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Both long-term grasslands and crop diversity are needed to limit pest and weed infestations in agricultural landscapes

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Increasing landscape heterogeneity has been suggested to be an important strategy to strengthen natural pest control in crops, especially through enhancing the amount of seminatural habitats. Increasing crop diversity is also a promising strategy to complement or replace seminatural habitat when seminatural habitat is scarce. However, their relative or possibly interactive effects on pest and weed infestation remain poorly investigated, and the role of different types of seminatural habitats has been understudied. Using an extensive sampling effort in 974 arable fields across 7 y, we evaluated the separate and interactive effects of crop diversity (seven arable crop types) and the amount of four types of seminatural habitats (meadows, hay, forests, and hedgerows) in the landscape on pest and weed control. Meadows and crop diversity, respectively, supported insect pest and weed control services in agricultural landscapes through a complementarity effect. Crop diversity increased weed seed predation rate (by 16%) and reduced weed infestation (by 6%), whereas long-term grasslands (to a much higher degree than hay or woody habitats) increased insect pest predation rates (by 23%) and reduced pest infestation (by 19%) in most arable crops. Our results demonstrate that diversification of the agricultural landscape requires long-term grasslands as well as improved crop diversity to ensure the delivery of efficient pest and weed control services.

natural enemies | sentinel cards | landscape heterogeneity | hay | seminatural habitat

Significance

Increasing landscape heterogeneity through crop diversity and amount of seminatural habitats have both been suggested to improve natural pest control in arable fields. However, despite decades of research, very little is known about the respective contributions of the various components of landscape heterogeneity in reducing weed and insect pest infestations in arable fields. We show that among landscape features, grasslands rather than woody elements, and long-term grasslands rather than temporary grasslands (hay), increased the top–down control of insect pests, especially in crops where pest infestation was high. Conversely, weed control was best explained by crop diversity at the landscape scale. Our findings suggest that public policies should target landscape mosaics harboring long-term grasslands and crop diversification.

Crop pests and weeds are considered to be a major threat for food security. Overall, they reduce crop yield by an estimated 20 to 30% (1, 2), which has led to ever-increasing pesticide use (3), with its associated negative impacts on biodiversity and human health (4, 5). Pest damage is predicted to increase with climate change while pest resistance to insecticides is of increasingly serious concern (4). Collectively, the negative externalities of pesticide use and the expected effects of climate warming threaten the sustainability of modern food production systems and necessitate other pest management strategies in agricultural landscapes (6). A promising alternative to pesticide use is to harness natural pest control services delivered by enemies of pests and weeds (7–9). The abundance of natural enemies, however, depends on critical resources provided by seminatural habitats, such as grasslands or woody habitats (10–12), but rarely considered by farmers (13). Recently, crop diversification has been suggested as a possible surrogate for seminatural habitats (14), as it enhances biodiversity (15) and ecosystem services (14, 16). Increasing crop diversity, rather than converting arable land to seminatural habitats, may be highly appealing to reconcile biodiversity conservation and commodity production because it would avoid competition with food production (17).

However, crop diversity has been seldom compared to seminatural habitat in its ability to provide natural pest control services (13, 18). These two management strategies are nonexclusive and rely on different ecological processes. For instance, promoting the presence of seminatural habitats at the landscape scale may increase top–down control by natural enemies (8, 9) since heterogeneous landscapes with seminatural habitats benefit natural enemies (7, 8, 19). In contrast, increasing crop diversity may limit pest abundance (20), with higher pest abundance being found in landscapes with low crop diversity in space and time because of higher resource concentration for pests (20, 21). To date, most studies have focused on the role of seminatural habitats on natural enemies or pests (9), whereas the impact of crop diversity on natural enemies and pest abundances has remained less studied (but see ref. 20). Moreover, how seminatural habitats and crop diversity may interact synergistically or antagonistically remains largely unclear (22), thus limiting our ability to design management strategies leading to effective pest control.

Ultimately, among seminatural habitats, grasslands are expected to provide stronger pest control compared with other types of seminatural habitats, such as woody habitats, because they shelter greater abundance of natural enemies (10). However, grassland is a generic term and several types of grasslands can actually be implemented by farmers:

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meadows, or long-term grasslands, which are intended to remain in place for many years and harbor high plant richness; temporary grasslands, hay or fodder (lasting usually up to 4 y), such as alfalfa (*Medicago sativa*); and short-lived (<1 y) artificial grasslands such as ryegrass (*Lolium* spp.), which are rather similar to annual crops (23). Each grassland type differs in its ecological properties and is likely to deliver different levels of natural pest control (23). Grassland types also differ in their management as well as in their agricultural benefits, and therefore are differentially attractive to farmers. Indeed, temporary grasslands such as hay, which are managed as crops (inputs such as fertilizers and pesticides are used in alfalfa), are generally preferred by farmers to long-term grasslands or meadows (24, 25). Despite these major differences, the effect of grasslands on pest control is generally examined by aggregating all grassland types (19, 26, 27), assuming that hay support natural pest control in a similar manner as long-term grasslands (i.e., acting as reservoirs). However, if hays are more similar to crops, they may improve pest control through increasing crop diversity and reduce resources concentration for pests rather than acting as a source for natural enemies as seminatural habitats. Such information is crucial to guide effective policies aiming to reduce the environmental footprint of agriculture.

