

RESEARCH ARTICLE

Grasslands enhance ecosystem service multifunctionality above and below-ground in agricultural landscapes

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Abstract

1. Managing agricultural landscapes integrate production, biodiversity conservation and the flow of ecosystem services (ES) is of paramount importance to simultaneously meet production goals and environmental challenges. However, the response of farmland biodiversity and multiple ES to land-use change at multiple spatial scales remains poorly understood.
2. We explored the effects of land-use at local (grassland vs. oilseed rape fields) and landscape scale (cover of permanent grasslands) on the provision of biodiversity (plants, arthropods, birds), five ES (pollination, pest control, soil fertility, carbon storage and water regulation) and overall ES-multifunctionality.
3. ES-multifunctionality was higher in grasslands than in crop fields, by 25.2% above-ground and by 106.1% below-ground. Multiple threshold analyses highlighted a particularly poor level of performance for below-ground functions in crop fields. This habitat type was however capable of providing numerous above-ground functions simultaneously, although at low levels of performance when compared to the maximum values recorded in the study. Grasslands supported higher biodiversity and provision of pollination, soil fertility, carbon storage and water regulation.
4. Landscape composition influenced the provision of multiple ES: a 10% increase in grassland cover in the landscape enhanced above-ground ES-multifunctionality by 11.0% in both habitats. In particular, grasslands cover in the landscape supported the provision of arthropod diversity, pollination and pest control provided by carabids.
5. *Synthesis and applications.* The results of this field study show the key importance of preserving semi-natural grasslands in agricultural landscapes for the conservation of farmland biodiversity, for the protection of soils and the delivery of multiple ES critical for crop production. Maximization of multifunctionality necessitates the integration at the landscape scale (0.5–2 km) of semi-natural patches within the intensively farmed agricultural matrix. This would require not only the protection of existing grasslands, but also their restoration in simplified

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landscapes. The promotion of mixed farming (i.e., both crop and livestock production) might increase semi-natural grassland cover at the landscape scale.

KEYWORDS

agroecosystem, farmland biodiversity, multiple ecosystem services, pest control, pollination, soil protection, sustainable agriculture

1 | INTRODUCTION

Maintaining and enhancing farmland biodiversity and the flow of ecosystem services (ES) in agroecosystems is considered pivotal for the long-term sustainability of agriculture and food security (Seppelt et al., 2020). However, the provision of critical ES for crop production such as pollination, pest control, water regulation and soil fertility is threatened by a range of global drivers of change such as the intensification and expansion of agricultural land (Ramankutty et al., 2018). The response of farmland biodiversity and multiple ES to land-use change at multiple spatial scales remains little understood, making sustainable planning of agroecosystems difficult.

The expansion and the intensive management of crop fields through implementation of monocultures, continuous cropping and the use of agrochemicals restrict many animal and plant species to non-cropped areas that are hence pivotal for the maintenance of farmland biodiversity (Tscharntke et al., 2021). Landscape simplification with the consequent loss of semi-natural habitats has also been shown to negatively impact the provision of several above-ground ES linked to crop production such as pollination and pest control (Dainese et al., 2019). These ES are in fact delivered by mobile organisms that also depend on resources, such as alternative hosts, food, shelter and overwintering sites, provided by semi-natural habitats (Holland et al., 2016). Nevertheless, semi-natural habitats can also represent an important source of pests so that their contribution to pest control is often context dependent (Tamburini et al., 2020). Moreover, species' responses to landscape characteristics often depend on sets of biological traits (Martin et al., 2019) so that abundance of semi-natural habitats in the landscape could affect different organism groups (e.g., crop specialists vs. habitat generalists) and ES in contrasting ways, potentially generating trade-offs (Lundin et al., 2021). Studies exploring landscape impact on the diversity of multiple taxa and the provision of multiple ES are hence important to adequately inform sustainable planning of agroecosystems. Moreover, although agricultural landscapes are heterogeneous and often complex mosaics of different habitat types, the effect of landscape composition has been rarely investigated across multiple habitats.

Semi-natural grasslands, that is, extensively managed hay meadows and pastures, are considered key components of agroecosystems producing an array of goods and benefits, although only few have market value (i.e., fodder and livestock production; Bengtsson et al., 2019). The area of such grassland habitats has declined worldwide in recent decades, mainly through expansion of agriculture or land abandonment, jeopardizing biodiversity conservation and ecosystem functioning in several agricultural systems (Lark et al., 2020).

Grasslands support farmland biodiversity by having a high diversity of plants and animals, harbouring many rare or declining species, and are essential contributors of ES (Bardgett et al., 2021). Above-ground, grasslands support pollinator and natural enemy communities, enhancing the flow of both pollination and biological control services in neighbouring areas (Werling et al., 2014). Grasslands have also been shown to provide important below-ground ES such as carbon sequestration and water regulation, more than crop fields and sometimes as much as forests (Bardgett et al., 2021; Bengtsson et al., 2019). Nevertheless, studies exploring the multifunctional role of grasslands are still scarce compared to other production systems such as crop fields and forests (but see Boetzi et al., 2021; Neyret et al., 2021).

