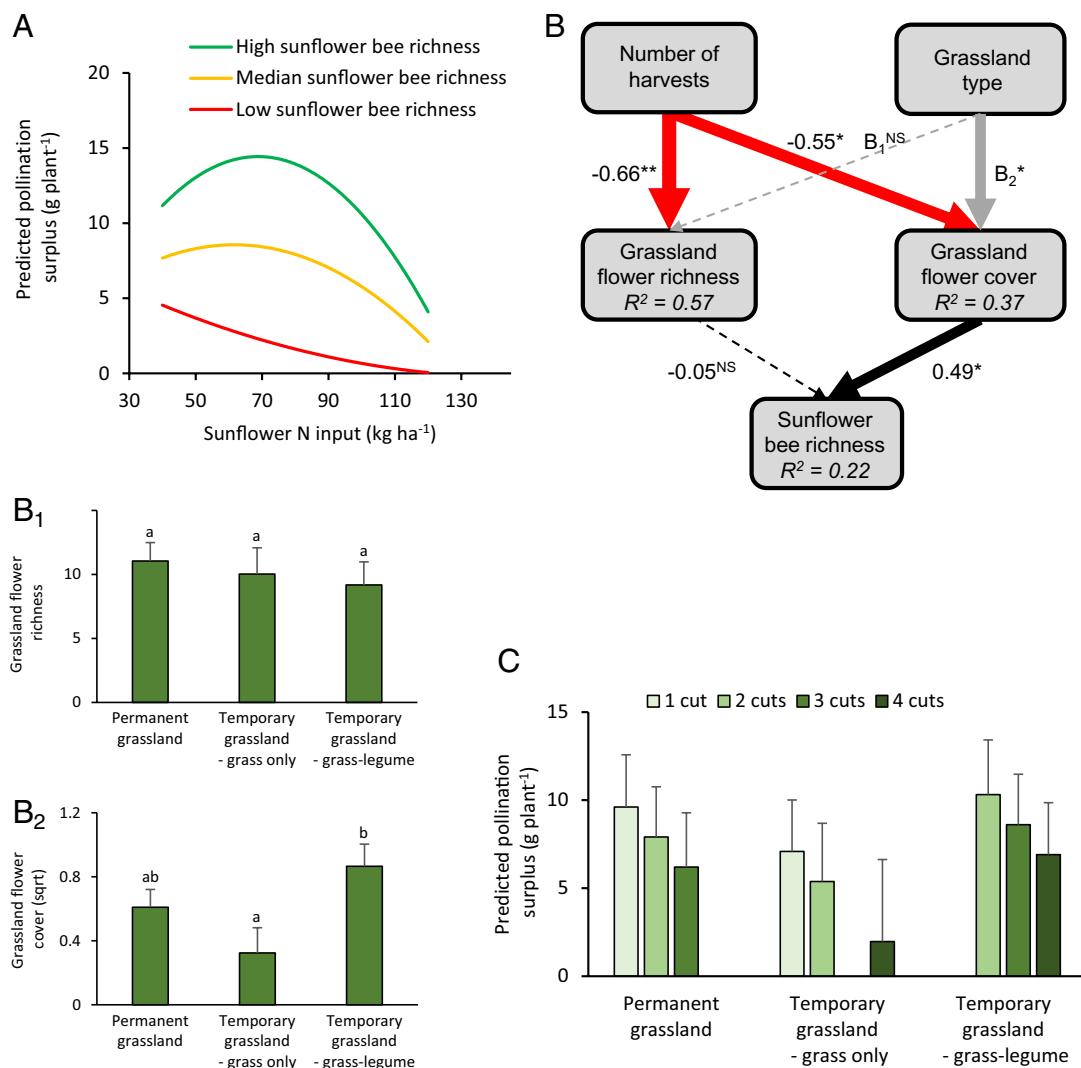


Fig. 2. The contribution of pollination to sunflower yield (pollination surplus) increases with species richness of bees, which in turn is mainly determined by the management intensity of neighboring grasslands. (A) Pollination surplus (i.e., the difference in yield between plants with and without pollinators) increases with species richness of bees visiting sunflower heads, but pollination benefits depend on nitrogen (N) application, with largest benefits at intermediate fertilizer application rates. Lines show predictions of the best model explaining pollination surplus, at first, second, and third quartile bee richness (*SI Appendix, Fig. S1*). (B) Bee richness on sunflower heads is primarily related to flower cover in neighboring grasslands. Flower cover, in turn, is determined by the number of times grasslands are being harvested and by grassland type. Depicted are the results of a structural equation model based on pollinator data of two survey rounds during sunflower bloom and grassland flower data of two survey rounds just prior to sunflower bloom. The hypothesized paths (*SI Appendix, Fig. S2*) were well supported by the data (Fisher's C = 6.43, df = 6, $P = 0.377$). Solid arrows and asterisks indicate (level of) statistical significance ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$). Red arrows indicate negative and black arrows indicate positive relationships between continuous variables. Numbers represent correlation coefficients. Gray arrows indicate effects of the categorical variable grassland type, with marginal model-estimated means (at two harvests) for flower richness and cover in each grassland type displayed in Fig. 2 B₁ and B₂, respectively. (C) The contribution of pollination to sunflower yield (pollination surplus) decreases linearly with the number of times neighboring grasslands are being harvested, with grass-legume-sown temporary grasslands yielding systematically higher than permanent grasslands and grass-sown temporary grasslands. Depicted are model estimates based on the best linear mixed-effects model explaining sunflower pollination surplus, under typical N application rate (60 kg ha⁻¹ y⁻¹) in the region, and incorporating sunflower bee species richness values for different grassland management estimated by the SEM analysis. Error bars represent one SE.

