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RESEARCH ARTICLE

Increasing crop richness and reducing field sizes provide higher yields to pollinator-dependent crops

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Abstract

1. Agricultural landscapes cover >60% of terrestrial landscapes. While biodiversity conservation and crop productivity have been seen as mutually exclusive options for a long time, recent research suggests that agricultural landscapes represent significant opportunities for biodiversity conservation outside of traditional protected areas.
2. Here, we use a unique dataset that includes annual monitoring of 12,300 permanent 25-ha plots over two decades across Spain to assess how agricultural landscapes are changing over time. We focus particularly on landscape composition and configuration variables such as the diversity of crops grown within a landscape, average plot size or the cover of natural habitats and assess how changes to these variables affect the ability of agricultural landscapes to ensure high yields.
3. We find potential synergistic strategies that are good for biodiversity conservation and can also lead to increasing crop yields. Specifically, we find that management practices that favour increasing biodiversity values such as maintaining small field sizes and high crop richness values at the landscape scale actually led to the greatest average yield values across 54 crops, 41% of which depend on pollinator activity for reproduction.
4. *Policy implications*: While our analysis does not factor in economic costs and benefits, we show that synergy scenarios that are good for biodiversity conservation and crop productivity are possible, yet not as widespread as they could be.

KEYWORDS
agricultural intensification, agricultural landscape, crop yield, pollination service, yield gaps

1 | INTRODUCTION

Across the globe, landscapes are undergoing a series of dramatic changes because of human activities (Foley, 2005). The human footprint has already reached >75% of terrestrial land, and the main driver of these changes is the expansion and intensification of agriculture (Venter et al., 2016), which is done in most cases at the expense of semi-natural habitats (Venter et al., 2016). The widespread loss of semi-natural habitats has led to significant negative impacts for the biodiversity they host (Seibold et al., 2019), as well as for their ability to provide several of Nature's contributions to people (Emmerson et al., 2016) that have been demonstrated to increase crop yield (Tamburini et al., 2020).

Crop yield is a consequence of a complex combination of anthropogenic, climatic, edaphic and natural inputs (Schröter et al., 2021), with the latter including the contribution of wild pollinators in the case of pollinator-dependent crops, or the role of pest control biological agents (Alexandridis et al., 2021; Holland et al., 2017) among others. Although the development of artificial inputs (e.g. synthetic fertilizers or pesticides) for agriculture has increased yields and reduced yield gaps for some crops and areas around the globe (Foley et al., 2011), a strong body of research has demonstrated that natural inputs still show beneficial impacts on yield despite the predominance of artificial inputs (Cohen et al., 2019). Actually, apart from farm-level management practices, crop yield has been related to different landscape-level variables, such as the proportion of arable land or the cover of semi-natural habitats (Redhead et al., 2020), the diversity of crop species (Renard & Tilman, 2019) or the heterogeneity in habitat types across the landscape (Hass et al., 2018; Martin et al., 2019; Sirami et al., 2019). Furthermore, different aspects of crop production (e.g. yield vs. stability) have been shown to respond to different landscape structure variables (Redhead et al., 2020).

Crop productivity can be affected by the loss of semi-natural habitats across agricultural landscapes because this leads to a decrease in the level of Nature's contributions to people provided (e.g. crop pollination, pest control services, favourable microclimates, soil health or reduced disease risk; Aguilera et al., 2020; Cheatham et al., 2009; Connelly et al., 2015; Dainese et al., 2019; Holland et al., 2016, 2017; Miner et al., 2020). However, although the number of research studies evaluating landscape effects on Nature's contributions to people is extensive, we are still missing detailed large-scale real-world observations of the relationship between landscape structure (composition and configuration) and crop yields (although see Beckmann et al., 2019; Karp et al., 2018). The few studies that have analysed landscape-yield relationships have used single-year datasets (Holland et al., 2017), have been based on average values of yield at regional levels (e.g. Martin et al., 2016, 2019) or have used meta-analytical tools to join results from multiple studies (Beckmann et al., 2019), but still fail to account simultaneously for spatial and temporal trends. Especially scarce are the studies looking at changes in landscape configuration and composition and their effect on crop yield at small spatial scales (sub-national), across multiple crop types and through time. Although local studies using space-for-time substitutions are extremely useful to test different hypotheses, only temporal analyses focusing on the changes experienced by agricultural landscapes can reveal a full picture of their current situation (Deguines et al., 2014).

Understanding the temporal trends of productivity within agricultural landscapes is particularly pressing in the case of the Mediterranean areas in Europe, which represent one of the world's biodiversity hotspots (Myers et al., 2000), and are currently charged with producing a large portion of the agricultural products in Europe (particularly fruits and vegetables, EUROSTAT, 2021), thus suffering the most dramatic changes (Newbold et al., 2020). Among the changes suffered by agricultural landscapes in Europe, two main processes appear: an abandonment of some areas and an intensification of others. Land abandonment is particularly widespread in temperate regions of the world, representing 11% of the area that was being farmed at the start of the century in the European Union alone (van der Zanden et al., 2017). Conventional intensification, aimed at boosting agricultural production, is also a widespread phenomenon across temperate regions. Agricultural intensification can take different forms and includes among others: an increase in field size with associated reductions in the presence of field margins or hedgerows (Clough et al., 2020), a decrease in the diversity of crops planted in an area (with an extreme being monocultures) and an increase in the use of chemical fertilizers, pesticides and machinery (Emmerson et al., 2016). In contrast to this conventional intensification processes, more and more research points towards the potential benefits of ecological intensification, or the replacement of artificial inputs by environmentally friendly practices to enhance productivity through an optimal management of the ecological functions provided by biodiversity (Bommarco et al., 2013). Among these practices is the conservation of semi-natural areas to act as source of many of these functions. Although the benefits of biodiversity for primary productivity are clear, both within agricultural (Albrecht et al., 2020) and ecological studies (Oehri et al., 2017; Tilman et al., 1996), there is less empirical evidence of the uptake of these practices among farmers and their impact on crop productivity (although see Kleijn et al., 2019).

Here, we used a comprehensive dataset gathered annually by the Spanish Ministry of Agriculture from 2001 to 2019 to explore fine-scale spatial and temporal dynamics in crop yields for different crops. Our aims are (1) to provide an overview of how agricultural landscapes have changed through time, (2) to assess how landscape structure and management affect crop yields and yield gaps and (3) to identify the strategies followed by growers that are simultaneously improving their crop yields while favouring management practices that are identified as positive for conserving biodiversity.

2 | MATERIALS AND METHODS

2.1 | Dataset

We used the Spanish Survey on Cultivar Area and Yield (ESYRCE), a public database collected annually by the Ministry of Agriculture across a representative area of the country (434 K–523 K ha per year which covers ~1% of the total country surface) for the period between 2001 and 2019. The national territory is subdivided into 1-km^2 cells, integrated into larger 100 km^2 blocks. The basic sample is constituted by three 1-km^2 cells chosen randomly within each larger block. Sample plots are 700-m square plots located at the lower left corner of each 1-km^2 cell. In areas with smaller plot structure (greater fragmentation of the territory), this unit can be reduced to 500-m square plots, hence rendering 49 and 25 ha plots. Plots are surveyed by professional surveyors during field visits with the aid of cartography and/or aerial photographs. At each plot, the surface of different land cover types is assessed, as well as crop yield for productive crops. Data on crop yield are collected within most of the plots in the areas with great agricultural cover, and within 1/5 of the plots in the areas with lower agricultural cover. Data collection is conducted each year from mid-June to mid-September and is adapted to sowing and collecting periods and to the phenology of the different crops to allow for correct crop identification. The result is a spatially explicit annual sample of square plots with internal polygons depicting different land use types and crop species (see Figure S1 for an example of one of these plots through time). Because our comparison is for the same plots across time, we kept both 25 and 49 ha plots and only modified plot size (reduced it from 49 to 25 ha, 3.25% of cases) if plot size changed for the same plot in different years.