The aim of this study was to explore the effects of land-use at multiple spatial scales on ecosystem multifunctionality. Assessing the ability of agroecosystems to support biodiversity and the flow of multiple ES is in fact considered fundamental to inform a sustainable management of agricultural landscapes that limits the multifaceted impacts of human activities on the environment (Nilsson et al., 2017). However, major gaps still remain for an efficient use of the multifunctionality concept in land management and planning, such as the scale of application (Hölting et al., 2019). For example, the response of local multifunctionality to landscape characteristics is still little understood.

Here, we measured the provision of biodiversity and five ES in two important habitats of European agroecosystems, oilseed rape fields and semi-natural grasslands: diversity of plants, arthropods, birds and the provision of pollination, pest control, soil fertility, carbon storage and water regulation. We further assessed the response of biodiversity and multiple ES to landscape composition, measured as the cover of grasslands around the selected sites. We then calculated above- and below-ground ES-multifunctionality (Manning et al., 2018). We hypothesized that (i) locally, grasslands would present higher biodiversity, ES provision and above- and below-ground ES-multifunctionality compared to crop fields, and that (ii) sites located in landscapes rich in grasslands would present higher diversity and ES provision related to mobile organisms.

2 | MATERIALS AND METHODS

2.1 | Site selection

The study was conducted in the agricultural landscape of the province Skåne in southern Sweden (centred on longitude 55°56'10"N, latitude 13°37'57"E). This region is characterized by temperate

climate (mean annual precipitation = 652 mm, mean annual temperature = 9.0°C) and it consists of intensively farmed plains interspersed with grasslands and forest patches. We selected 10 non-overlapping circular landscapes with a 1 km radius along a gradient in the cover of permanent grasslands (range = 3.5%–24.8%, Figure 1). Permanent and extensively managed grasslands (typically grazed) are considered the most important semi-natural habitat in the region for the maintenance of biodiversity and for the provision of ES (Bengtsson et al., 2019; Öckinger & Smith, 2007). Landscapes were separated by at least 2.5 km (average minimum distance = 9.1 km). ArcGIS 9.3 was used for landscape analyses of regional land-use maps (Swedish land use map, 2020), verified and ameliorated with aerial photograph interpretation and field surveys. Since different service providers are often characterized by different mobility, they can be influenced by landscape features at different scales. We hence considered and measured landscape composition in a 0.5 and 2-km buffer in addition to the 1 km one, distances considered appropriate for the taxonomic groups studied here (correlations among landscape variables at different scales are presented in Table S1; Boetzel et al., 2021). Within each landscape, we selected one oilseed rape field and one permanent grassland (distance between paired sites: 0–527 m, median distance = 190.5 m) for a total of 20 sites. Oilseed rape was selected as study crop as it is economically important worldwide, an important component of the typical crop rotation in the region, and it depends on ES both above (pest control, pollination) and below-ground (Bartomeus et al., 2015). The oilseed rape fields were managed conventionally according to local practices. Eight grasslands were used for extensive livestock grazing with comparable livestock units (LSU) per unit of area (0.63–1.49 LSU/ha, mean = 1.11 LSU/ha) and two were managed for hay production and hence mowed twice per year. Sampling was performed between 6 May and 5 September 2017.

2.2 | Assessing biodiversity and ES provision

Following established methodology (Garland et al., 2021; Manning et al., 2018), we measured 20 variables to estimate the provision of biodiversity and multiple ES in both oilseed rape fields and grasslands (13 variables above-ground and 7 below-ground, Figure 1). The variables were then used to quantify 13 indicators (9 above-ground and 4 below-ground) and the provision of above-ground biodiversity and five ES. Variables and indicators represented either ecosystem functions underpinning ES (e.g., flower visitation for pollination) or were general indicators of the service (e.g., bee diversity and abundance for pollination). The variables and indicators evaluated here are considered to be critical determinants of ecosystem functioning in agroecosystems (Bengtsson et al., 2019; Garland et al., 2021). Some components of above-ground biodiversity affect or are good proxies for service provisioning (e.g., spider diversity can be considered as a measure of both biodiversity and predation) and were hence included for the provision of both biodiversity and ES (Figure 1). We checked whether the inclusion of repeated variables in the dataset affected our results (see below).

2.2.1 | Above-ground biodiversity and ES

We quantified above-ground biodiversity measuring the diversity of birds (one 500m transect per site, two sampling rounds), bees (five pan trap clusters, two rounds), butterflies (one 500 m transect, four rounds), carabid beetles and spiders (five pitfall traps, three rounds) and plants (ten 1 × 1 m plots, two rounds) in each site (see Table S2). These organisms are considered effective umbrella groups for farmland biodiversity (Gerlach et al., 2013). We quantified pollination