flower cover just prior to sunflower bloom. Grassland type affected sunflower pollinators as well through effects on flower cover, with flower cover being lowest in temporary grass-sown grasslands and highest in temporary grass-legume-sown grasslands. Consequently, the contribution of pollination to sunflower yield increased when land-use intensity on neighboring grassland decreased, and was consistently higher in sunflower fields next to grass-legume-sown grasslands than in those neighboring permanent or temporary grass-sown grasslands (Fig. 2C). The importance of flower cover rather than flower richness for sunflower pollinators can be explained by the fact that common bumblebee species (especially *Bombus lapidarius* and *B. terrestris*) made up the vast majority (86%) of the wild bee visits. Bumblebees are generalist, dominant crop-pollinating species (22) that generally forage for pollen and nectar on a broad spectrum of plants, even though when given a choice they prefer leguminous plants such as alfalfa and clover species that were sown in the grass-legume temporary grasslands (36, 37). This suggests that enhancing pollination service delivery may require only modest changes in grassland management to enhance the amount of flowers and promote wild bees (38), and that including leguminous species in seed mixes may be particularly effective (39).

Analyzing the relationship between management intensity and grassland bee biodiversity revealed that reducing the harvesting frequency drastically increased total and locally rare wild bee species

in the grasslands (SI Appendix, Table S4). Interestingly, the main mechanisms driving grassland bee diversity differed from the ones driving bee diversity in neighboring sunflower fields, with the effects of harvesting frequency operating through flower richness rather than cover (as indicated by SEMs; Fig. 3). This suggests that to maintain diverse grassland bee communities, a diverse flowering vegetation is more important than an abundantly flowering vegetation (40). Note that for both total richness (Fisher's $C = 31.77$, $df = 6$, $P < 0.001$) and rare bee richness (Fisher's $C = 27.24$, $df = 6$, $P < 0.001$), tests of d-separation revealed missing paths from the hypothesized SEM model (SI Appendix, Fig. S2), with mechanisms differing between total and rare bee richness as well. In particular, total bee richness was additionally indirectly influenced by flower richness through effects on flower cover (Fig. 3A), while rare bee richness was additionally negatively affected by a direct effect of harvesting frequency (Fig. 3B). Direct effects of harvesting probably reflect disturbance of nesting sites or instant mortality due to grassland harvesters, which may disproportionately affect the smaller populations of rare bee species. The highest bee diversity values, including rare species such as *Anthophora pubescens*, *Lasioglossum discum*, and *Rhophitoides canus*, were attained in the most extensively used permanent grasslands, confirming the importance of low-input grasslands as biodiversity hotspots in Europe (41). Taken together,