The present study did not require ethical approval or fieldwork permits to be conducted.

2.2 | Change in agricultural landscapes through time

To provide a general description of the spatial and temporal changes in crop species identity across all our plots, we used crop species presence–absence data to calculate Sørensen beta-diversity indices (Sørensen, 1948) for each province-year combination, which provides a matrix of beta-diversity indices. We then used a PERMANOVA (Anderson, 2017) as implemented in the VEGAN package (function *adonis*; Oksanen et al., 2020) to assess whether changes in species composition were greater across space or time by fitting a model including the beta-diversity matrix as response variable and the interaction between year and province as explanatory variables. Given that we detect an interaction between province and time, for visualization purposes, we plot for each province the correlation between the beta-diversity observed each year for that province and time, with positive values indicating this province is becoming more unique in its crop cultivation patterns, and negative values indicating that it is becoming more similar to the rest of regions.

2.2.1 | Landscape metrics and trajectories through time

We calculated a series of metrics at the plot level that reflect measures of habitat composition (semi-natural habitat cover, crop richness, the proportion of pollinator-dependent crops in the landscape) and configuration (field size, edge density, see Table S1 for all land use categories). In the case of semi-natural habitats, we estimated the proportion of a plot covered by three different types of habitats: forests, natural meadows and the combination of pastures and shrubs (Table S1). Thus, these categories differentiate between more open (meadows and pastures) and closed habitats (forests), as well as between areas with greater potential livestock presence (meadows vs. pastures). Furthermore, for each plot, we calculated the richness of crops being grown per hectare, where crops are defined based on the categories included in the original dataset and include differentiated varieties such as table olives and oil olives. We also calculated the average size of crop fields, as well as the proportion of pollinator-dependent crops in the landscape for each plot, which gives an idea of the aggregated amount of resources available for pollinators at the landscape scale. This metric was calculated as the combination of the average dependence of crops on pollinators weighted by the area they occupied within a plot,

$$\text{Proportion of pollinator dependent crops} = \sum_{\text{plot polygons}} (\text{Demand}(\text{polygon}) \times \text{Area}(\text{polygon}))/\text{Area}(\text{plot}).$$

In this case, for each pollinator-dependent crop, their average crop dependence was assigned based on four categories (little, modest, great and essential; Klein et al., 2006), which cover a range of production reduction in the absence of pollinators. For each category, we used the mean value of the range. In the case of crop dependence, we used the same classification (Klein et al., 2006), to develop a binary factor describing whether a particular crop's productivity increased with pollinator activity. Edge density, a measure of habitat fragmentation, was calculated using GeoPandas in Python (Jordahl, 2014) as the sum of the length of the edges between different land uses within each plot divided by the area of the plot. We selected edge density as a measure of fragmentation in the landscape because it offers a measure of landscape heterogeneity which is independent of composition, and is commonly used in fragmentation studies (Hargis et al., 1998).

We then evaluated the trajectories followed by the main explanatory variables. To simplify results and to visually represent the main slopes through time, we aggregated these variables at the province level, which also reflects the scale at which many policy decisions that define agricultural practices are taken in Spain.

2.3 | Effect of land use and management practices on crop yield and yield gaps

To evaluate whether changes in land use across Spain might have impacted crop yield for the 54 crops with yield data considered in the dataset between 2001 and 2019, we ran a general linear mixed-effects model (LMM). First, given the presence of some unlikely values for some of the crops, we removed all yield values that were above or below three standard deviations within each crop (3.4% of the data) and we transformed the variable using a log transformation. Then, we normalized yield values within crop types

$$(x - \min(x)) / (\max(x) - \min(x)),$$

to have comparable values across crops with very different production values. We also tried a normalization based on subtracting the mean and dividing by a standard deviation, which provided highly correlated values to the former ($r = 0.71$) and do not affect the conclusions (data not shown). Second, we fit a full model with crop yield per individual crop within plot as dependent variable. Explanatory variables included several variables that represent the main factors traditionally responsible for crop yield. Specifically, these included several climatic variables (total precipitation, minimum annual temperature) commonly used in crop yield analyses (Beillouin et al., 2020; Kukal & Irmak, 2018), landscape configuration variables (average crop field size, edge density) and landscape composition variables (crop richness, the proportion of pollinator-dependent crops in the landscape, and the cover of semi-natural habitats, Redhead et al., 2020). We also included as predictors whether a particular crop depended on pollinators to set fruit (coded as a qualitative factor with two categories, pollinator dependent or independent; Klein et al., 2006), and whether the crop was an annual or perennial crop. We considered three types of semi-natural habitats: forests, meadows and the combined cover of pasture, grasslands and shrub areas. Prior to any analyses, we checked for the existence of multi-collinearity amongst all the explanatory variables using variable inflation factors (VIF). As all VIF values were <2.5 (Table S2), we retained all the variables within our full model. Given the left-skewed distribution of some of the independent variables (average field size, crop richness and total precipitation), we log-transformed them before including them in the full model. All independent variables were then scaled for direct comparison between them. Furthermore, we included two-way interactions between all the variables considered as well as three- and four-way interactions between these and the dependence of a crop on pollinators and whether the crop was an annual or perennial crop. We do not include management practices such as fertilizer or insecticide usage as this information is not available at the same spatial and temporal resolutions. Because plots were repeatedly measured through time, we included plot and crop type as random effects. We also included an autocorrelation structure of order one to account for the temporal correlation of yield values within plots. We used a logit transformation for normalized yield given its range between 0 and 1.

We used the same approach to evaluate whether the same variables might explain annual yield gaps for these crops. Yield gap was calculated by subtracting the value observed in a particular plot from the average of the five largest yield values for that crop observed at the province level for a given year. In this case, we also included plot and crop type as random effects and an autocorrelation structure to account for temporal correlation. In both cases, we checked the normality of model residuals using qqplots.

2.4 | Identifying synergies

We evaluated yield changes through time and related these changes with those experienced by the key variables that are both important in the models and related to clear ecological expectations using a tree diagram. To this end, we selected (i) the average slope values for log average field size and log crop richness/ha through time at the plot level and (ii) the amount of semi-natural habitat surrounding a plot. Note that we did not use the rate of change for this variable given the expected smaller changes observed through time (slopes between −0.05 and 0.05). For simplicity, we classified plots into two categories based around a 20% semi-natural habitat threshold, which previous studies suggest is the threshold needed to sustain a number of ecological functions that are crucial within agricultural landscapes (Garibaldi et al., 2021), plots with >20% semi-natural habitat cover and those with <20% cover. Variables entered the tree based on variable importance, in this case based on estimate size in LMMs. Given the different combinations of these three variables, we identified areas of (1) synergy, (2) intensification, (3) loss and (4) compromise. Synergy refers to situations where there is simultaneously an increase in crop yield through time (positive slope) and an increase in biodiversity-friendly practices (positive slope for crop richness and semi-natural habitat cover>20% and negative slope for average field size). Intensification refers to increasing crop yield (positive slope) and decreasing biodiversity-friendly practices (negative slope for crop richness, <20% semi-natural habitat cover and positive slope for average field size). Compromise refers to areas where crop yields decrease (negative slope) with increasing biodiversity-friendly practices and finally, loss refers to decreases in crop yield (negative slope) with decreasing biodiversity-friendly practices.