Using 974 farmers' fields in an intensive arable landscape surveyed over 7 y (2013 to 2019), we conducted an in-depth analysis of pathways through which landscape heterogeneity (estimated at increasing spatial scales, from 500 to 2,000 m) affects natural control of pests and weeds, contrasting the effects of crop diversity and the area of seminatural habitats. As landscape effects may vary according to prey type (28), we used four types of sentinel prey to quantify predation rates, i.e., adult insects on the ground or in the crop canopy, weed seeds, and insect eggs. The intra-annual dynamic of pests and natural enemies was captured by quantifying pest presence and pest predation rates in two winter (cereal and oilseed rape) and two spring (maize and sunflower) planted crops. Pest presence and pest predation were also quantified in meadows and hay. First, we explored the separate and interactive effects of crop diversity, the amount of grasslands (combining hay and meadows) as well as the amount of woody habitats on predation rates. We predicted that seminatural habitats would be more beneficial to pest predation than crop diversity, given that the former support a greater abundance of natural enemies. We also tested whether crop diversity would increase pest predation in landscapes harboring a high amount of seminatural habitats through a synergistic effect (15). Among seminatural habitats, we hypothesized that grassland-rich landscapes would enhance weed and pest control services in crops more efficiently than woody-rich landscapes because of the stronger habitat similarity for natural enemies. Next, we focused on the specific role of hay (short-term grasslands) to determine whether they behave more like meadows or (annual) crops, by including them in either category and recalculating all landscape metrics (i.e., crop diversity or grassland amount). We expected meadows to exert stronger effects than hay on natural weed and pest control (26, 27). Finally, we investigated how variation in predation rates (surrogate of natural control) cascades to within-field weed and pest abundances, hence their regulation.

Results

Predation Rates and Pest/Weed Abundance According to Crop. Predation rates of the four pests differed significantly between the six land-use cover types (Fig. 1 *A*, *C*, *E*, *G*). For ground-level pests, predation rates were highest in meadows (Fig. 1*A*; $F_{5,957} = 21.73$, $P < 0.001$), whereas for weed seeds, predation rates were higher in arable crops, especially cereals (Fig. 1*C*; $F_{5,665} = 9.13$, $P < 0.001$). No differences were detected for egg predation (Fig. 1*G*; $F_{1,163} = 3.69$, $P = 0.06$) and for canopy-level pest predation rates (Fig. 1*E*; $F_{1,165} = 0.32$, $P = 0.57$). A different pattern emerged when considering pest abundance, with the highest values observed in oilseed rape, followed by meadows and hay, and finally cereals, regardless of the insect pest type (all $P < 0.001$; Fig. 1 *B*, *D*, *F*). Meadows showed the third-highest pest abundances and the highest predation rates of ground pests, whereas oilseed rape showed the highest abundances of ground pests but the lowest pest predation rate and second-highest level for weed seed abundance and seed predation rate (Fig. 1).

Stronger Effect of Grasslands than Woody Habitats or Crop Diversity on Pest Predation Rates. The spatial extent at which landscape features affected predation rates varied among preys. It was smaller for canopy-level insect pests (buffer radius of 750 m), than for ground-level insect pests (1,250 m), weed seeds (1,500 m), and pest eggs (2,000 m). The amount of grasslands (considering both permanent meadows and temporary hay) significantly enhanced predation rates of ground-level pests in all arable crops (Fig. 2*A*, see *SI Appendix*, Table S2 for associated statistic), as well as of pest eggs in oilseed rape (Fig. 2*J* and *SI Appendix*, Table S2). In the former, predation rates improved by 23% [average amount over year, 95% CI (17 to 28%)] when grasslands amount increased from 0 to 40% within a given year (Fig. 2*A*). No effects of grasslands were observed on weed seed predation rates in cereal, maize, and sunflower but a significant negative effect was observed in oilseed rape (Fig. 2*D*). The amount of woody habitats never increased pest or weed predation rates (Fig. 2, *Central* column), while crop diversity only improved seed predation rates, in cereal, maize, and sunflower, but not in oilseed rape (Fig. 2 *F*, *Right* column; see also *SI Appendix*, Table S2). Overall, merging all crops and years, seed predation rates increased by 16% [(11 to 22%)] when crop diversity doubled. No significant interaction was observed between grassland and crop diversity on predation rate of any pest type (*SI Appendix*, Table S2). Therefore, for all pests except canopy pests, the amount of grasslands in the landscape improved predation rates (Fig. 2).