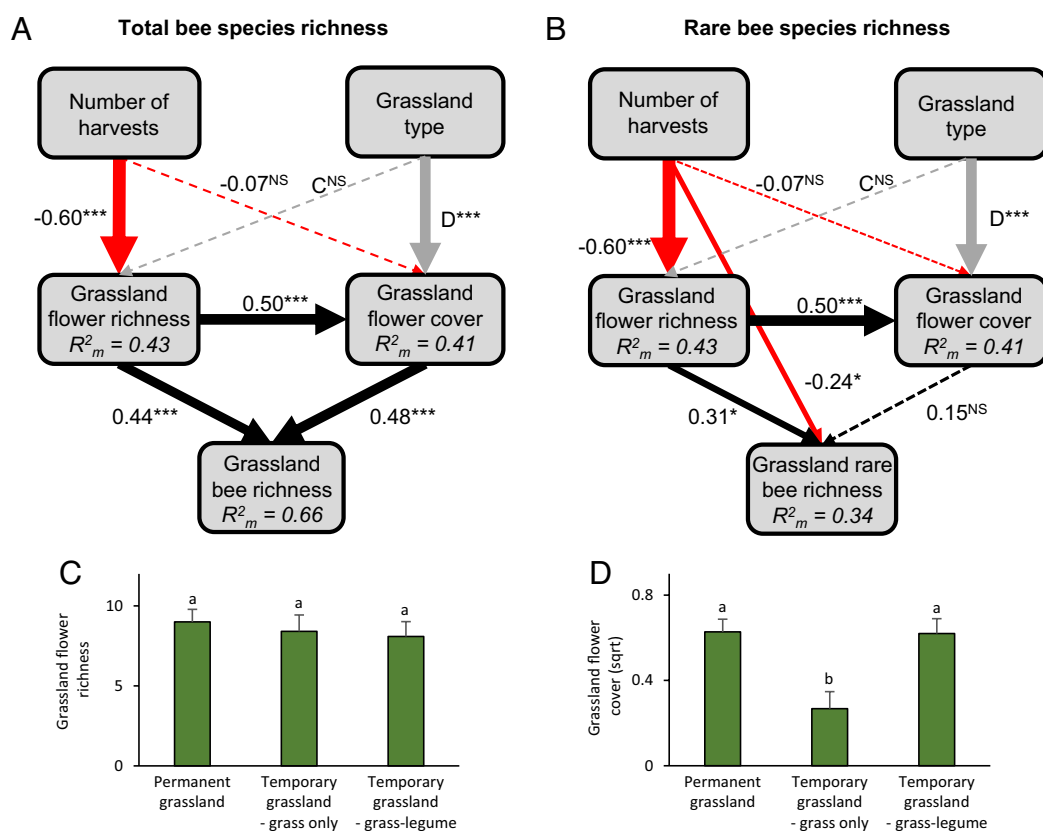


Fig. 3. Bee richness in grasslands' neighboring sunflower fields is negatively influenced by harvesting frequency of the sward. (A) Total bee richness in grasslands is positively related with grassland flower richness and flower cover. In turn, flower richness is negatively affected by harvesting frequency but does not differ among grassland types (Fig. 3C). Flower cover depends on grassland type, with permanent grasslands and temporary grass-legume grasslands having higher cover than that in temporary pure-grass grasslands (Fig. 3D), and is indirectly negatively affected by harvesting frequency via effects on flower richness (SEM model fit: Fisher's $C = 7.83$, $df = 4$, $P = 0.098$). (B) Rare bee species richness is almost exclusively influenced by harvesting frequency through direct negative effects and indirect negative effects via flower richness (SEM model fit: Fisher's $C = 0.058$, $df = 2$, $P = 0.971$). Depicted are the results of the structural equation model based on pollinator data of four survey rounds before and after crop flowering. Solid arrows and asterisks indicate (level of) statistical significance ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$). Red arrows indicate negative and black arrows indicate positive relationships between continuous variables. Numbers represent correlation coefficients. Gray arrows indicate effects of the categorical variable grassland type, with marginal model-estimated means (at two harvests) for flower richness and cover in each grassland type displayed in Fig. 3 C and D, respectively.

the differing SEM results for grassland bee diversity and sunflower bee diversity suggest that, although extensifying grassland management benefits crop pollinators as well as wider bee diversity, maximization of ecosystem services and intrinsic biodiversity values requires different management strategies (22, 42).

Economic Costs and Benefits. Finally, we estimated the economic consequences for farmers when choosing a more pollinator-friendly grassland management. The positive spillover effects of a reduced grassland management intensity on pollination of adjacent sunflower fields resulted in higher sunflower gross margins. In our study system, the largest reductions in harvesting frequency resulted in a 10%, 17%, and 10% higher gross margin in sunflower fields adjacent to permanent (from three to one harvest), temporary grass-sown (from four to one harvest), and temporary grass–legume-sown grasslands (from four to two harvests), respectively. On the cost side, reducing harvesting frequency decreases total forage biomass and lowers forage quality and associated market value. In permanent grassland, this meant that reducing harvesting frequency from three to two times per year resulted in a 41% decline in gross margin (*SI Appendix, Table S4*). However, going from three harvests to only one harvest yields much more drastic declines in gross margins (117%) since the most extensively used permanent grasslands were mulched (not harvested) because of agri-environment scheme prescriptions and consequently are not used to produce forage. Temporary grasslands showed similar, but much more moderate economic consequences when going from the most intensive to the most extensive grassland management scenario. However, under all scenarios, the costs associated with reduced grassland management intensity exceeded the benefits of enhanced sunflower pollination (*SI Appendix, Table S4*). As a result, accumulated grassland forage and sunflower gross margins were highest when grassland forage production was most intensive, despite lower pollination service delivery to sunflower. Our results therefore indicate that managing grasslands less intensively may produce win-win situations for grassland bee diversity and delivery of pollination services to sunflower fields, but not for overall farmer profit.