3 | RESULTS

3.1 | Change in agricultural landscapes through time

Over all plots and years, we recorded 128 crop species that have been grown in Spain during the past two decades (i.e. crop gamma diversity). The richness of crops grown across the country has steadily increased, from 100 crops grown in 2001 to 125 in 2018. Partitioning this gamma diversity into its temporal and spatial components revealed that provinces have a mean alpha crop diversity within a particular year of 43.8 crops, and at the national level the average number of crops grown per year is 115. The PERMANOVA analysing the contribution of spatial (across provinces) and temporal (through time) components to dissimilarity in crop species composition shows that province explains 78% of the variance while year only accounts for 2%. In addition, we find an interaction between province and year. In this case, this interaction appears because while most provinces tend to become more similar to other provinces through time, a few become more different (Figure S3). In particular, provinces in the South and NW tend to become more similar in the crops they grow to the national average, while provinces in the E and W become more different in their cultivation patterns (Figure S3). Repeating this analysis for annual and perennial crops separately yields very similar results, with province explaining >75% of the variance and year accounting for <3%.

3.2 | Land use change trajectories

A closer inspection at how landscape-level variables that affect crop yield have changed through time showed some general as well as regional and province-specific changes (Figure 1; Table S3). While meadow cover has generally decreased across the country, forest cover has mostly increased (Figure 1). In turn, pasture and shrub areas have decreased particularly in the N, central and SW, and increased or remained stable in much of the rest of the country (Figure 1). Average crop field size has decreased everywhere, while crop richness has increased across most of the country (Figure 1). Overall, cropland has decreased across many areas, although that of pollinator-dependent crops has increased particularly in the central and N part of the country. In turn, fallow land has decreased almost everywhere with some increases in the E and NW.

3.3 | Crop yield and yield gaps

Our analysis of drivers of crop yield using uncorrelated (Figure S2) climatic, landscape configuration and landscape composition variables shows that the most important variables included landscape configuration and climate variables and their interaction with crop pollinator dependence, as well as management practices like average field size or crop richness in the landscape (Table 1). Our full model including all variables and their interaction presented a marginal R^2 of 0.08, and a conditional R^2 of 0.57. Given the variability in crops and varieties analysed, and the fact that we do not analyse important known variables such as fertilizer or pesticide use, the model presents a large unexplained variation, but nonetheless some clear patterns emerge. It is also important to note that our analysis considers the temporal correlation of yield values, meaning that we account for the non-independence of yield values through time. The variable with the greatest effect size was whether a crop was annual or perennial (Table 1). We found that equally important was the interaction between log average field, pollinator dependence and annual versus perennial status such that crop yield decreased in areas with larger field sizes particularly in the case of annual crops with a reliance on pollinators to set fruit (Figure 2a). Following in importance, based on effect sizes, were climatic variables minimum temperature and total precipitation and their interaction with pollinator dependence and annual versus perennial status. Log crop richness/ha and its interaction with pollinator dependence and annual versus perennial status also showed an important effect such that maximum yield values were observed within more diverse landscapes for both annual and perennial pollinator-dependent crops (Figure 2b).

In the case of yield gaps, our model showed a marginal R^2 of 0.08, and a conditional R^2 of 0.44. Here, the most important variable was again whether a crop was annual or perennial, followed by climatic variables minimum temperature and total precipitation (Table 2). As before, log average field size and log crop richness/ha also showed some of the largest effects observed such that crop yield gaps were minimized within small fields and more crop-diverse landscapes (Figure 3a,b). We also find an effect of the interaction between two semi-natural habitat types (forest and meadows) and whether a crop is annual or perennial which shows that yield gaps are smaller at high meadow covers and medium or low forest covers (Figure 3c).

3.4 | Identifying synergies

Our analysis of changes in yield through time related to changes in landscape-scale variables shows that 28% of the plots surveyed have increased their yield through time (positive slopes), while 30% have suffered decreases in their yields (negative slopes). Within the remaining 42%, yield shows no directional trend through time (slope > −0.001, <0.001). From now on, we will focus on the results for this 58% of plots where yield has suffered changes. Our results show that *synergies*, that is, situations in which increasing yield values and biodiversity-friendly practices (decreased field sizes, increased crop richness, >20% semi-natural habitat cover) occur simultaneously can be observed across 19% of all the plots where yield has increased in the past two decades. At least one of these biodiversity-friendly management practices, such as increasing crop richness, decreasing field size or maintaining at least 20% of semi-natural habitat cover, can be observed within 92.8% of these more productive plots (Figure 4). In turn, only 7.2% of the plots that have increased their yield during the past two decades have done so while intensifying the landscape (*intensification* category), that is, increasing field sizes, decreasing crop richness and keeping semi-natural habitat below 20% (Figure 4), and 80.9% show increasing yields while showing at least one intensification management practice. However, among the plots whose productivity has decreased in the past two decades, 21.35% followed all biodiversity-friendly practices (*compromise* category), while 5% followed the opposite more intensified-related ones (*loss* category, Figure 4). Reducing semi-natural habitat cover to <20% represented the main driver of yield decreases, with 66.74% of the plots showing reduced yields while also showing lower semi-natural habitat cover (Figure 4).

4 | DISCUSSION

Our analysis of temporal trends in agricultural landscapes in Spain shows that, despite province-specific changes, several general patterns appear in the evolution of agricultural landscapes in the past two decades at the national level. These patterns include a general