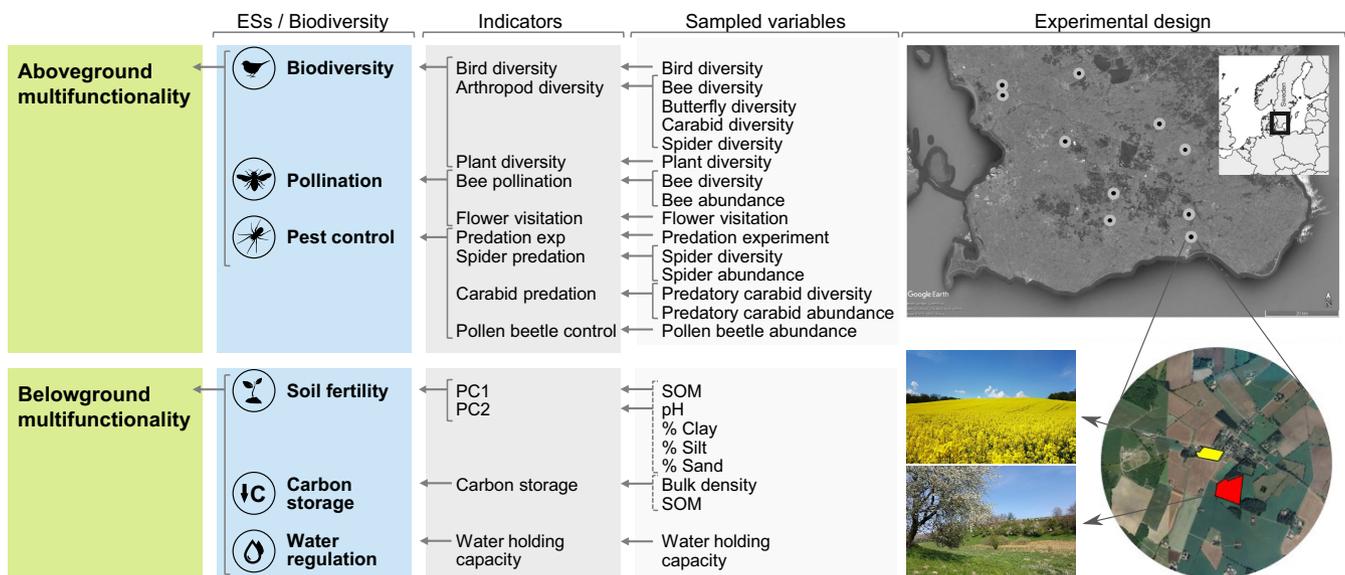


FIGURE 1 Experimental design and list of sampled variables grouped into indicators, biodiversity, ecosystem services and above- and below-ground ES-multifunctionality. Solid line brackets indicate averaging of components, dashed brackets indicate other type of analyses (see text for details). Pollen beetles were measured only in oilseed rape fields.

measuring bee diversity and abundance (pan trapping) and flower visitation (twenty 1 × 1 m plots, two rounds; Dainese et al., 2019). The provision of pest control was estimated by measuring the diversity and abundance of predatory carabids (i.e., a subset of all carabids) and spiders (pitfall trapping) and through a predation experiment where sentinel preys were deployed in the field for 24 h (five alive larvae of *Calliphora vomitoria* glued to a small tray, five trays per site, two rounds; Dainese et al., 2019; McHugh et al., 2020). We also estimated adult pollen beetle abundance as an indicator of pest control, but only in oilseed rape fields at flowering (50 plants, two rounds) since *Meligethes aeneus* is considered a major pest for this crop (Bartomeus et al., 2015). Pollen beetle abundance was reversed so that lower values signalled higher service provision. To achieve one value per site, we further averaged all abundance and rate variables and reported the total number of species across sampling rounds. For details on sampling methods, see Table S2. Carabid and spider data from oilseed rape fields have been previously published by Aguilera et al. (2020).

2.2.2 | Below-ground ES

We quantified below-ground ES measuring several soil characteristics (three core samples per site, one sampling round). Soil fertility was estimated by quantifying soil organic matter (SOM) content, soil structure (i.e., proportion of clay, silt and sand) and pH. Since it is not always straightforward to relate single soil indicators to service provision (e.g., soil structure and pH), we used principal component analysis to extrapolate two independent variables to describe soil characteristics (Byrnes et al., 2014). Soils richer in SOM and characterized by higher (i.e., less acid) pH and lower amount of sand were considered more fertile (Williams & Hedlund, 2013). Soil fertility PC1 was reversed so that higher values signalled higher service provision. Carbon storage was quantified as the total amount of carbon in the soil, calculated through SOM content and bulk density. Water regulation was quantified measuring water-holding capacity. This study did not require ethical approval.