Discussion

Our findings provide an explanation for the reticence of farmers to adopt ecosystem service-enhancing management. Farmers are generally risk averse (43), and our results show that they cannot be reasonably sure that ecosystem service-based approaches (e.g., refs. 8 and 24) work both ecologically and economically. It should however be noted that cost-benefit analyses of biodiversity-enhancing management are context dependent. For example, in a highly pollinator-dependent, high-revenue crop such as blueberry (17), pollination benefits will be significantly higher and the balance could be tipped in favor of a win-win-win for biodiversity, pollination, and profit. Yet, the most widely cultivated insect-pollinated crops in Europe such as oilseed rape and sunflower are modestly pollinator-dependent, comparatively low-revenue crops (44, 45). The results obtained in the agricultural landscapes of our study area therefore probably hold for most European intensively managed agricultural landscapes.

Farmers are not only motivated by profit (46, 47), and many farmers carry out unsubsidized biodiversity-friendly practices voluntarily (48). Yet, economic constraints and incentives are principal factors in farmer decision-making (49, 50), and without financial triggers adoption of ecosystem service-enhancing management will probably mainly be restricted to farmers that are intrinsically motivated to work with biodiversity (46). Increased uptake by mainstream farming requires financial incentives that

at least compensate for income losses resulting from biodiversity-enhancing measures. Our study focused on the private benefits of ecosystem services to farmers, but integrating biodiversity management into farming practices also provides public goods that go beyond pollination service provision, such as carbon sequestration, clean air and water (51), landscape esthetics (52), and conservation of rare species (53). For a transition toward more biodiversity-based farming systems, it is essential that farmers are financially rewarded for providing these public goods, for example through public payments in the form of agri-environment schemes, or through private payments in the form of higher market prices. In fact, more than half of the extensively managed grasslands in our study system were part of agri-environment schemes targeting rare farmland birds, for which farmers received average payment rates of 337, 408, and 334 euro ha⁻¹ for permanent, temporary grass-sown, and temporary grass–legume-sown grasslands, respectively. These payments would more than compensate for any loss of accumulated gross margin associated with the more extensive grassland management in the grassland–sunflower system (*SI Appendix, Table S4*). However, the abovementioned payment rates included compensations for conversion from arable to grassland farming, which makes it impossible to link them directly to the economic costs and benefits of managing grasslands more extensively (*Materials and Methods*). Nevertheless, it does suggest that agri-environment schemes targeting biodiversity can export ecosystem service's net benefits to neighboring fields.

Our results furthermore suggest that, from both a pollination service and a biodiversity conservation perspective, it makes sense to improve grassland habitat quality through reducing grassland land-use intensity. In mixed crop–livestock farms, reducing land-use intensity on grasslands may therefore pose a promising strategy to promote ecosystem service delivery to adjacent crop fields (54). However, our study indicates that considering the quality of habitats for service-providing organisms, in our case grassland floral resource availability for wild bees, is essential for achieving biodiversity and ecosystem service delivery benefits of such habitats (26). To be effective, environmental policy instruments that aim to enhance biodiversity and ecosystem services on farmland, such as the new European Union's Common Agricultural Policy, should therefore target not only the quantity but also the quality of semi-natural habitats in agricultural landscapes.

Materials and Methods

Experimental Design. In spring 2015, we selected 21 study sites consisting of a sunflower field and an adjacent grassland located in the Long-Term Socio-ecological Research site "Zone Atelier Plaine & Val de Sèvre" in southwestern France (31). Sunflower (*Helianthus annuus* L.) is the main oilseed crop in Europe (45) and is, together with oilseed rape, the most widely grown insect-pollinated crop in the study region (31). Grassland study sites included permanent grasslands (>5 y old), temporary grasslands sown with grass species (≤5 y old), and temporary grasslands sown with mixtures of grass and legume species (≤5 y old). Sunflower–grassland pairs covered a gradient in grassland-harvesting frequency, a proxy for land-use intensity (32, 55). The harvesting frequency ranged from one to four times a year, with frequencies ranging from one to three times for permanent grasslands, one to four times (excluding three times) for temporary pure-grass grasslands, and two to four times for temporary grass–legume grasslands (*SI Appendix, Table S1*). Grasslands were harvested for hay or silage with the exception of the most extensively used single-harvest permanent grasslands that were only mulched as part of an agri-environment scheme prescription, targeting the conservation of the little bustard (*Tetrax tetrax*), a highly threatened bird species (56). Most of the other less intensively managed grasslands were under agri-environment scheme prescription as well (*SI Appendix, Table S1*). To minimize confounding effects of landscape composition (e.g., ref. 11) on cost-benefit

trade-offs of biodiversity management, the main focus of our study, we minimized variation in the composition of the landscape surrounding our study sites. We used ArcGIS 10.0 (Environmental Systems Research Institute) to determine landscape composition (% cover of grassland, woody habitats, total arable land, and sunflower; *SI Appendix, Table S2*) in radii of 500 m and 1,000 m around the study sites. Analyses revealed that cover of the dominant land-use types was not significantly correlated with grassland-harvesting frequency or with grassland type (*SI Appendix, Table S2*). The minimum distance between study sites was 0.9 km (range: 0.9 km to 3.8 km; mean \pm SD: 1.7 ± 1.0 km).