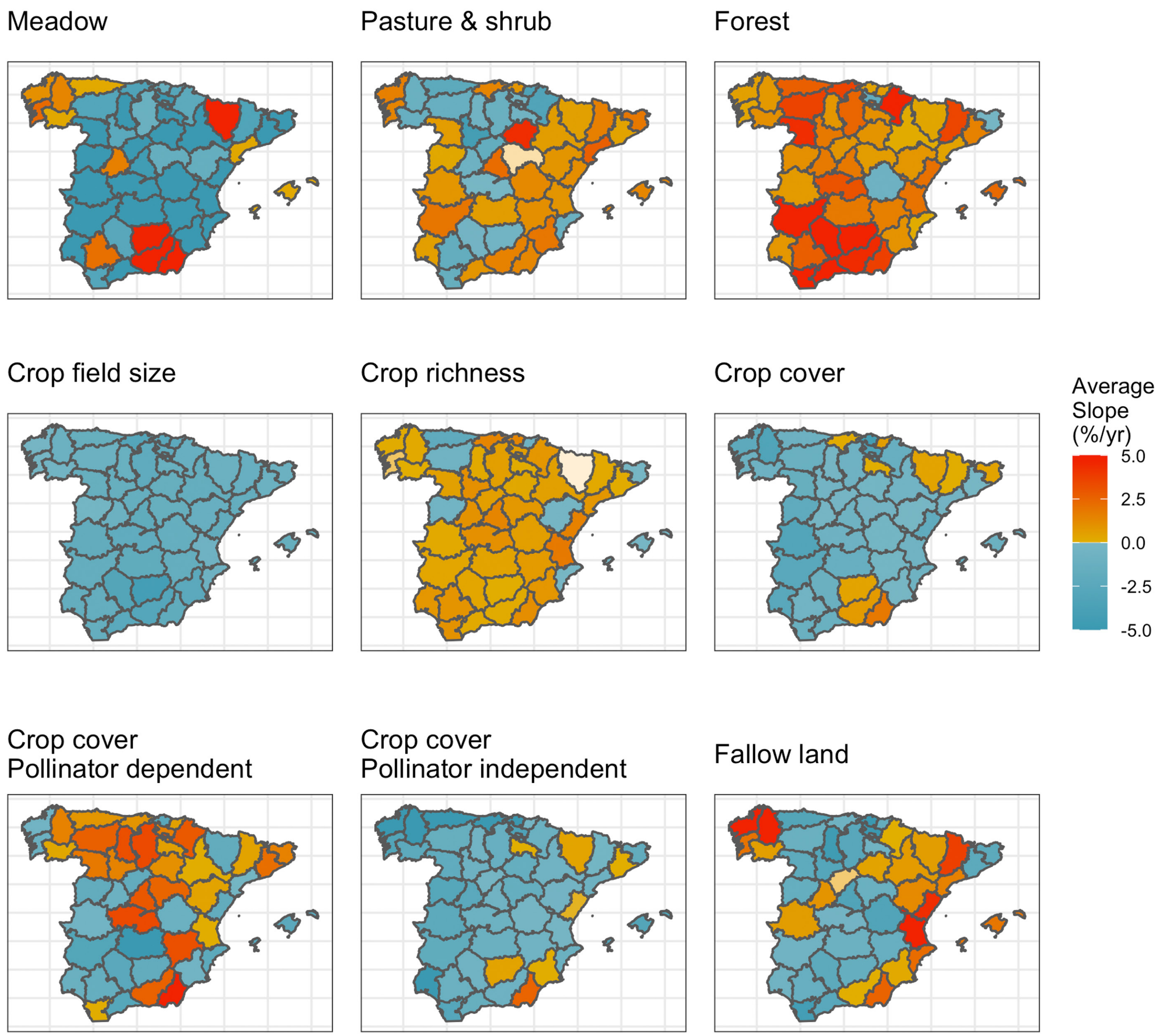

FIGURE 1 Maps depicting magnitude of slope of temporal changes in main landscape metrics averaged across provinces in Spain.

decrease in the area covered by cropland, although the area covered by pollinator-dependent crops has increased across most of the country (as also shown globally in Aizen et al., 2008). Changes also include an increase in crop richness, a general decrease in crop field sizes, as well as in the cover of most semi-natural habitats, except for forest areas, which have expanded. Our analysis of crop species turnover through space and time further shows that crop species composition tends to be conserved for a particular province through time, and most of the differences found in crop composition are due to differences across provinces in what is being grown. However, we also find that some provinces are changing the identity of the crops they grow and becoming more singular. Our analysis of crop yields and yield gaps shows that different management (e.g. crop richness, field size) and landscape-level variables related to habitat heterogeneity (e.g. semi-natural habitat cover) affect productivity.

Our results indicate that, in addition to climatic variables, crop yield is most affected by variables related to management (e.g. crop field sizes and crop richness), but we also find that a diverse cover of semi-natural habitats contributes to reducing yield gaps, therefore suggesting that overall, landscape heterogeneity is an important driver of crop productivity. Unfortunately, we do not measure agronomic practices such as varieties planted, or fertilizer or pesticide use, which can help explain part of the unexplained variance. Our results showing larger effects of ecological intensification on pollinator-dependent crop productivity are similar to those shown in a previous analysis focusing on the effect of intensification on the aggregated productivity of crops distributed across France (Deguines et al., 2014) but using finer resolution 25-ha plots surveyed repeatedly through time rather than aggregated measures.

TABLE 1 Results of linear mixed-effects model (LMM) showing estimates and lower and upper confidence interval values for each of the variables included in the full model evaluating differences in crop yield. Bold letters indicate variables whose confidence intervals do not overlap 0. Effects are ordered by estimate value

	Lower	Estimate	Upper
(Intercept)	0.72	0.74	0.75
Annual_perennial	−0.21	−0.18	−0.15
Log average field size:Pollinator dependence:Annual_perennial	0.12	0.18	0.25
Minimum temperature:Pollinator dependence	0.13	0.16	0.18
Minimum temperature:Pollinator dependence:Annual_perennial	0.11	0.16	0.20
Total precipitation:Pollinator dependence:Annual_perennial	0.11	0.14	0.17
Log crop richness/ha:Pollinator dependence:Annual_perennial	0.09	0.14	0.19
Log average field size:Pollinator dependence	−0.17	−0.13	−0.09
Total precipitation	0.11	0.12	0.12
Prop pollinator-dependent crops:Pollinator dependence:Annual_perennial	0.08	0.11	0.14
Pollinator dependence	0.06	0.09	0.12
Total precipitation:Pollinator dependence	−0.11	−0.09	−0.07
Edge density:Pollinator dependence	0.03	0.07	0.10
Log average field size:Annual_perennial	0.03	0.07	0.10
Pollinator dependence:Annual_perennial	−0.12	−0.07	−0.02
Log crop richness/ha	0.04	0.05	0.06
Semi-natural pasture and shrub	−0.06	−0.05	−0.03
Semi-natural forest:Pollinator dependence	−0.08	−0.05	−0.01
Total precipitation:Annual_perennial	−0.07	−0.05	−0.04
Edge density:Annual_perennial	−0.08	−0.05	−0.02
Log crop richness/ha:Annual_perennial	0.02	0.05	0.07
Semi-natural forest:Semi-natural meadow:Annual_perennial	0.01	0.04	0.07
Edge density:Pollinator dependence:Annual_perennial	−0.09	−0.04	0.01
Proportion pollinator-dependent crops:Pollinator dependence	−0.05	−0.03	−0.01
Semi-natural pasture and shrub:Annual_perennial	−0.05	−0.03	−0.01
Semi-natural forest:Semi-natural pasture and shrub:Pollinator dependence	−0.08	−0.03	0.03
Semi-natural pasture and shrub:Pollinator dependence:Annual_perennial	−0.01	0.03	0.08
Semi-natural forest:Semi-natural pasture and shrub:Pollinator dependence:Annual_perennial	−0.04	0.03	0.10
Minimum temperature	−0.03	−0.02	0.00
Semi-natural forest	−0.03	−0.02	−0.01
Log crop richness/ha:Pollinator dependence	−0.05	−0.02	0.01
Semi-natural forest:Annual_perennial	−0.04	−0.02	0.01
Semi-natural meadow:Annual_perennial	−0.03	0.02	0.06
Semi-natural meadow:Semi-natural pasture and shrub:Pollinator dependence	−0.02	0.02	0.05
Edge density	0.00	0.01	0.03
Proportion pollinator-dependent crops	−0.01	0.01	0.02
Semi-natural meadow	−0.02	−0.01	0.01
Semi-natural forest:Semi-natural meadow	−0.02	−0.01	0.00
Semi-natural meadow:Pollinator dependence	−0.04	−0.01	0.02
Semi-natural pasture and shrub:Pollinator dependence	−0.04	−0.01	0.03
Proportion pollinator-dependent crops:Annual_perennial	−0.03	−0.01	0.01
Semi-natural forest:Pollinator dependence:Annual_perennial	−0.03	0.01	0.06
Semi-natural meadow:Pollinator dependence:Annual_perennial	−0.05	0.01	0.06
Semi-natural forest:Semi-natural meadow:Pollinator dependence:Annual_perennial	−0.05	−0.01	0.03
Log average field size	−0.02	0.00	0.02
Semi-natural forest:Semi-natural pasture and shrub	−0.02	0.00	0.02
Semi-natural meadow:Semi-natural pasture and shrub	−0.02	0.00	0.01
Minimum temperature:Annual_perennial	−0.03	0.00	0.03
Semi-natural forest:Semi-natural meadow:Pollinator dependence	−0.02	0.00	0.02
Semi-natural forest:Semi-natural pasture and shrub:Annual_perennial	−0.03	0.00	0.03
Semi-natural meadow:Semi-natural pasture and shrub:Annual_perennial	−0.04	0.00	0.04
Semi-natural meadow:Semi-natural pasture and shrub:Pollinator dependence:Annual_perennial	−0.05	0.00	0.06

(Continues)

TABLE 1 (Continued)