Stronger Effect of Meadows than Hay on Pest Predation Rates. Given that the amount of grasslands, among landscape variables, had the strongest effect on predation rates, we disentangled the relative effects of permanent meadows versus temporary hay. A first model restricted the grassland category to only meadows (hay being shifted to the crop category and included in crop diversity calculation), and was compared to the previous model in which the two types of grasslands were aggregated. For ground-level pests and pest eggs, slopes and significance of effects were identical between the two models, indicating that the previously detected effect of grasslands on these pest predation rates was mainly attributable to meadows (Fig. 3 *A* and *G*). No effects of meadows were observed for the predation rates of weed seeds (Fig. 3*D*) or canopy-level pests (*SI Appendix*, Fig. S4), which is again similar to what was found when considering all grasslands (*SI Appendix*, Table S2). In addition, we found that increasing age of meadows significantly improved predation rates of ground-level pests and pest eggs (Fig. 3 *B* and *H*), a pattern not found for hay (Fig. 3 *C* and *I*; see also *SI Appendix*, Table S3) nor for weed seeds (Fig. 3 *E* and *F*). Switching hay from the grassland to the crop category, so that hay contributed to the calculation of crop diversity, did not alter crop diversity effects (*SI Appendix*, Fig. S4): All nonsignificant effects remained nonsignificant, and the significant effect of crop diversity in interaction with crop type on weed seed predation remained significant (*SI Appendix*, Fig. S4 and Table S3). As an alternative to the first model which considered only meadows in

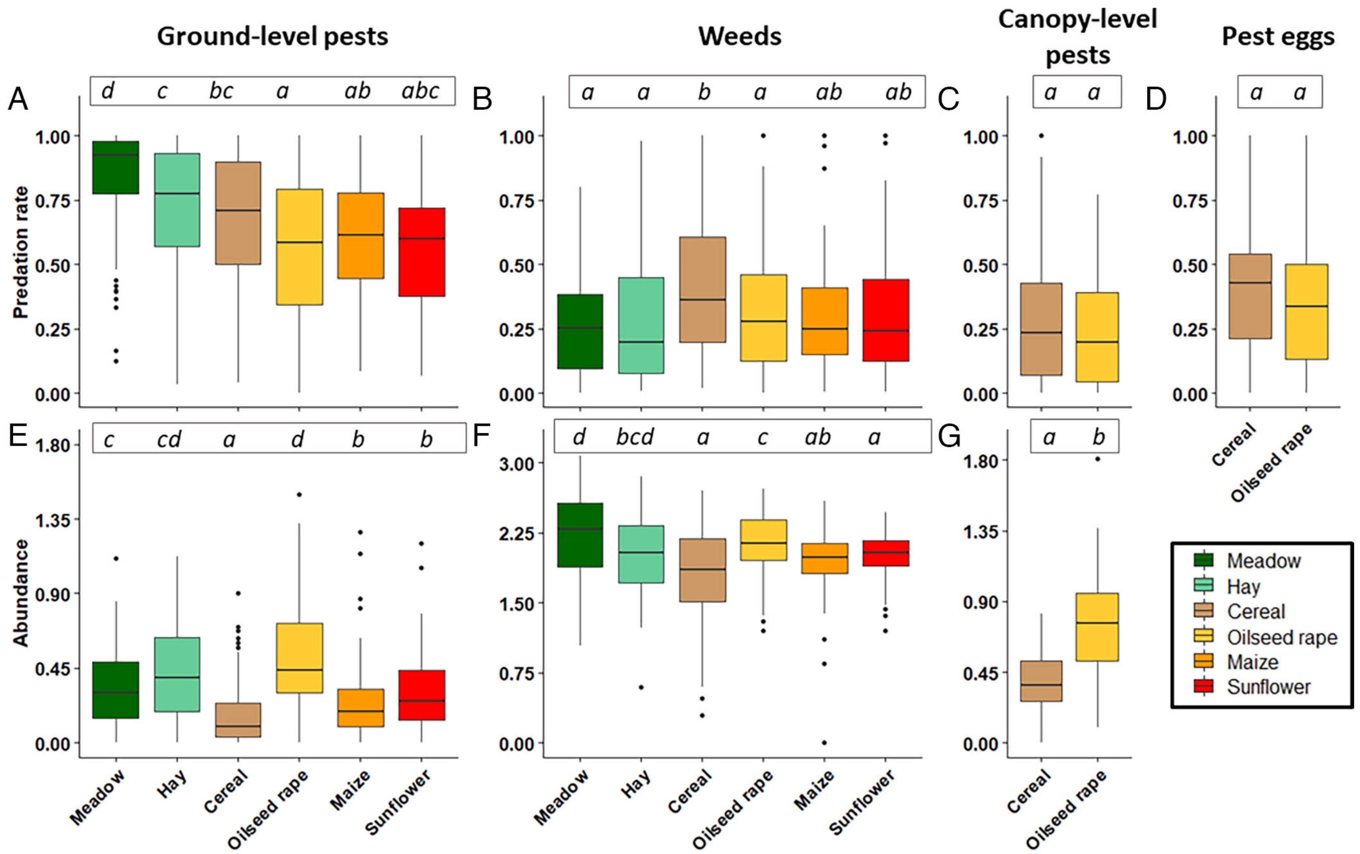

Fig. 1. Effects of crop type on predation rate and pest abundance of ground-level pests (*A* and *B*), weeds (*C* and *D*), canopy-level pests (*E* and *F*), and pest eggs (*G*). Crop types are shown by different colors: dark green for meadows, light green for hay, brown for cereal, yellow for oilseed rape, orange for maize, and red for sunflower. Pest and weed abundances are log(x+abs(min)+1) transformed. Letters represent a significant difference between crops for predation rates or pest abundances.

the grassland category, we fitted a second model including only hay in the grassland category, i.e., meadows were removed from the model. The results indicated that the amount of hay in the landscape had no significant effect on predation rates of pests and weeds (Fig. 3*A* and *SI Appendix*, Table S3).