2.3 | Assessing ES-multifunctionality

We applied two different approaches proposed in the literature to estimate ES-multifunctionality above-ground and below-ground for each site, the averaging and the multiple threshold approach (Byrnes et al., 2014). The averaging approach is widely used in multifunctionality studies since it provides a straightforward measure to evaluate the ability of ecosystems to simultaneously provide multiple functions and services (Garland et al., 2021; Manning et al., 2018). We first normalized (log-transformed when needed) and standardized (0–1 scale) each of the 20 variables considering the maximum and minimum value measured during the sampling, to meet model assumptions and to make different measures comparable. Closely related standardized variables were averaged to

obtain service indicators: butterfly, bee, carabid and spider diversity were averaged into 'arthropod diversity', bee abundance and diversity into 'bee pollination', spider diversity and abundance into 'spider predation', predatory carabid diversity and abundance into 'carabid predation' (Figure 1). Indicators were averaged to obtain a measure of above-ground biodiversity and five ES, which were then averaged to obtain values of ES-multifunctionality above-ground and below-ground. We adopted this multiple-step approach to avoid the overweighting of certain aspects of overall ecosystem functioning (e.g., diversity of arthropods) and to study different components of ES-multifunctionality. Nevertheless, to test whether this variable grouping could affect our results, we also calculated ES-multifunctionality directly averaging the 13 standardized variables for above-ground ES-multifunctionality and the four indicators for below-ground ES-multifunctionality, where variables and indicators were included only once. Pollen beetle abundance was only used to estimate pest control and above-ground ES-multifunctionality in oilseed rape fields. Correlation values between different variables, indicators and ES are presented in Figure S1.

The multiple threshold approach evaluates whether multiple functions are simultaneously performing at high levels. It hence considers the number of functions which perform higher than a given threshold, that is, a percentage of the maximum observed value of each function. Since choosing specific thresholds can be arbitrary, this approach considers the full range from 0% to 100%. This approach better handles the presence of unevenly strong functions in the dataset (i.e., few highly performing functions do not drive the multifunctionality index) and it allows to see potential trade-offs between functions (i.e., when some functions maximize and others minimize; Byrnes et al., 2014; Wittwer et al., 2021). We therefore calculated for each site the number of functions which performed higher than a given threshold (thresholds between 1% and 98% of the maximum value of each variable were considered). We considered 12 standardized variables and 4 indicators for above- and below-ground ES-multifunctionality, respectively. We did not include pollen beetle abundance in this analysis to keep the number of functions equal between habitats. Preliminary multiple threshold analyses considering different variable grouping produced qualitative similar results.

2.4 | Statistical analyses

We used linear mixed-effects models to test the effects of habitat type and landscape composition on above- and below-ground ES-multifunctionality (averaging approach), biodiversity and ES provision, indicators and on their components. The analyses of above-ground response variables included habitat type (categorical, grassland vs. oilseed rape field) and the cover of permanent grasslands in the landscape (continuous) as predictors. The interaction between the two predictors was included only when significant (i.e., in one model, bee abundance), even though full models yielded qualitatively comparable results. Landscape ID was included as

random factor. Since pollen beetle abundance was measured only in oilseed rape fields, it was analysed with a linear model only considering the cover of grasslands in the landscape. We also ran two additional linear models to analyse the response of above-ground ES-multifunctionality to landscape composition in the two habitats, separately. For each above-ground response variable, we tested the effect of the cover of grasslands using three scales (0.5, 1 and 2 km), separately. Moreover, since changes at low values of the landscape predictor might have more impact than at high values (Martin et al., 2019), we run three additional models including the log-transformed landscape predictor at each scale. The model displaying the lowest AIC was considered as the best fitting model (Table S3). Preliminary analyses showed no consistent effects of other landscape features on tested response variables and are therefore not presented here. The analyses of below-ground response variables included only the habitat type as local predictor and the landscape ID as random factor as we did not expect the cover of grasslands in the landscape to influence the provision of below-ground ES at these scales (but see Supplementary Information for the analyses including landscape variables). Model residuals approximated a normal distribution and exhibited homogeneity of variance.

To analyse the impact of local and landscape predictors on the number of functions working beyond a certain level of performance (i.e., multiple threshold approach, from 1% to 98% of the maximum observed value of each function), we followed the methodology by Byrnes et al. (2014). We first analysed and plotted the relationship between habitat type, landscape composition and the number of functions maximized at different threshold levels (from 1% to 98%). Then, to better understand how predictors influenced ES-multifunctionality, we evaluated and plotted the effect sizes of the predictors (slope of regression and 95% confidence interval) at each threshold level. Analyses were performed using the NLME

and MULTIFUNC packages (Bates et al., 2014; Byrnes, 2017; Pinheiro et al., 2014) implemented in R.

3 | RESULTS

Locally, ES-multifunctionality was higher in grasslands than in crop fields, by 25.2% above-ground and by 106.1% below-ground (Figure 2; Figure S2; Table S4). The multiple-threshold approach further confirmed that the number of high-performing functions was higher in grasslands. This effect was significant across the whole threshold range below-ground, but only when considering thresholds between roughly 50% and 90% of the maximum observed value of each function above-ground (Figure 3d,f). Grasslands were generally characterized by higher provision of above-ground biodiversity and pollination service than oilseed rape fields, but comparable levels of pest control. The overall higher level of biodiversity found in grasslands was reflected by its constituent indicators: we found higher bird, arthropod and plant diversity in grassland sites compared to oilseed rape fields. The higher arthropod diversity was mainly driven by the higher diversity of spiders and butterflies, since bee diversity did not differ between the two habitats and carabid diversity was found to be marginally lower than in oilseed rape fields (Figure S3). The higher level of pollination in grasslands was mainly driven by the higher visitation rate, since bee pollination (both bee diversity and abundance) did not clearly differ between the two habitats. Habitat type had variable impact on pest control indicators. We found no effect on predation (i.e., predation experiment), higher spider predation in grasslands (higher diversity and abundance) and higher carabid predation in oilseed rape fields (higher abundance but equal diversity of predatory carabids; Figure S3). Below-ground, grasslands presented higher soil carbon storage and higher provision