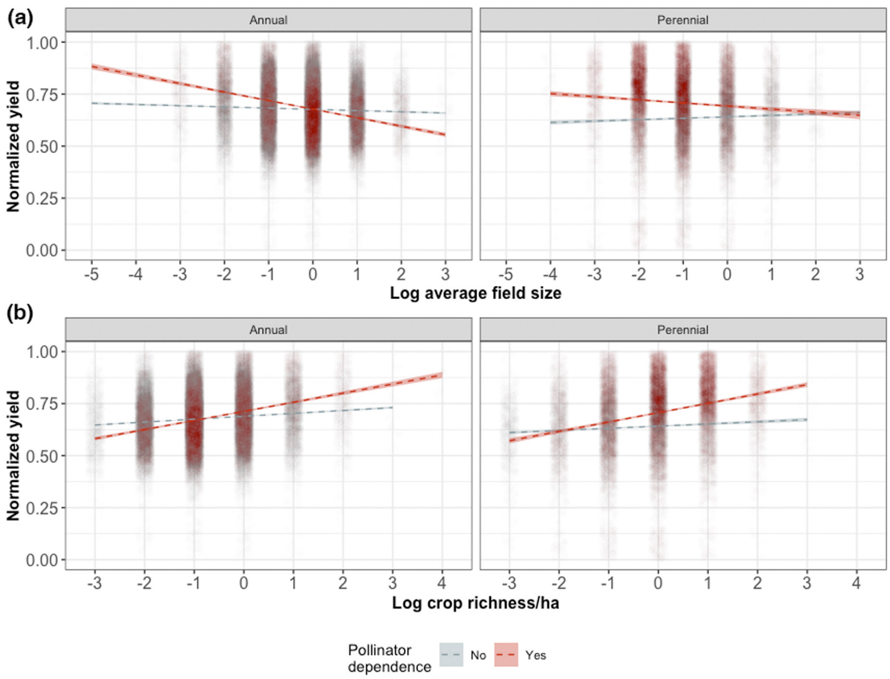

FIGURE 2 Scatterplots showing the effect of different landscape-scale variables on crop yields for 54 crops. (a) Log average crop field size and (b) log crop richness/ha. Different colours represent crops that depend on pollinators for fruit production (red) and crops that do not depend on pollinators (grey). Ranges for different untransformed variables are: Average field size 0–49 ha, edge density 0–3244.57, crop richness 1–17.25.

The importance of landscape heterogeneity for crop productivity is probably related to some Nature's contributions to people, such as crop pollination or pest control, that are positively affected by landscape complementarity (Dunning et al., 1992; Fahrig et al., 2010). Note that Spain has a large proportion of pollinator-dependent crops, in contrast to northern latitudes cropping systems. The organisms providing these services have requirements provided by different habitats across their life cycles (Alexandridis et al., 2021; Lami et al., 2020). In our study, landscapes show patterns of natural habitat and crop type heterogeneity that are independent from each other (i.e. we find no correlation between semi-natural habitat cover and crop richness, Table S2) as opposed to what Fahrig et al. (2010) find to be a common feature across many agricultural landscapes. Therefore, our findings demonstrate that both semi-natural habitats and diverse croplands are important in determining increases in crop yield, particularly for pollinator-dependent crops. These pollinator-dependent crops show slightly larger yield gaps than non-dependent crops, which shows they have more variable productivities and are more susceptible to landscape-level processes.

Recent studies have demonstrated that increases in crop field sizes and reductions in crop richness that accompany many agricultural intensification processes have a negative effect on biodiversity (Martin et al., 2019; Sirami et al., 2019). Our study complements these studies by demonstrating that increasing field size and decreasing crop richness further translates into decreasing crop productivity, at least when measured as production per hectare. A full cost–benefit analysis, including the potential increase in labour costs associated with small fields, or harvesting diverse crops within the same farm is beyond the aims of this study. The observed patterns can be related to different mechanisms. In many instances, an increase in field size is accompanied by a decrease in the density of field edges, grass margins and hedgerows (Clough et al., 2020), which have been shown to act as habitat for many important pollinator species (Ponisio et al., 2015). Coupled with the reduction in crop richness, and thus resource availability, these changes could be affecting the abundance of mobile organisms, like pollinators, that seem to rely on the presence of a certain level of heterogeneity in the landscape (Hass et al., 2018; Magrach et al., 2017). Furthermore, the ability of wild pollinators to forage within crop fields is reduced with field size as distance to nesting sites, usually located outside of crop fields, increases (Garibaldi et al., 2016; Martin et al., 2019). The decrease in pollinator-suitable habitats at these margins could be directly affecting crop productivity. In addition, landscape simplification as a consequence of agricultural intensification does not only affect the delivery of pollination (Garibaldi et al., 2011; Kennedy et al., 2013), but also that of pest control services (Emmerson et al., 2016; Östman et al., 2001, 2003), something that could be affecting the yield of both the pollinator-dependent and -independent crops we analyse in our study. While we could not account for pesticide use in our analysis given the lack of this data, previous research has shown that landscape intensification tends to be accompanied by an increasing use of pesticides, which further reduces populations of beneficial organisms (Emmerson et al., 2016).

As suggested previously (Benton et al., 2003), a focus on changing just one specific management practice will not be enough to recover the loss of important contributions from nature that are being lost, and a multivariate approach that ensures that landscape-level heterogeneity is maintained should be pursued. The dependence of pollinators on landscape heterogeneity means they cannot be managed by taking a field-based approach, but rather need of landscape-scale approximations to farming (Ricketts et al., 2008). Furthermore, mobile ecosystem services need to be managed at the scales of their home ranges.

TABLE 2 Results of linear mixed-effects model (LMM) showing estimates and lower and upper confidence interval values for each of the variables included in the full model evaluating differences in crop yield gaps. Bold letters indicate variables whose confidence intervals do not overlap 0. Effects are ordered by estimate value

	Lower	Estimate	Upper
(Intercept)	0.05	0.06	0.06
Annual_perennial	0.04	0.04	0.04
Minimum temperature:Annual_perennial	0.01	0.02	0.02
Total precipitation:Pollinator dependence:Annual_perennial	−0.02	−0.02	−0.01
Log average field size:Pollinator dependence:Annual_perennial	−0.03	−0.02	−0.02
Log crop richness/ha:Pollinator dependence:Annual_perennial	−0.02	−0.02	−0.01
Total precipitation	−0.01	−0.01	−0.01
Log crop richness/ha	−0.01	−0.01	−0.01
Semi-natural forest:Semi-natural meadow:Annual_perennial	−0.01	−0.01	0.00
Semi-natural pasture and shrub	0.00	0.01	0.01
Minimum temperature:Pollinator dependence	−0.01	−0.01	0.00
Log average field size:Pollinator dependence	0.01	0.01	0.02
Semi-natural pasture and shrub:Annual_perennial	0.00	0.01	0.01
Pollinator dependence:Annual_perennial	0.00	0.01	0.01
Minimum temperature:Pollinator dependence:Annual_perennial	−0.02	−0.01	−0.01
Prop pollinator-dependent crops:Pollinator dependence:Annual_perennial	−0.02	−0.01	−0.01
Minimum temperature	0.00	0.00	0.00
Edge density	0.00	0.00	0.00
Proportion pollinator-dependent crops	0.00	0.00	0.00
Log average field size	0.00	0.00	0.00
Semi-natural forest	0.00	0.00	0.00
Semi-natural meadow	0.00	0.00	0.00
Pollinator dependence	0.00	0.00	0.00
Semi-natural forest:Semi-natural meadow	0.00	0.00	0.00
Semi-natural forest:Semi-natural pasture and shrub	0.00	0.00	0.00
Semi-natural meadow:Semi-natural pasture and shrub	0.00	0.00	0.00
Total precipitation:Pollinator dependence	0.00	0.00	0.01
Edge density:Pollinator dependence	−0.01	0.00	0.00
Proportion pollinator-dependent crops:Pollinator dependence	0.00	0.00	0.00
Log crop richness/ha:Pollinator dependence	0.00	0.00	0.01
Semi-natural forest:Pollinator dependence	0.00	0.00	0.01
Semi-natural meadow:Pollinator dependence	0.00	0.00	0.00
Semi-natural pasture and shrub:Pollinator dependence	−0.01	0.00	0.00
Total precipitation:Annual_perennial	0.00	0.00	0.01
Edge density:Annual_perennial	0.00	0.00	0.00
Proportion pollinator-dependent crops:Annual_perennial	0.00	0.00	0.00
Log average field size:Annual_perennial	−0.01	0.00	0.00
Log crop richness/ha:Annual_perennial	−0.01	0.00	0.00
Semi-natural forest:Annual_perennial	0.00	0.00	0.01
Semi-natural meadow:Annual_perennial	−0.01	0.00	0.01
Semi-natural forest:Semi-natural meadow:Pollinator dependence	0.00	0.00	0.00
Semi-natural forest:Semi-natural pasture and shrub:Pollinator dependence	−0.01	0.00	0.00
Semi-natural meadow:Semi-natural pasture and shrub:Pollinator dependence	−0.01	0.00	0.00