Similarly, the goodness-of-fit of models including only meadows as the amount of grassland in the landscape and hays in the crop diversity calculation were similar to those of models including all grasslands in the landscape variable (*SI Appendix*, Fig. S5; see Akaike information criterion (AIC)/R^2 scores and variance analyses). By contrast, restricting grasslands to hay-only strongly decreased the goodness-of-fit except for predation rates of weed seeds, which showed a similar goodness-of-fit (*SI Appendix*, Fig. S5). Finally, the amount of variance explained in predation rates of ground-level pests, canopy-level pests, and pest eggs was mostly accounted for by the amount of meadows, whereas crop diversity explained most of the variance in predation rates of weed seeds (*SI Appendix*, Fig. S5).

Top–Down Effects of Predation Rates on Pest Abundance. Abundances of ground-level pests and weeds decreased with increasing predation rates in all crops resulting in respective decreases of 19.5% [(16.6 to 22.1%)] and 5.6% [(0.5 to 10.3%)] with an increase of 20% in predation rate within a given year (Fig. 4 *A* and *B*, see *SI Appendix*, Table S4 for associated statistics). This negative effect was not found for canopy-level pests (Fig. 4*E*). An interactive effect with crop identity was further found in the case of ground-level pests with a strong negative effect in oilseed rape (*SI Appendix*, Fig. S6*C*). These negative relationships between predation rates and abundances of ground-level pests and weeds suggest a clear top-down effect of natural enemies on these types of prey. Such top-down effect is mediated by grassland amount in the case of ground level (Fig. 2*A*), and by crop diversity for weed seeds (Fig. 2*F*), suggesting that these habitats support natural enemies, respectively, for insect pest and weeds. Increasing the amount of seminatural habitats or lowering crop diversity could have rather benefitted pests and weeds in crops through resource complementation across crop/noncrop habitats or through resource concentration effects. These hypotheses were actually not supported by our data, either for meadows (Fig. 4*B*), crop diversity (Fig. 4*D* and *SI Appendix*, Fig. S6), or woody habitats (*SI Appendix*, Fig. S6), none of which affected positively or negatively any of the insect pests or weeds. We even found that the amount of meadows decreased abundance of weeds in maize (*SI Appendix*, Fig. S6*E*) and canopy-level insects in oilseed rape (Fig. 4*F*). Finally, we ran statistical models with interactive effects between predation rate and either meadow amount or crop diversity, for each pest category. We found no significant effect of this interactive term in any of the models (Fig. 4 and *SI Appendix*, Fig. S7 and Table S4). Instead, we only found additive effects of predation rate and meadow amount for weeds in maize fields (Fig. 4*H* and *SI Appendix*, Fig. S6*E* and Table S4).

Discussion

Our study provides strong evidence that two facets of landscape heterogeneity are simultaneously needed to support both pest and weed control services in agricultural landscapes. On the one hand,