Surveying Bees and Flowering Plants. We surveyed flower-visiting bees and flowering plant species from June to August 2015 using standardized transect walks following Scheper et al. (53). Sunflower fields were sampled in two survey rounds during sunflower bloom, while grasslands were sampled twice just before and twice shortly after sunflower bloom. The timing of the survey rounds in each study site was determined by the phenology of the individual focal sunflower field. In each field, we established two 150 m² transects, with transect dimensions measuring 1 m \times 150 m in the sunflower fields and 2 m \times 75 m in the grasslands. In sunflower fields, one transect was located at the crop edge (the outer 2 to 3 crop rows) adjacent to the grassland and one transect was located in the interior of the crop, at 25 m distance parallel to the edge transect. In grasslands, the two transects were located in representative flower-rich parts of the grasslands. Bees were sampled using insect nets for a total of 15 min net surveying time per transect per survey round, between 9:00 and 06:00 h on dry, sunny days with low wind speeds and temperatures above 17 °C. We identified and recorded all entomophilous plant species that flowered during the survey and estimated flower cover of each species as the total number of flower units \times the mean surface area of the flower unit, divided by the transect area. Total flower cover per transect was determined as the sum of the cover of all observed flowering species (53).

Agricultural Management. Early 2016, we used semi-structured interviews to survey the farmers participating in the study to obtain information on characteristics and agronomic practices on the sunflower fields and grasslands. Agronomic information obtained included sunflower variety, sunflower field size, sunflower total nitrogen fertilizer application (organic and inorganic), grassland sowing year (age), sown forage plant species, grassland-harvesting frequency (number of harvests in 2015), and grassland size. The nitrogen content of different types of organic fertilizers was calculated following the approach of Kleijn et al. (57).

Quantifying Sunflower Pollination and Yield. We assessed the contribution of insect pollination to sunflower crop yield using pollinator exclusion treatments (58). In June, prior to anthesis, we selected ten pairs of sunflower plants in each field. The pairs were evenly distributed along a 45-m transect perpendicular to the crop edge. Plants within each pair were selected so that they had similar developmental stage, vigor, and stem diameter (measured between the third and fourth internodes) (59), and were located within the same crop row, within a maximum distance of 1 m of each other. We randomly selected one plant of each pair and covered its flower head with a fine mesh nylon bag (<1 mm \times 1 mm), allowing self- and wind-pollination but excluding insect pollination. The flower head of the other selected plant was not bagged and remained accessible to all flower-visiting insects. All bags were removed after flowering. For each plant, we quantified surrounding plant density by counting the number of plants in the same row within 50 cm distance from the focal plant and by measuring the distance to the next row. We measured plant stem diameter and flower head diameter during flowering (July) and at the time of harvest (September). After harvest, flower heads were dried for 72 h in a ventilated heat chamber at 37 °C, and seeds were removed from the flower heads using a threshing machine (Criquet, Moulis). We sorted full and empty seeds and dried the full seeds at 80 °C for 48 h. Full seeds were counted and weighed using an automatic counter (Contador, Pfeuffer) and an electronic balance (0.01 g accuracy), respectively. Thirty-five plants were affected by mold at the time of harvest and excluded from further analysis. Yield analyses were therefore based on a total of 385 experimental plants.

Varietal Differences in Pollination Dependency and Yield. The farmer interviews revealed that 12 different varieties of hybrid sunflower had been grown in the 21 examined sunflower fields. This made it impossible to establish whether, at a certain level of management intensity, differences in yield between fields were caused by pollination or by variety. To disentangle and correct for pollination and