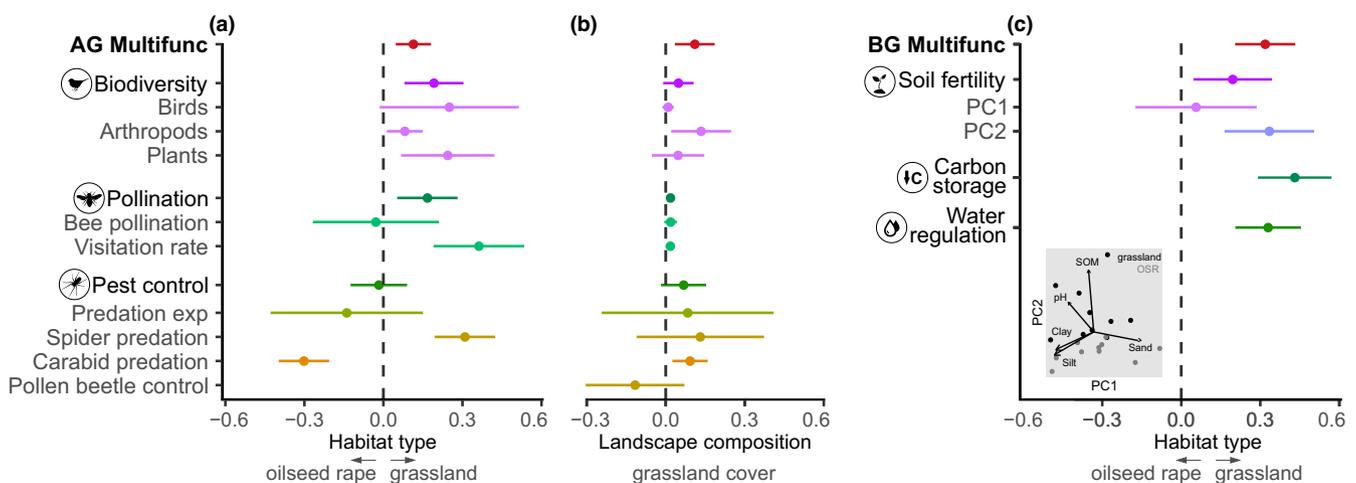


FIGURE 2 Model effect sizes and 95% confidence intervals for the (a and c) local (grassland vs. oilseed rape field habitat) and (b) landscape (increase in 10% of grassland cover) predictors explaining above- and below-ground ES-multifunctionality, biodiversity and ecosystem service provision and their indicators, measured following the averaging approach. AG = above-ground and BG = below-ground. Confidence intervals overlapping 0 indicate the predictor has no effect on related variable. Principal component analysis plot shows the relationship between the two soil fertility indicators (i.e., PC1 and PC2) and soil characteristics. Pollen beetle abundance ('Pollen beetle control' indicator) was measured only in oilseed rape fields. For details on indicators and statistical analyses, see Figure 1 and Table S4.