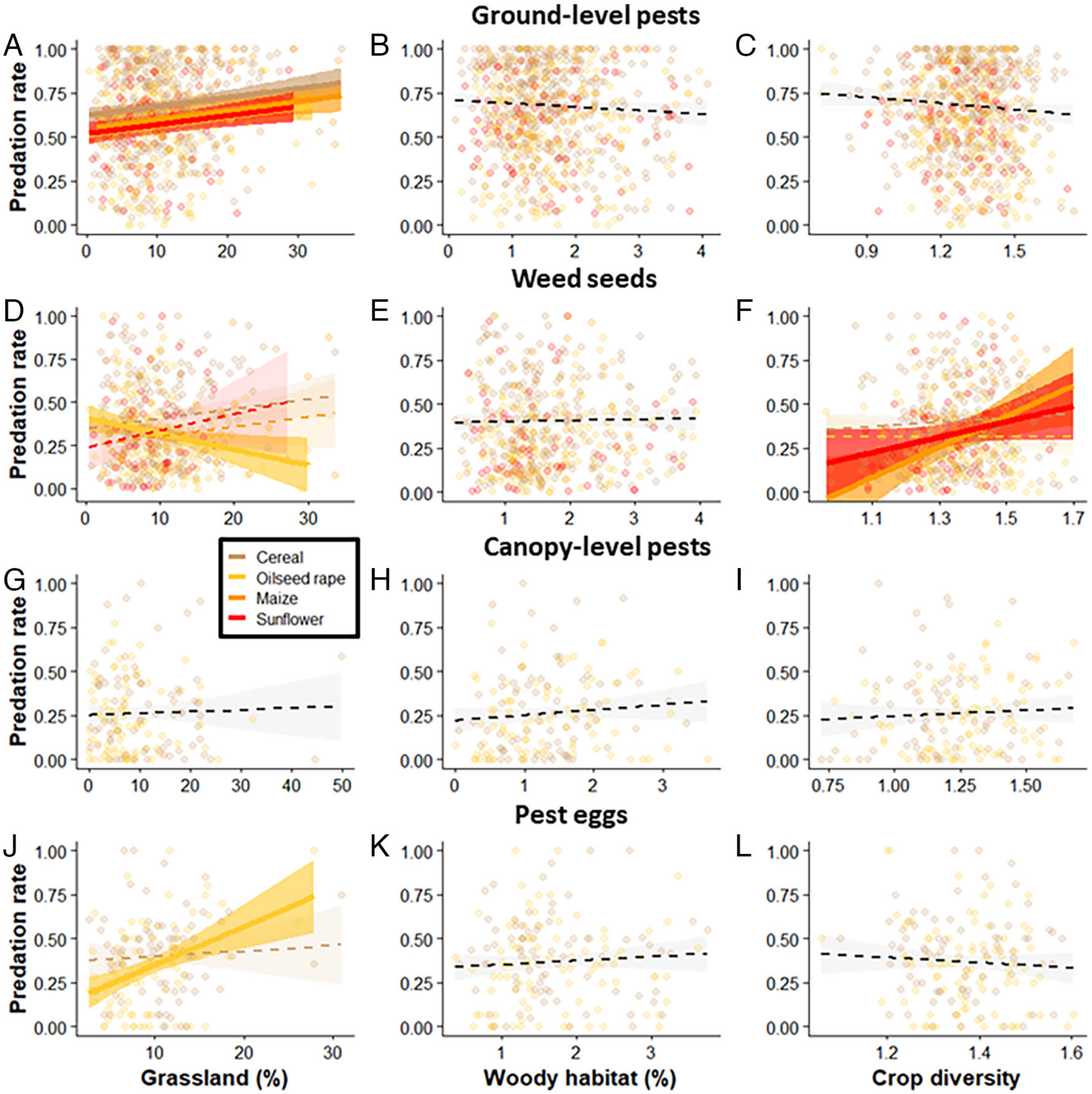

Fig. 2. Effects of grasslands, woody habitats, and crop diversity on the predation rates of ground-level pests (*A*–*C*), weed seeds (*D*–*F*), canopy-level pests (*G*–*I*), and pest eggs (*J*–*L*). Landscape features were calculated at 750 m buffer for canopy-level insect pest, 1,250 m for ground-level insect, 1,500 m for weed seed, and 2,000 m for pest egg. Grassland includes both meadows and hay. Crop diversity was estimated by the Shannon index computed on seven crop types. Color lines represent the relationship between predation rate and landscape variables per crop type (brown for cereal, yellow for oilseed rape, orange for maize, and red for sunflower). Solid lines show significant relationships, and nonsignificant relationships are dashed (see *Materials and Methods* for the model that was ran and the procedure used to account for multiple testing). When no significant effect of landscape feature is detected whatever the crop type, relationship over the four crop types is aggregated and represented by a dashed black line. Shades represent 95% CI of predicted values. Woody habitats are log(x+abs(min)+1) transformed.

long-term grasslands support the bulk of insect pest control services, while on the other hand, crop diversity increases weed seed control. Importantly, meadows, especially older permanent grasslands, rather than hay or woody habitats, increase natural pest control services and limit pest abundance, making them major habitats.

Recently, a global synthesis recently pinpointed inconsistencies in the effects of seminatural habitats on pest control (9), suggesting that other aspects of landscape heterogeneity were probably involved. The present results reveal that habitat types, and therefore their quality, have unforeseen impacts on the magnitude and direction of landscape-scale effects on pest control. Beneficial effects of meadows can be attributed to the fact that they are largely undisturbed habitats, without soil tillage or pesticide applications, providing more stable environments than arable crops or hay for natural enemy communities (23, 26). The increased magnitude of such beneficial effects with age of meadows further supports such interpretation. The temporal stability of meadows combined with high plant diversity has documented beneficial effects on multitrophic biodiversity (26, 29–31). Our results demonstrate that these beneficial effects trickle down to ecosystem services in surrounding crops suggesting that meadows behaved as sources of natural enemies that probably spillover into adjacent crop fields, ensuring pest control services. While we did not examine natural enemy communities sheltered in meadows, several studies demonstrate that natural enemies, such as spiders, lacewings, or syrphids, do spillover from seminatural habitats to crops and are involved in top-down control of pests (31–34).

The beneficial effects of meadows on pest control may also derive from direct bottom-up effects on pest populations as observed here for canopy insect pest in oilseed rape (12). Maintaining such habitats in an agricultural landscape might contribute to limit pest populations by diluting resources for pests independently of the control delivered by natural enemies (20, 35). Moreover, despite positive effects of meadows on predation rates of various pests,