variety effects, we set up a pot experiment at Wageningen University Experimental Farm (the Netherlands) in the summer of 2016 to quantify pollination dependency and crop yield for each of the 12 varieties under standardized conditions. Seeds of the different varieties were obtained from the commercial seed suppliers in the study region and grown outdoors under ambient conditions in 11 L pots. Plants were drip irrigated and received 50 kg ha⁻¹ of nitrogen fertilizer. We established five experimental randomized blocks, with each block containing a pair of plants of each variety. Just before anthesis, a randomly selected plant of each pair received a pollinator exclusion treatment (1 mm \times 1 mm fine mesh nylon bag), using the same approach as in the field study. We monitored pollinator visitation rates on open-pollinated plants for a total of 60 min on two occasions during sunflower bloom (30 min each), following the approach of Fijen and Kleijn (60). The analysis of visitation data showed that visitation rates did not significantly differ among varieties (linear mixed-effects model with square-root transformed visitation rate as response variable, variety as fixed factor, and block as random factor; likelihood ratio test $\chi^2_{(11)} = 8.74, P = 0.65$). After harvest, flower heads were dried for three weeks at 35 °C. Seeds were manually extracted and sorted. Dry full seeds were counted using a seed counter (Contador, Pfeuffer) and weighed using an electronic scale.

For each variety, we used a linear model to estimate sunflower seed yield for the two pollination treatments while correcting for variation in stem diameter. We subsequently used the relative differences in yield between varieties in the pot experiment to standardize yield measurements obtained in the field study. To this end, we used the yield of the variety that was most commonly used by farmers in the field study (variety X1, grown in four fields), and, based on the pot experiment, calculated yield conversion ratios for the bagged and unbagged plants of the other varieties (*SI Appendix, Table S5*). In other words, estimated yield for variety X1 in the experiment was set at 1, varieties that had higher yields than variety X1 in the pot experiment had a conversion ratio that was smaller than 1, and varieties with a lower yield than X1 had a conversion ratio larger than 1. Yield data obtained in the field study were then multiplied by the corresponding variety conversion ratio to express all yields in the field study in "units of variety X1," thereby correcting for inherent differences in yield and pollination dependency between sunflower varieties.

To assess the sensitivity of our results from the field study to the uncertainty in the conversion ratios for the different sunflower varieties from the pot experiment, we repeated the model selection procedure with which we analyzed the sunflower yields in the field study (*Statistical Analyses*) in 25 runs. In each run, the standardized, converted sunflower yields were based on variety conversion ratios that were randomly varied within mean \pm SE of the respective variety conversion ratio (*SI Appendix, Table S5*). The sensitivity analysis showed that the results of our main analysis based on the converted sunflower yields were robust for uncertainty in the variety conversion ratios, with the best model from our main analyses (*SI Appendix, Table S3*) consistently remaining the highest ranked model in all runs (*SI Appendix, Table S6*). All further yield analyses and results are therefore based on the converted, standardized yields (i.e., expressed in yields for variety X1).

Statistical Analyses.

Estimating the pollination contribution to sunflower yield. We used LMMs and a multimodel inference approach to analyze the standardized sunflower yield data. We first used an information theoretic approach to identify covariables that were strongly related to sunflower yield and that could therefore be used to correct for inherent differences in yield that were unrelated to our variables of interest. We constructed a set of LMMs with yield as response variable and all possible combinations of sunflower field size, distance from the field edge, plant density, stem diameter, and head diameter as explanatory variables. The latter three variables were included both as an average value per field and as a within-field centered value to separate across and within field effects of these variables, respectively (61). Yield was square-root transformed (which gave better residual diagnostic plots than log-transformation) to improve normality and homogeneity of residuals. Field ID and pollination treatment nested within field ID were included as random factors. Variance inflation factor values indicated no problems with multicollinearity (all VIFs < 3). The model containing within-field centered stem diameter, within-field centered head diameter, and averaged head diameter per field was the most parsimonious and best-performing model within $\Delta AIC_c < 6$ (62) (*SI Appendix, Table S7*), and these correcting covariables were included in all subsequent yield analyses.

To examine to what extent the contribution of insect pollination to sunflower yield was explained by the abundance and diversity of flower-visiting wild bees and honeybees in the sunflower fields, we built a set of LMMs that included

pollination treatment (pollinator excluded vs. open pollinated) and two-way interactions between pollination treatment and either the abundance of honeybees, abundance of wild bees, or wild bee species richness. As preliminary analyses showed that none of the bee variables differed significantly between crop edge and crop interior (LMMs with bee variables as response variables, transect location as fixed factor, and field ID as random factor: honeybee abundance $\chi^2_{(1)} = 0.00, P = 0.95$; wild bee abundance $\chi^2_{(1)} = 0.90, P = 0.34$; wild bee richness $\chi^2_{(1)} = 1.41, P = 0.24$), bee data were pooled over transects and averaged over survey rounds. To test for interacting effects of the bee variables, we also included models containing three-way interactions between pollination treatment and all pair combinations of the different bee metrics. As pollination benefits may be affected by nitrogen fertilizer inputs, both linearly and nonlinearly (33, 34), we furthermore included models containing two-way and three-way effects between pollination treatment and linear or quadratic effects of total (organic and inorganic) nitrogen fertilizer levels in the sunflower fields and bee variables. Finally, for reference, we included a null-model that only contained the stem and flower head diameter covariables (*SI Appendix, Table S3*). Yield models included field ID, with pollination treatment nested within field ID (to account for yield measurements on multiple bagged and open-pollinated plants per field), as random factors. The models were ranked based on their corrected Akaike's Information Criterion (AIC_c). Variance inflation factor values indicated no problems with multicollinearity in any of the examined models (all VIFs < 4). Yield of one sunflower field was excluded from the analyses because the variety grown in this field was used to produce bird food instead of sunflower oil, and was the only field that was irrigated. Analyses including data from this field gave qualitatively similar results though (*SI Appendix, Table S8*).