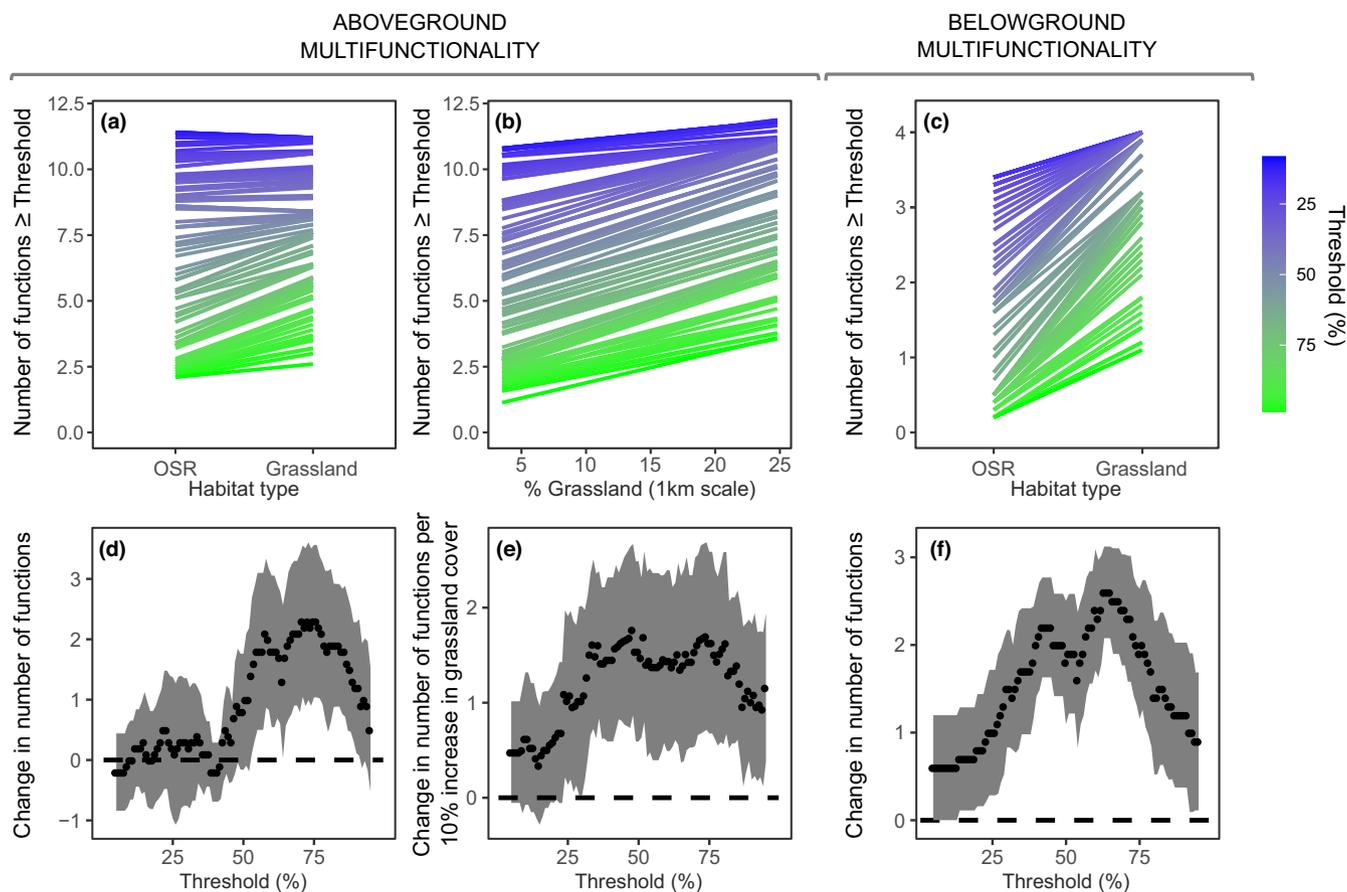


FIGURE 3 Impact of the local and landscape predictors on above- and below-ground ES-multifunctionality adopting the multiple threshold approach. Panels a–c show the relationships between local habitat type (grassland and oilseed rape fields) or landscape composition (cover of grasslands) and the number of functions which performed higher than a given threshold (thresholds between 1% and 98% of the maximum value of each variable were considered). Colours indicate different thresholds (see legend). Panels d–f show the slope of the relationship between predictors and the number of functions reaching a certain threshold. Black dots indicate fitted values and shading the 95% confidence interval; confidence intervals overlapping 0 indicate the threshold values at which the local/landscape factor has no effect on ES-multifunctionality.

of water regulation. The higher level of soil fertility found in grasslands was mainly related to PC2 (i.e., higher SOM content and higher, less acid pH), whereas PC1 (i.e., soil texture) did not differ between the two habitats.

At the landscape scale, a 10% increase in grassland cover in the landscape (2 km scale) enhanced above-ground ES-multifunctionality by 11.0% in both in oilseed rape fields and grasslands (Figures 2b and 3b). These results were maintained when analysing the landscape effect on ES-multifunctionality in the two habitats, separately (Table S5). The multiple-threshold approach showed that ES-multifunctionality was positively related to the grassland cover in the landscape at thresholds between roughly 25% and 98% (Figure 3e). Landscapes with high grassland cover were characterized by higher provision of pollination and, marginally, higher biodiversity and pest control (at 0.5, 2 and 1 km scale, respectively). Regarding biodiversity indicators, grassland cover at 2 km scale increased arthropod diversity and had no effect on bird and plant diversity. The increase in arthropod

diversity was mainly driven by the positive response of carabids and marginally of bees to grassland cover, since grassland cover in the landscape did not affect butterfly and spider diversity. The positive impact of grassland cover on pollination was mainly driven by the positive response of visitation rate and, marginally, bee pollination (increased bee diversity and abundance; the latter only in grasslands, Figure S3c). Regarding pest control, the cover of grasslands in the landscape positively influenced carabid predation (increased predatory carabid diversity but not abundance), but had no effects on spider predation, overall predation (i.e., predation experiment) and pollen beetle control. Both conditional and marginal R^2 for all models were generally high (mean cR^2 0.52 ± 0.22 , mean mR^2 0.44 ± 0.22), suggesting that the variance explained by the fixed factors was high (Table S4). The effects of the local habitat type and landscape composition on above- and below-ground ES-multifunctionality were confirmed when the indexes were measured directly averaging the 12 standardized variables and indicators (Table S6).