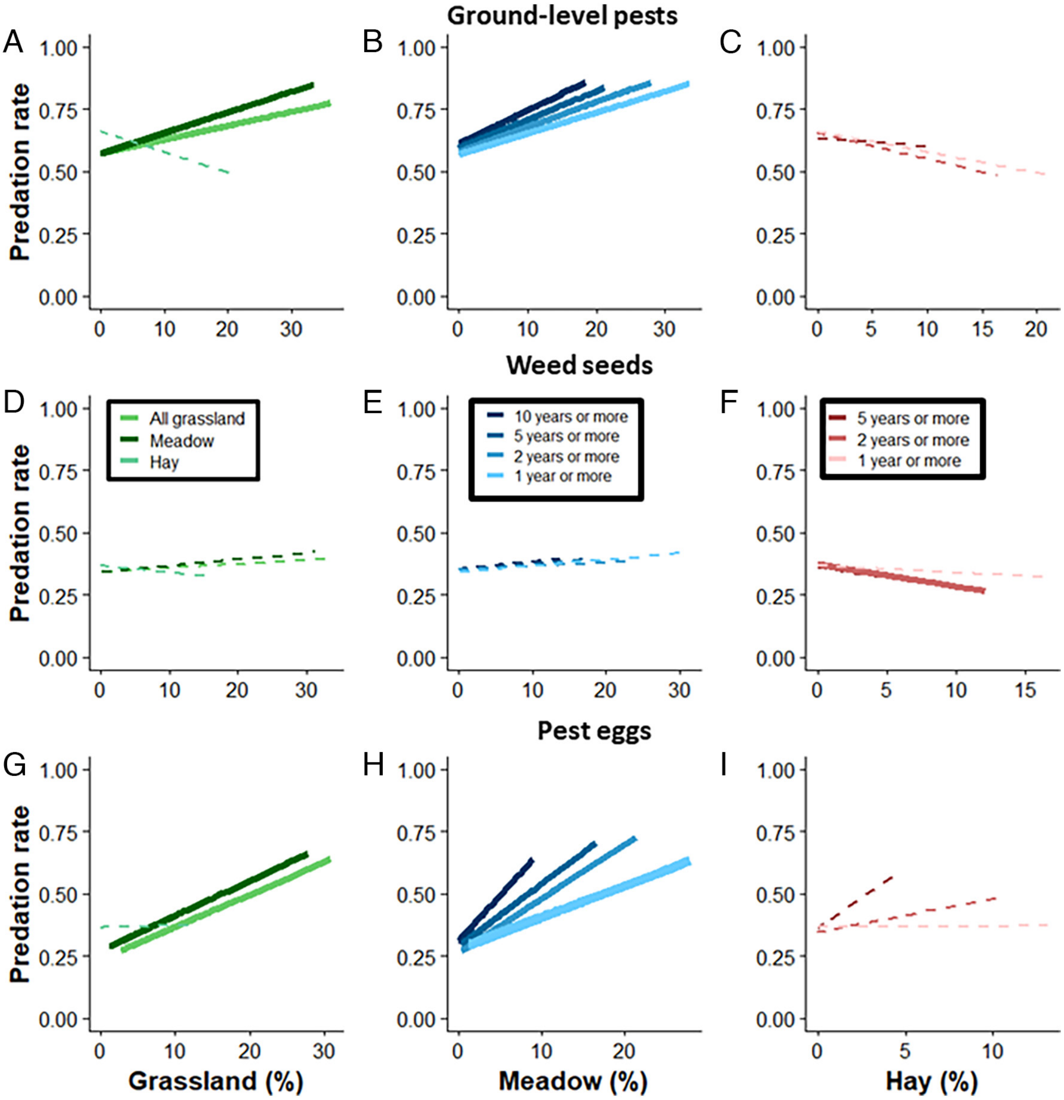

Fig. 3. Effects of grassland (left column), age of meadows (median column), and age of hay (right column) on predation rate of (*A*–*C*) ground-level pests, (*D*–*F*) weed seeds, and (*G*–*I*) pest eggs. On the left column, the model predictions are shown for either all grasslands (medium green), or only meadows (dark green) with hay being shifted to the crop category, or only hay (blue green) with meadows being excluded from the model (*Materials and Methods*). For the median and right column, grasslands are split into meadow and hay, with color intensified with age (color according to meadow/hay age from blue green for the most recent meadow to dark blue for the oldest meadow and light brown for the most recent hay to dark grown for oldest hay). The model includes either all meadows/hay (1 y or more), meadows/hay aged 2 y or more, meadows/hay aged of 5 y or more, or meadows aged of 10 y or more (there was no hay of 10 y or more). Lines represent the relationships as predicted by linear models over all crop types. Solid lines represent significant relationship, and nonsignificant relationships are dashed.

higher predation rates did not always lead to lower pest abundances in the fields (e.g., in maize, *SI Appendix*, Fig. S6). In such cases, other processes, such as intraguild predation between predators or higher benefit of meadows on pest populations than on natural enemies, might have affected the beneficial effects of meadows among natural enemies (36, 37).

While several studies recently claimed that crop diversity can compensate for, or even magnify, the effects of seminatural habitats on biodiversity and associated functions (15, 22, 38), the present results do not support this suggestion, despite extremely high sampling effort across multiple crops and years. Rather, seminatural habitats and crop diversity appear as complementary aspects of landscape heterogeneity that are both needed to limit insect pests and weeds in agricultural landscapes. We also observed that the beneficial effects of crop diversity on weed control were mediated by a strong top-down control of weed seeds by their natural enemies (38, 39). Suitable candidates for weed seed control in arable crops are carabid beetles (38), which feed on many weed seed species (40), are known to contribute to seed bank regulation (41) and respond positively to crop heterogeneity (42, 43). Although we cannot rule out that crop rotation (44) may have contributed to the crop diversity effect detected in our analyses, we are confident that weed seed control delivered by natural enemies contributed to the observed pattern given the correlation found between seed predation rate and weed abundance in this study as in others studies (41, 45). Overall, our results suggest that the amount of long-term grasslands and crop diversity affect two distinct trophic networks, respectively, those of insect pests and of weeds, and consequently, that pest and weed control services are mediated by different taxa. Spiders that are sheltered in meadows are one of the main groups of natural enemies of insect pests (29), while carabids known to regulate weeds found in arable land used a wide range of crops and are less dependent on seminatural habitats for their life cycle (42).