Explaining variation in pollinator diversity on sunflower heads. Next, we used piecewise structural equation models (SEM) (63) to examine whether the results of the previous analysis of sunflower yield could be linked to the characteristics of the grasslands neighboring the sunflower fields. Because the highest ranking LMM explaining variation in sunflower yield included wild bee richness as a predictor (*SI Appendix, Table S3*), we combined several linear models in an SEM to examine whether and how wild bee richness in sunflower fields was affected by grassland type and grassland-harvesting frequency. We hypothesized that harvesting frequency would indirectly negatively affect wild bee richness in sunflower fields by reducing the amount and diversity of flower resources present in the adjacent grassland prior to sunflower bloom (i.e., during the first two survey rounds in grasslands). Furthermore, we expected that wild bee richness in sunflower fields would depend on the type of the adjacent grassland, via differences in floral resource availability among grassland types (*SI Appendix, Fig. S2*). The SEM fit was assessed using Shipley's test of d-separation (64). Although we aimed to minimize variation in landscape composition during selection of study sites, and none of the landscape variables was significantly correlated with sunflower wild bee richness (all $|r| < 0.35$, all $P > 0.12$), we nevertheless checked whether including landscape composition increased model performance because this variable has been shown to be an important determinant of pollinator diversity and abundance in crop fields (65, 66). This set of analyses indicated that even the landscape variable that was most strongly correlated with sunflower wild bee richness (% woody habitats in 500 m radius, $r = 0.35, P = 0.12$) did not improve SEM model performance ($\Delta AIC_c = 42.75$). Similarly, we assessed whether including grassland size improved SEM model fit, but this was not the case (SEM $\Delta AIC_c = 44.62$). This made us confident that the variation in landscape composition and grassland size observed in our study did not affect its outcome, and these variables were not further considered.

Estimating biodiversity benefits of grassland management. We used piecewise SEM to examine the effects of grassland-harvesting frequency on wild bee communities in the grasslands themselves. Separate analyses were performed for total wild bee species richness [$\log(x + 1)$] and the species richness of locally rare bees [$\log(x + 1)$], with species being classified as locally rare if their abundance accounted for <1% of the total number of wild bee individuals in the grassland dataset (55). Analyses were based on data from all grassland survey rounds, with data pooled over transects per round. SEM analyses examined similar hypothesized paths as in the analysis of sunflower bee richness (see above, *SI Appendix, Fig. S2*), with paths analyzed using LMMs that included survey round as random factor. When Shipley's test of d-separation suggested lack of SEM model fit, we sequentially added missing paths until a satisfactory model fit was achieved [as indicated by Fisher's C-statistic (63)]. As with the SEM analyses of wild bee richness

in the sunflower fields, we checked whether including the most strongly correlating landscape variable improved SEM model performance, but this was not the case (total wild bee richness: % sunflower in 500 m radius, $r = -0.47, P = 0.03, SEM \Delta AIC_c = 11.99$; rare bee richness: % total arable land in 500 m radius, $r = -0.36, P = 0.10, SEM \Delta AIC_c = 15.86$). Including grassland size did not improve SEM model performance either (total wild bee richness: SEM $\Delta AIC_c = 6.58$; rare bee richness: SEM $\Delta AIC_c = 8.82$).

Economic costs and benefits of managing grasslands for sunflower pollination. To calculate the economic benefits and costs attributed to increased sunflower pollination due to extensification of grassland management, we combined the results from the best LMM describing sunflower yield and the SEM describing wild bee richness in sunflower fields. For simplicity, we assumed that paired sunflower fields and grasslands belonged to the same farmer. Mixed-farming is the main farming system in the study area (31) and farmers that own grasslands and sunflower fields are common. However, even if fields in reality belong to different farmers, the analyses are still relevant for collective farming systems and working landscapes. It is increasingly recognized that reconciling biodiversity conservation and food production requires an across-farm, landscape-scale approach (24, 67) in which farmer collaboratives play an important role (68, 69).