4 | DISCUSSION

Our analyses show that land-use influences the provision of above- and below-ground ES-multifunctionality in agroecosystems. Locally, grasslands had higher biodiversity, pollination, soil fertility, carbon storage, water regulation and overall ES-multifunctionality provision compared to crop fields. Moreover, high cover of grasslands in the landscape enhanced above-ground ES-multifunctionality in both grasslands and crop fields, supporting higher arthropod diversity, pollination and pest control provided by carabids.

4.1 | Biodiversity

Biodiversity was influenced by habitat type and, marginally, by landscape composition. Overall, we found grasslands to locally harbour more diverse communities compared to oilseed rape fields. This is not surprising, given that permanent grasslands are known to be biodiversity hotspots in the agricultural landscapes, and is probably the result of the overall lower disturbance, greater habitat stability, higher niche diversity and resource partitioning of semi-natural habitats, characteristics that promote both species coexistence and persistence (Silvertown, 2004). The difference in plant diversity between grasslands and oilseed rape fields is to be ascribed to soil management and high inputs of soil amendments and herbicides typical of crop fields. Similar to previous studies, we found that spider, butterfly and bird diversity was higher in grasslands compared to disturbed annual crops (Lemoine et al., 2007; Mestre et al., 2018; Pe'er et al., 2011). Contrary to our hypothesis, we found no differences in bee diversity between the two habitats. Although grasslands are generally expected to host a more diverse community of pollinators than arable fields (Öckinger & Smith, 2007), bees are mobile multi-habitat users that can forage several hundred meters from their nesting site (Jauker et al., 2009). The proximity of the sampled habitats within each landscape and the abundance of floral resources in oilseed rape fields during flowering might explain this result. Similar to other studies, carabid communities were found to be more diverse in cropland than in semi-natural habitats (Wang et al., 2021), although the difference between the two habitats was only marginally significant ($p = 0.051$; Table S4). Oilseed rape fields provide in fact abundant resources during spring and summer such as agricultural pests and weed seeds, potentially attracting a large range of carabid species (Marrec et al., 2015).

High cover of permanent grasslands in the landscape was positively correlated with arthropod diversity, in particular with the species richness of carabid beetles and bees ($p < 0.001$ and 0.095 , respectively; Table S4), in both habitats. These organisms benefit in fact from the presence of this type of habitat in the landscape for overwintering, nesting and alternative food resources (Boetzel et al., 2021; Purtauf et al., 2005). Surprisingly, grassland cover in the landscape did not affect the diversity of butterflies, spiders, birds

and plants, in contrast to what has been observed in many previous studies (Mestre et al., 2018; Öckinger & Smith, 2006; Tamburini, De Simone, et al., 2016), and even though the local species richness of these groups was higher in grasslands than in oilseed rape fields. Other factors might have masked diversity responses to the tested landscape variable, such as species traits, local management and differences in landscape configuration at different spatial scales (Dover & Settele, 2008; Lami et al., 2021; Redlich et al., 2021; Tamburini, Pevere, et al., 2016).

4.2 | Provision of above-ground ES

Pollination service was influenced by both habitat type and by landscape composition. The cover of permanent grasslands in the landscape had the most consistent effect on pollination, being positively correlated to visitation rate, bee abundance (but only in grasslands) and marginally to bee diversity. This result is consistent with previous findings showing the importance of landscape composition in shaping pollinator communities and related service delivery (Dainese et al., 2019). Locally, flower visitation rates were higher in grasslands than in oilseed rape fields. This result can be explained by the higher plant diversity that might have attracted and supported a more diverse and abundant community of (specialized) pollinators, and, partially, by the higher bee abundance detected in the grasslands located in landscapes with high grassland cover (Figure S3c). Our findings highlight the importance of preserving and restoring semi-natural habitats in agricultural landscapes to support the provision of pollination services for both food production and the reproductive success of grassland species.

The response of pest control to land-use was variable, depending on the scale and on the organism group or function considered. Grasslands locally harboured more diverse and abundant communities of spiders, increasing the potential for spider predation in this habitat, whereas predatory carabids were more abundant, but not more diverse, in oilseed rape fields. Only predatory carabid diversity was positively related to the cover of permanent grasslands in the landscape, resulting in an increased potential for carabid predation in both grasslands and arable fields. These results suggest that spiders and carabids use habitats in the landscape matrix in different ways. Spiders are strongly linked to grasslands, with landscape composition probably affecting community structure rather than the overall diversity (Nardi et al., 2019). Predatory carabids rely on non-crop habitats most likely for overwintering (Holland et al., 2016) and disperse within the landscape matrix during spring and summer for food, visiting mostly arable fields where preys are probably more abundant. We found no effect of local habitat type and landscape composition on predation rate. The methodology adopted here might not have been sensible enough to correctly detect predation rates, as the small number of preys exposed to natural enemies were equally well controlled in both grasslands and arable fields and in different landscape contexts. Moreover,

caution should be taken in the interpretation of these results as experiments using immobilized sentinels have been shown to not be representative for predation of live, mobile preys in other systems (Zou et al., 2017). Landscape composition did also not affect pollen beetle abundance in oilseed rape fields. Although non-crop habitats can be used by this important pest for overwintering, other factors might have influenced pollen beetle immigration into arable fields such as the area of oilseed rape crops in the landscape (Riggi et al., 2017). As previously shown, it is not always possible to find a consistent effect of landscape composition on natural enemies and pests because different functional groups or species respond differently to landscape characteristics (Martin et al., 2019). Nevertheless, our results indicate that permanent grasslands are key habitats in agricultural landscapes for the maintenance of diverse communities of spiders and predatory carabid beetles, important agents of biological control for several crops, potentially promoting a more efficient regulation of pest populations (Dainese et al., 2019).