However, four limitations of our study warrant further analyses. First, the range of variation of crop diversity, which ranged from

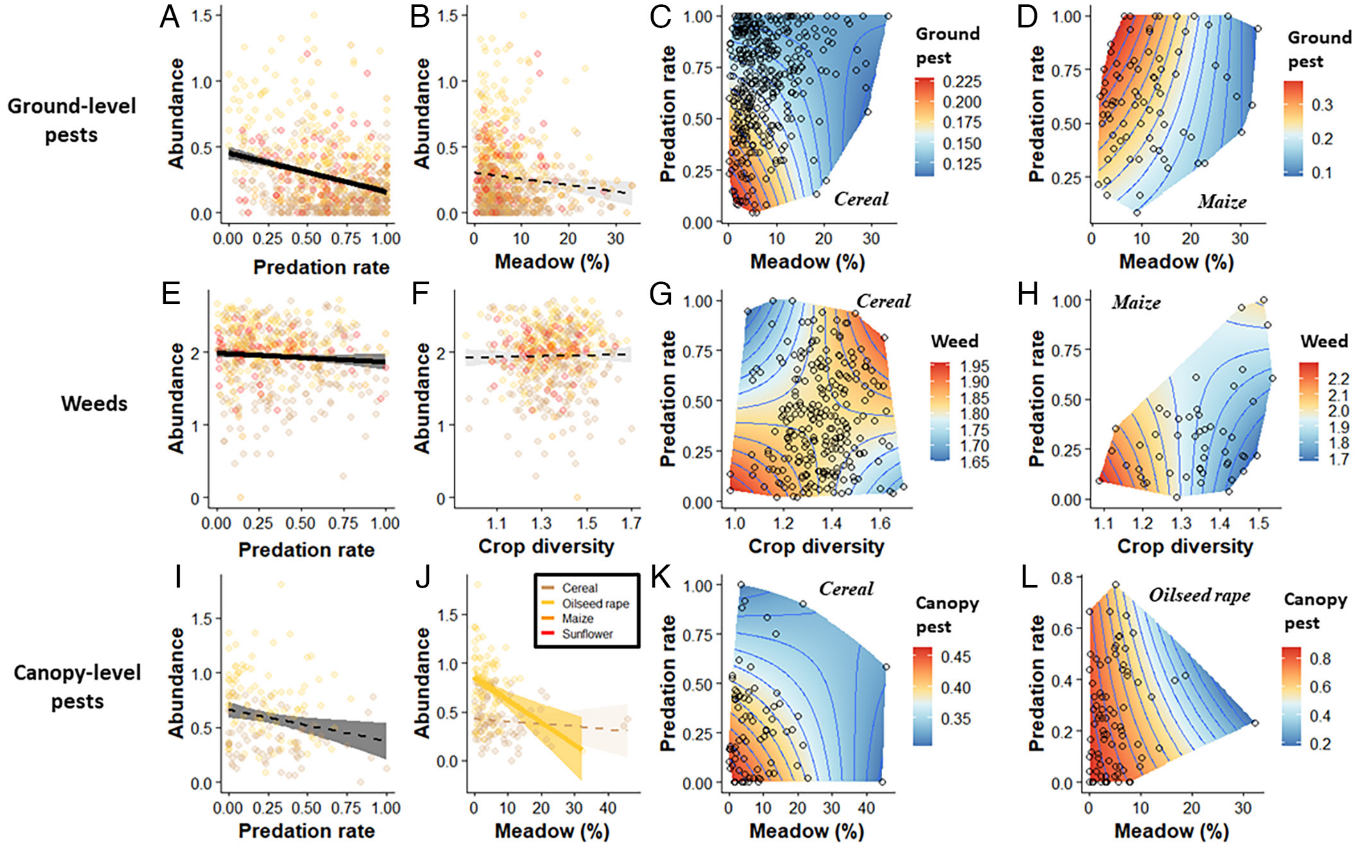

Fig. 4. Effects of predation rate (left column) or amount of meadow in buffer or crop diversity (second left column) on ground-level pest (*A* and *B*), weeds (*C* and *D*), and canopy-level pest (*E* and *F*) abundances. The two right columns show the model results with simple and interactive effects (predation rate and amount of meadows) for cereal and maize crop for ground-level pest (*G* and *H*) and weeds (*I* and *J*) or for cereal and oilseed rape for canopy-level pest (*K* and *L*). See model specifications in *Materials and Methods*. Black lines represent the relationship over the four crop types aggregated; color lines represent the relationship between predation rate and landscape variables per crop type (brown for cereal, yellow for oilseed rape, orange for maize, and red for sunflower) when crop type significantly interacts with % Meadows. Solid lines show significant relationships, and nonsignificant relationships are dashed. For presenting the results of the interactive model, heat maps were used, with color range (from blue to red) accounting for low to high abundance. The color range is specific to each model. All abundances are log(x+abs(min)+1) transformed.