(Continues)

TABLE 2 (Continued)

	Lower	Estimate	Upper
Semi-natural forest:Semi-natural pasture and shrub:Annual_perennial	−0.01	0.00	0.00
Semi-natural meadow:Semi-natural pasture and shrub:Annual_perennial	−0.01	0.00	0.00
Edge density:Pollinator dependence:Annual_perennial	0.00	0.00	0.01
Semi-natural forest:Pollinator dependence:Annual_perennial	−0.01	0.00	0.00
Semi-natural meadow:Pollinator dependence:Annual_perennial	−0.01	0.00	0.01
Semi-natural pasture and shrub:Pollinator dependence:Annual_perennial	−0.01	0.00	0.00
Semi-natural forest:Semi-natural meadow:Pollinator dependence:Annual_perennial	0.00	0.00	0.01
Semi-natural forest:Semi-natural pasture and shrub:Pollinator dependence:Annual_perennial	0.00	0.00	0.01
Semi-natural meadow:Semi-natural pasture and shrub:Pollinator dependence:Annual_perennial	−0.01	0.00	0.00

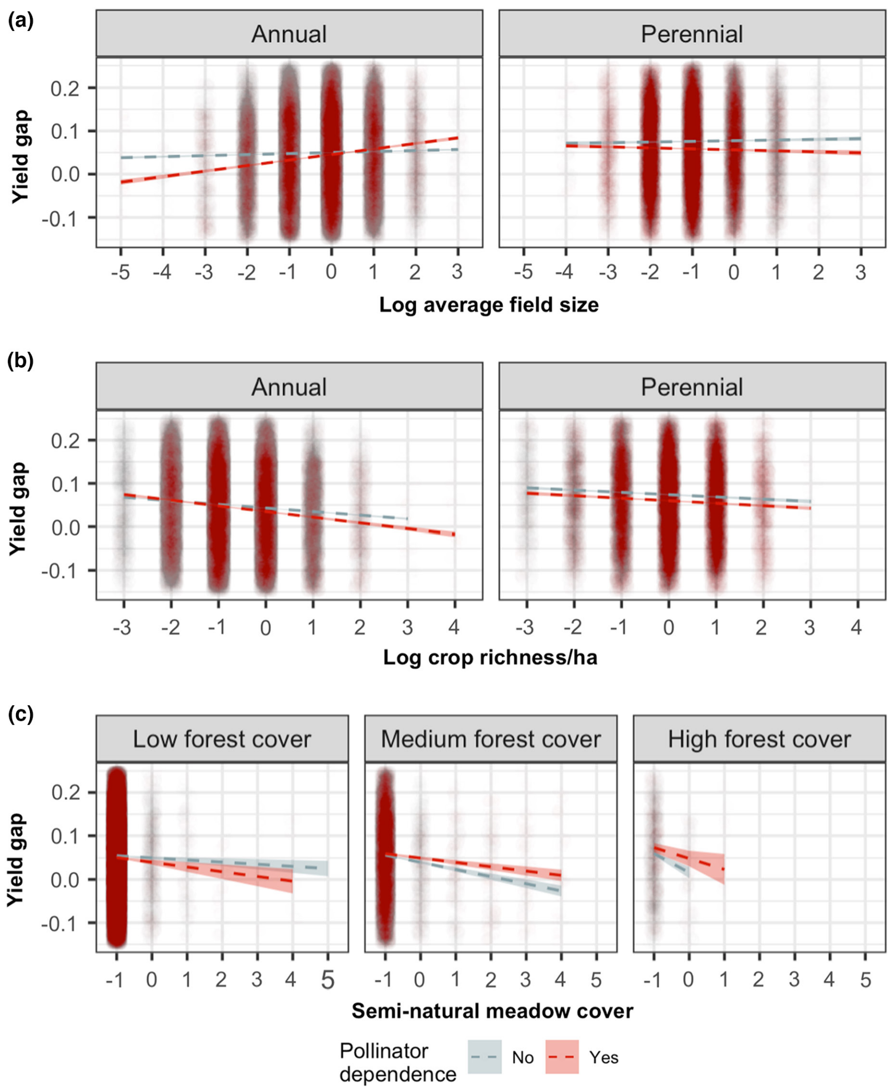

FIGURE 3 Scatterplots showing the effect of different landscape-scale variables on crop yield gaps for 54 crops. (a) Crop richness, (b) average field size and (c) semi-natural meadow and forest cover. Continuous variables were used in every case for the analysis, but they have been transformed into categories for visualization purposes. Similarly, outliers have been removed. Different colours represent crops that depend on pollinators for fruit production (red) and crops that do not depend on pollinators (grey).

Our study presents a number of caveats, particularly regarding other management practices that have not been included. For example, we do not include whether the plots were organic or followed conventional practices, which could also help to explain some of the results. However, at present data on organic versus conventional management do not exist at the resolution and spatial coverage used