4.3 | Provision of below-ground ES

As expected, we found a strong impact of habitat type on the delivery of below-ground ES. Grasslands had higher soil fertility, carbon storage and water regulation than arable fields. These results are mostly driven by the difference between the two habitat types in the amount of SOM, that influences soil fertility, the amount of carbon stored below-ground and the capacity of soil to absorb water (Schmidt et al., 2011). The lower quantity of SOM in cultivated soils compared to non-crop habitats has been extensively investigated and it is linked to the removal of crop residues, enhanced mineralization of organic matter and enhanced soil erosion (Wiesmeier et al., 2012). Grassland soils are instead generally less disturbed than cultivated ones, they are vertically more stratified, and the dense root system of herbaceous plants provides abundant carbon sources to soil. We found no effect of habitat type on soil structure (i.e., soil fertility PC2, see Figure 2), which is probably due to the paired experimental design (i.e., close sites probably shared similar soil characteristics). Although management intensity can strongly affect soil characteristics and functioning, our results confirm the importance of permanent grasslands for soil protection and carbon storage in agroecosystems (Bengtsson et al., 2019).

4.4 | Above- and below-ground ES-multifunctionality

Multifunctionality was influenced by both habitat type and landscape composition. Locally, grasslands presented higher ES-multifunctionality than arable fields both above and below-ground. However, the impact of habitat type was stronger for below-ground than for above-ground ES-multifunctionality: grasslands supported

a maximum of 2.3 functions more than oilseed rape fields above-ground (peak at around a threshold of 73%) and a maximum of 2.6 functions more than oilseed rape fields below-ground (peak at around a threshold of 63%). Moreover, below-ground ES-multifunctionality was significantly higher in grasslands across almost the entire threshold range (Figure 3), suggesting a very low level of performance for below-ground functions in arable soil. Above-ground instead, the effect of habitat type on ES-multifunctionality was significant only above a threshold of 50%, suggesting that oilseed rape fields can provide numerous above-ground functions, although at low performance levels. It is important to acknowledge that in this study we did not define levels of function, service or ES-multifunctionality above which the provision is considered sufficient (Manning et al., 2018). Compared to habitat type, the impact of landscape composition on above-ground ES-multifunctionality was lower, although comparable: an increase in 10% of grassland cover in the landscape resulted in fact in an increase of maximum 1.8 functions (peak at around a threshold of 48%). Lastly, the decreasing slope at higher thresholds indicates that neither of the predictors considered here could simultaneously drive all functions to their highest levels. Thus, other factors probably influence ES-multifunctionality in this system (e.g., local management; Wittwer et al., 2021).

It is important to consider that the findings of the present study are necessarily limited by the experimental setup. The measurements of ES and multifunctionality, for example, depend on the variables selected and might not be of direct interest for the stakeholders (e.g., predatory carabid diversity might be less important than pollen beetle abundance as an indicator of pest regulation in oilseed rape for farmers). Moreover, the present experimental design (sites selected along a gradient in grassland cover) might have narrowed our ability to detect the impact of landscape characteristics other than the abundance of grasslands, such as landscape configuration and diversity.

5 | CONCLUSIONS

Our results highlight the key importance of preserving semi-natural grasslands in agroecosystems for the conservation of farmland biodiversity and the delivery of multiple ES critical for crop production. Moreover, maximization of multifunctionality necessitates the integration at the landscape scale (0.5–2 km) of semi-natural grassland patches within the intensively farmed agricultural matrix. This would require not only the protection of existing grasslands, but also their restoration in simplified landscapes. However, landscape strategies are notoriously difficult to implement, they are highly sensitive to the type of ES desired by stakeholders, and trade-offs often emerge (e.g., production and biodiversity conservation). At the farmscape scale, the promotion of mixed farming, which involves both the growing of crops and the raising of livestock and was once common in Europe, might increase semi-natural grassland cover at the landscape scale. Moreover, the establishment of wildlife friendly habitats (e.g., long-term fallows and temporally stable flowering fields) might act

synergistically with semi-natural grasslands in enhancing farmland biodiversity. Strong support from regional, national and international policy is needed to promote the integration of grasslands into agricultural production systems and land-use decisions (e.g., compensation for ES, agri-environmental schemes for mixed farming).

AUTHOR CONTRIBUTIONS

Giovanni Tamburini and Erik Öckinger conceived and designed the study. Giovanni Tamburini and Guillermo Aguilera performed the study. Giovanni Tamburini performed data analysis and led the writing. All authors participated in results' interpretation and drafting the manuscript.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.4b8gthtg6> (Tamburini et al., 2022).

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