We used the SEM-estimated species richness of bees for the different harvesting frequencies in the different grassland types as input in the highest ranked yield LMM to predict how grassland management ultimately translates into pollination benefits in adjacent sunflower fields. Yield model predictions were based on mean values for the correcting covariables and, as pollination benefits depended on nitrogen fertilizer input in the sunflower fields (Fig. 2A), were performed for different sunflower nitrogen input values ranging from 40 to 120 kg ha⁻¹ (First quartile to third quartile). Combining the LMM and SEM results allowed us to link harvesting frequency of grasslands via their effects on floral resources, to sunflower-visiting bee communities, and subsequently to sunflower yield. We did not find any indications for distance-decay effects for bees and sunflower yield ("*Estimating the pollination contribution to sunflower yield*" and *SI Appendix, Table S7*), likely because wild bee visitation of sunflower flowerheads was dominated by large-bodied bumblebees that have large foraging ranges (70, 71). We therefore extrapolated our transect-level results for sunflower yields to the whole-field scale. We estimated per ha yields by extrapolating the yield per sunflower-head estimation, assuming a sunflower plant density of 5.7 heads per square meter, which was the average across all fields.

Based on the yield and further agronomic information, we established our cost-benefit analysis from the point of view of farmers. Benefits originated from pollination-induced increased sunflower yields; costs from the lower forage production in the different grasslands. Since the studied changes in production systems did not require any new production methods, no investments into new machines were necessary and no changes in fixed costs took place. Thus, we based our economic calculations on gross margins, i.e., the difference between revenues and variable costs. Information on typical agronomic practices and costs (in 2015) of the sunflower fields and the different grassland types in the region was obtained from local agronomic experts and external sources. With regard to sunflower production, we calculated revenues by multiplying per ha yields with local market prices in 2015 [350 € t⁻¹ (72)]. Production costs comprised the following positions: costs for fertilizers (based on synthetic fertilizer use), seeds and pesticides (as far as used), as well as variable costs for the use of machinery and labor (73, 74). Economic benefits gained by an improved pollination performance in sunflower cultivation were calculated by comparing the estimated gross margins of sunflower fields adjacent to the different grasslands. Calculations of forage production were carried out applying the same approach and were established for different harvesting frequencies as well as for the different grassland types (permanent grassland, temporary grass-sown grassland, and temporary grass-legume sown grassland). Grassland yield levels in 2015 were estimated based on local information (details given in *SI Appendix, Supplementary text and Table S9*), whereby hay production only was assumed. Prices for hay in 2015 were taken from ref. 75. Production costs again comprised costs for fertilizers, seeds and pesticides (as far as used), as well as variable costs for the use of machinery and labor (73). All calculated gross margins mentioned above can be found in *SI Appendix, Tables S10-S12*. In a final step, we assumed an area proportionality of sunflower and forage production and calculated accumulated per-ha gross margins of sunflower production with adjacent forage production

per-ha gross margins. Gross margins of sunflower production were based on a nitrogen fertilizer application rate of 60 kg ha⁻¹ y⁻¹ which is the typical rate applied in the region. The overall accumulated gross margins show the economic value of a certain combination of forage and sunflower production and allow a direct cost-benefit comparison of the different scenarios. Using nitrogen fertilizer rates that maximize sunflower gross margins for the different grassland management scenarios resulted in qualitatively similar patterns in accumulated gross margins as those based on typical nitrogen fertilizer rates in the region (SI Appendix, Table S13).

Although 12 of the 21 grasslands in our study were under agri-environment scheme (AES) prescription, we were not able to directly link management intensity of the grasslands to the amount of AES payments received. Most (83%) of the AES grasslands were former arable fields that were part of a scheme where farmers were paid to convert arable fields into grasslands and maintain them for several years. As such, these particular payments were not directly linked to the management of the grasslands themselves after conversion from arable fields. To illustrate this, for the twelve grasslands that received AES payments in our study, there was no significant correlation between the amount of payment received and the number of harvests ($r = -0.24$, $P = 0.44$), or grassland flower richness (June: $r = 0.01$, $P = 0.98$; August: $r = 0.19$, $P = 0.55$) and cover (June: $r = -0.32$, $P = 0.30$; August: $r = -0.08$, $P = 0.82$). As we were unable to disentangle the payments for arable-to-grassland conversion from payments directly associated with management intensity restrictions, and because we wanted to calculate the pure and not the subsidy-driven financial advantage or disadvantage of managing grassland extensively, we did not explicitly include any AES payments in our economic analyses. Instead, we briefly discuss and explore the implications of AES payments for the profitability of the grassland-sunflower system.

Data, Materials, and Software Availability. All data associated with this manuscript are freely available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j6q573nkr> (76).

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