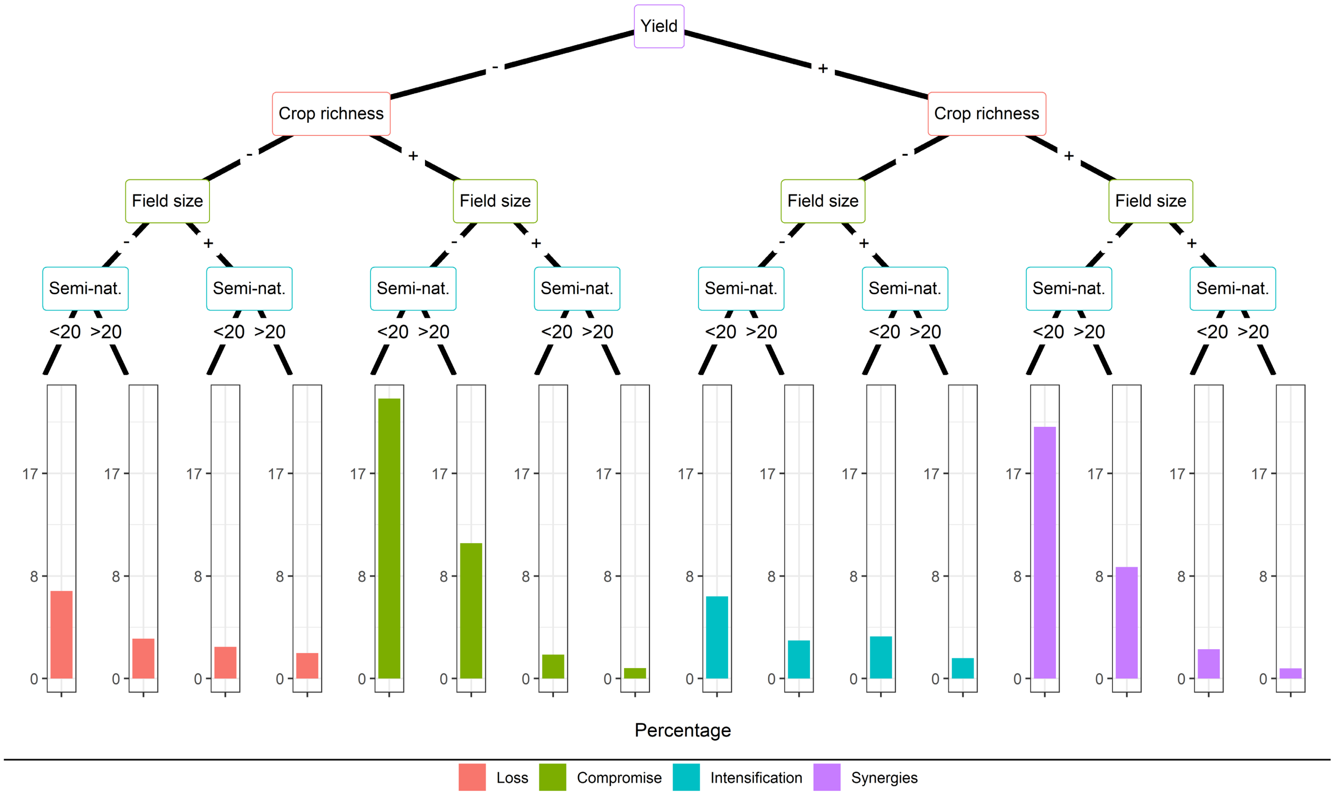

FIGURE 4 Tree plots showing the frequency of plots where yield has increased (positive slope through time) or decreased (negative slope) given different management practices related to crop diversity, average field sizes and semi-natural habitat cover. The combination of yield with these variables determine areas of loss (red), compromise (green), intensification (blue) or synergy (purple).

in this study. Furthermore, the dataset could also be used to explore regions and specific crops in more detail, yet the detail presented by these kinds of analyses is beyond the scope of this work.

Our results could help improve policy measures like the EU's Common Agricultural Policy (CAP) or the US Agricultural Policy, by providing scientific evidence of the importance of maintaining small field sizes, as well as a diversity of semi-natural habitats and crop species. At present, these CAP measures favour increasing field sizes (Peer et al., 2014) by providing larger estates with greater subsidy payments. Although there are number of capping and redistribution mechanisms in place, direct payments from the EU's CAP have still favoured larger field sizes (Scown et al., 2020). The redistribution to small farms is based on a moderate increase in the basic payment, which do not compensate for the greater costs incurred by farmers in terms of production costs when reducing field sizes (reviewed in Clough et al., 2020). However, no study has yet quantified the trade-offs between increasing production costs and improving biodiversity, Nature's contributions to people and productivity values for pollinator-dependent crops in smaller field sizes.

Changes in yield through time are due to myriad different factors that interact in complex ways and that are difficult to disentangle (Beckmann et al., 2019). Indeed, although the relationships identified in our study show weak effects in some cases, given this large number of unidentified factors that influence crop yield, the fact that we are still able to find statistically significant relationships is highly relevant. Specifically, our results clearly show that despite the intrinsic variability of crop production, agricultural practices like increasing crop richness and decreasing field size have a measurable average positive effect for crop productivity. We further find that a diversity of land uses (semi-natural habitats and crop types) favour productivity and decreased yield gaps. Finally, we find that semi-natural habitats have an unclear relationship with yield, but we find that they actually reduce yield gaps. Therefore, despite the decrease in yields that could arise as a consequence of retaining semi-natural habitats within agricultural landscapes, the buffering and insurance effect they provide against environmental fluctuations (Loreau et al., 2003), as seen here in the form of reduced yield gaps, but also as observed greater temporal stability in productivity (Montoya et al., 2019) will be invaluable, even more so under future global change conditions. Despite the general pessimistic view of agriculture and its practices, we find there is reason for hope. Our results show that >90% of the agricultural landscapes in Spain where yield has increased were following at least one agricultural practice that can be aligned with biodiversity conservation (decreased field size, increased crop richness, >20% semi-natural habitat), 70% were following two of these practices and 19% were following all three practices. In turn, only 7.2% of the plots where yield increased were following the opposite intensifying practices (i.e. increasing field sizes, decreasing crop richness and reducing semi-natural habitat cover <20%), 80% were following at least one intensifying practice and 30% were following at least two of those practices. Our call now is thus for those 10% who are not yet following any biodiversity-friendly practices, as well as for all those plots where yield has decreased in the past decades: a different way of producing food is possible. These results have direct implications for the design of CAP policies, which should capitalize on promoting conservation practices that are not conflicting with yield production such as decreasing field sizes and increasing the diversity of crops grown in agricultural landscapes.

AUTHOR CONTRIBUTIONS

Ainhoa Magrach and Ignasi Bartomeus conceived the study, Ainhoa Magrach, Angel Giménez García and Alfonso Allen-Perkins analysed the data. Ainhoa Magrach, Ignasi Bartomeus, Angel Giménez García, Alfonso Allen-Perkins and Lucas Garibaldi contributed to discussions and ideas. Ainhoa Magrach wrote the first draft of the manuscript. All authors contributed to multiple rounds of revision.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data come from a publicly available dataset that can be requested through https://www.mapa.gob.es/es/estadistica/temas/estadisticas-agrarias/agricultura/esyrce/.

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REFERENCES

Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S. A. M., Öckinger, E., Rundlöf, M., Rusch, A., Smith, H. G., & Bommarco, R. (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology*, *57*, 2170–2179.

Aizen, M. A., Garibaldi, L. A., Cunningham, S. A., & Klein, A. M. (2008). Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current Biology*, *18*, 1572–1575.

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., Entling, M. H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., … Sutter, L. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters*, *23*, 1488–1498.

Alexandridis, N., Marion, G., Chaplin-Kramer, R., Dainese, M., Ekroos, J., Grab, H., Jonsson, M., Karp, D. S., Meyer, C., O'Rourke, M. E., Pontarp, M., Poveda, K., Seppelt, R., Smith, H. G., Martin, E. A., & Clough, Y. (2021). Models of natural pest control: Towards predictions across agricultural landscapes. *Biological Control*, *163*, 104761.

Anderson, M. J. (2017). *Permutational multivariate analysis of variance (PERMANOVA)* (pp. 1–15). Wiley StatsRef: Statistics Reference Online.

Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceausu, S., Kambach, S., Kinlock, N. I., Phillips, H. R. P., Verhagen, W., Gurevich, J., Klotz, S., Newbold, T., Verburg, P. H., Winter, M., & Seppelt, R. (2019). Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. *Global Change Biology*, *25*, 1941–1956.

Beillouin, D., Schauberger, B., Bastos, A., Ciais, P., & Makowski, D. (2020). Impact of extreme weather conditions on European crop production in 2018. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*, 20190510.

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*, 182–188.

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*, 230–238.

Cheatham, M. R., Rouse, M. N., Esker, P. D., Ignacio, S., Pradel, W., Raymundo, R., Sparks, A. H., Forbes, G. A., Gordon, T. R., & Garrett, K. A. (2009). Beyond yield: Plant disease in the context of ecosystem services. *Phytopathology*, *99*, 1228–1236.

Clough, Y., Kirchweger, S., & Kantelhardt, J. (2020). Field sizes and the future of farmland biodiversity in European landscapes. *Conservation Letters*, *13*, e12752.

Cohen, F., Hepburn, C. J., & Teytelboym, A. (2019). Is natural capital really substitutable? *Annual Review of Environment and Resources*, *44*, 425–448.

Connelly, H., Poveda, K., & Loeb, G. (2015). Landscape simplification decreases wild bee pollination services to strawberry. *Agriculture, Ecosystems & Environment*, *211*, 51–56.

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*, eaax0121.

Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R., & Fontaine, C. (2014). Large-scale trade-off between agricultural intensification and crop pollination services. *Frontiers in Ecology and the Environment*, *12*, 212–217.

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*, 169.

Emmerson, M., Morales, M. B., Oñate, J. J., Batáry, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I., Bommarco, R., Eggers, S., Pärt, T., Tscharntke, T., Weisser, W., Clement, L., & Bengtsson, J. (2016). How agricultural intensification affects biodiversity and ecosystem services. *Advances in ecological research* (pp. 43–97). Elsevier.

EUROSTAT. (2021). *Eurostat: Regional statistics: Reference guide*. European Commission. https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Agricultural_production_-_crops

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J. L. (2010). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*, 101–112.

Foley, J. A. (2005). Global consequences of land use. *Science*, *309*, 570–574.

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., … Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*, 337–342.

Garibaldi, L. A., Carvalheiro, L. G., Vaissiere, B. E., Gemmill-Herren, B., Hipolito, J., Freitas, B. M., Ngo, H. T., Azzu, N., Saez, A., Åström, J., An, J., Blochtein, B., Buchori, D., Chamorro García, F. J., Oliveira da Silva, F., Devkota, K., de Fatima Ribeiro, M., Freitas, L., Gaglianone, M. C., … Zhang, H. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, *351*, 388–391.

Garibaldi, L. A., Oddi, F. J., Miguez, F. E., Bartomeus, I., Orr, M. C., Jobbágy, E. G., Kremen, C., Schulte, L. A., Hugues, A. C., Bagnato, C., Abramson, G., Bridgewater, P., Gomez Carella, D., Diaz, S., Dicks, L. V., Ellis, E. C., Goldenberg, M., Huaylla, C. A., Superman, M., … Zhu, C. D. (2021). Working landscapes need at least 20% native habitat. *Conservation Letters*, *14*, e12773.

Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., … Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, *14*, 1062–1072.

Hargis, C. D., Bissonette, J. A., & David, J. L. (1998). The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology*, *13*, 167–186.

Hass, A. L., Kormann, U. G., Tscharntke, T., Clough, Y., Baillod, A. B., Sirami, C., Fahrig, L., Martin, J. L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Burel, F., Georges, R., Giralt, D., Marcos-García, M. Á., Ricarte, A., Siriwardena, G., & Batáry, P. (2018). Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20172242.

Holland, J. M., Bianchi, F. J., Entling, M. H., Moonen, A.-C., Smith, B. M., & Jeanneret, P. (2016). Structure, function and management of semi-natural habitats for conservation biological control: A review of European studies. *Pest Management Science*, *72*, 1638–1651.

Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R. W., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, *37*, 31.

Jordahl, K. (2014). *GeoPandas: Python tools for geographic data*. https://github.com/geopandas/geopandas

Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Matinez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tscharntke, T., Wratter, S. D., Zhang, W., … Adler, L. S. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, E7863–E7870.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhöffer, J. H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., … Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, *16*, 584–599.

Kleijn, D., Bommarco, R., Fijen, T. P. M., Garibaldi, L. A., Potts, S. G., & van der Putten, W. H. (2019). Ecological intensification: Bridging the gap between science and practice. *Trends in Ecology & Evolution*, *34*, 154–166.

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2006). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 303–313.

Kukal, M. S., & Irmak, S. (2018). Climate-driven crop yield and yield variability and climate change impacts on the U.S. Great Plains Agricultural Production. *Scientific Reports*, *8*, 3450.

Lami, F., Bartomeus, I., Nardi, D., Beduschi, T., Boscutti, F., Pantini, P., Santoiemma, G., Scherber, C., Tscharntke, T., & Marini, L. (2020). Specieshabitat networks elucidate landscape effects on habitat specialisation of natural enemies and pollinators. *Ecology Letters*, *24*, 288–297.

Loreau, M., Mouquet, N., & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 12765–12770.

Magrach, A., Holzschuh, A., Bartomeus, I., Riedinger, V., Roberts, S. P. M., Rundlöf, M., Vujić, A., Wickens, J. B., Wickens, V. J., Bommarco, R., González-Varo, J. P., Potts, S. G., Smith, H. G., Steffan-Dewenter, I., & Vilà, M. (2017). Plant-pollinator networks in semi-natural grasslands are resistant to the loss of pollinators during blooming of mass-flowering crops. *Ecography*, *41*, 62–74.

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, *22*, 1083–1094.

Martin, E. A., Seo, B., Park, C.-R., Reineking, B., & Steffan-Dewenter, I. (2016). Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, *26*, 448–462.

Miner, G. L., Delgado, J. A., Ippolito, J. A., & Stewart, C. E. (2020). Soil health management practices and crop productivity. *Agricultural & Environmental Letters*, *5*, e20023.

Montoya, D., Haegeman, B., Gaba, S., Mazancourt, C., Bretagnolle, V., & Loreau, M. (2019). Trade-offs in the provisioning and stability of ecosystem services in agroecosystems. *Ecological Applications*, *29*, e01853.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.

Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology & Evolution*, *4*, 1630–1638.

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2017). Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 10160–10165.

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., de Caceres, M., Durand, S., … FitzJohn, R. (2020). *Vegan: Community ecology package* [software]. https://cran.r-project.org/web/packages/vegan/vegan.pdf

Östman, Ö., Ekbom, B., & Bengtsson, J. (2001). Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology*, *2*, 365–371.
Östman, Ö., Ekbom, B., & Bengtsson, J. (2003). Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics*, *45*, 149–158.
Peer, G., Dicks, L. V., Visconti, P., Arlettaz, R., Baldi, A., Benton, T. G., Collins, S., Dieterich, M., Gregory, R. D., Hartig, F., Henle, K., Hobson, P. R., Kleijn, D., Neumann, R. K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W. J., Turbé, A., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, *344*, 1090–1092.
Ponisio, L. C., MGonigle, L. K., & Kremen, C. (2015). On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. *Global Change Biology*, *22*, 704–715.
Redhead, J. W., Oliver, T. H., Woodcock, B. A., & Pywell, R. F. (2020). The influence of landscape composition and configuration on crop yield resilience. *Journal of Applied Ecology*, *57*, 2180–2190.
Renard, D., & Tilman, D. (2019). National food production stabilized by crop diversity. *Nature*, *571*, 257–260.
Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., Potts, S. G., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*, 499–515.
Schröter, M., Egli, L., Brüning, L., & Seppelt, R. (2021). Distinguishing anthropogenic and natural contributions to coproduction of national crop yields globally. *Scientific Reports*, *11*, 10821.
Scown, M. W., Brady, M. V., & Nicholas, K. A. (2020). Billions in misspent EU agricultural subsidies could support the sustainable development goals. *One Earth*, *3*, 237–250.
Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E. D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*, 671–674.
Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., … Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 16442–16447.
Sørensen, T. J. (1948). *A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons*. I Kommission Hos E. Munksgaard.
Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, *6*, eaba1715.
Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, *379*, 718–720.
van der Zanden, E. H., Verburg, P. H., Schulp, C. J. E., & Verkerk, P. J. (2017). Trade-offs of European agricultural abandonment. *Land Use Policy*, *62*, 290–301.
Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*, 12558.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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