three to seven crops (in the 1 km buffer, which is consistent with the range of variation found in European farms) in the present study might have limited our ability to detect crop diversity effects that may emerge at higher levels of crop diversification as observed in southern European countries (46). Second, crop diversity was calculated considering crop taxonomy while a better characterization of crop diversity based on phylogenetic distances or crop traits (e.g., sowing date, plant height, or nitrogen amount: see ref. 44) may help to understand more thoroughly the effect of crop diversity on pest and weed control services. Third, while we dedicated a major effort in analyzing landscape-scale compositional effects on pest control services, we did not consider interactions with local field management practices (e.g., soil tillage, pesticide use) that can act as local filters potentially modulating landscape scale effects (47, 48). Finally, our study mainly focused on the effects of landscape composition, ignoring those of landscape configuration such as field size, which are notably larger in other parts of the world (49), or edge density (15). We may assume a higher magnitude of natural pest control in landscape with high edge density because of greater connectivity between the elements of the landscape mosaic (50). This may lead to a higher effect of meadows and crop diversity, and further studies should account for this potential effect.

Implication for Farmland Landscape Management. The present study shows that combining old long-term grasslands meadows and crop diversity increases both insect pest and weed control in an agricultural landscape. Importantly, our results demonstrate that replacing long-term meadows by short-term meadows (such as hay, in our study) is not a viable option from an ecosystem-services perspective, because hay does not contribute to pest control services comparably to meadows. These findings are critically important in regard to agricultural policies of most industrialized countries (e.g., past and future European common agricultural policy) which has invariably advised farmers to increase crop diversity at the expense of long-term grasslands which are weakly protected (24) and globally highly degraded (25). In addition to pest control, meadows have other benefits as they support many ecosystem services such as biodiversity conservation, crop pollination, or carbon sequestration, underlying strong synergies between grassland conservation and sustainability of food production systems (51). Socioeconomical assessment of such nature-based solutions benefitting farmers and society is now urgently needed if we are to design multifunctional agricultural landscapes that better reconcile food production with biodiversity conservation.

Materials and Methods

Study Area and Field Selection. The study was conducted between 2013 and 2019 in the Long Term Social-Ecological Research site "Zone Atelier Plaine & Val de Sèvre" (ZAPVS), an agricultural landscape located in central western France (52), in the Nouvelle Aquitaine Region (46.23°N, 0.41°W). The ZAPVS area is 435 km^2 and includes c. 450 farms. Meadows and hay fields (alfalfa and clover crops) represent, respectively, 7.1% and 2.2% of the ZAPVS, whereas cereals, mainly winter wheat, are the dominant crop (37.1% cover). The other main crops comprise oilseed rape (7.1%), sunflower (7.4%), and maize (8.9%). Forests cover about 13.7% of the ZAPVS. The remaining area is composed of other crops, such as pea, linseed, or ryegrass, and urbanized surfaces.

Surveys were conducted in farmers' fields. Each year, we randomly selected 40 to 60 squares of 1 km² area in the ZAPVS distributed along three gradients of landscape features: woody habitats (hedges and forest fragments), grasslands (meadow and hay), and crop diversity estimated with the Shannon diversity index (52). We used a moving window to select the squares (53) and create statistically independent gradients. Within each square, we selected one field of cereal, oilseed rape, maize or sunflower, and alfalfa or meadow when they were present (resulting in three to four fields per window). A total of 974 fields were selected, comprising 164, 234, 138, 144, 102, 111, and 81 from 2013 to 2019, respectively. See *SI Appendix*, Fig. S8 for partitioning of the crop fields in 2015 and the associated sampling method described below. All selected fields were conducted under conventional farming practices management. Field size varied from 0.17 to 35.18 ha (mean: 5.74 ha).

Estimation of Predation Rates of Pests and Weeds. We used sentinel cards to estimate predation rates of different prey types by their natural enemies (54). We used three pest types as prey: aphids (*Acyrthosiphon pisum* 55), weed seeds (*Viola arvensis* 56), and lepidopteran eggs (*Ephestia kuehniella* 28). Sentinel cards were positioned either on the ground or in the crop canopy to differentiate between predation rates of ground-dwelling and canopy-dwelling insects. We estimated ground-level predation rates in 963 fields (all crops surveyed) from 2013 to 2019 and canopy-level predation in 165 fields from 2014 to 2018 [only in oilseed rape and cereal as a significant part of pest control services in those crops are assumed to take place in the canopy (57, 58)] We estimated weed seed predation rates from 2014 to 2019 in 671 fields (all crops surveyed) and egg sentinel cards were used to insect egg predation rates from 2014 to 2018 in 167 fields (only in oilseed rape and cereal). Details on the distribution of fields per crop and prey types are given in *SI Appendix*, Table S5. On each card, three aphids (*A. pisum*) or ten weed seeds (*V. arvensis*) were glued (organic glue Aero'Colle, Cléopâtre) on the rough side of 5 cm × 6 cm sandpaper cards (28, 54). Aphid cards were deployed in the field for 24 h while seeds cards were collected after 4 d. Because their size prevented precise counting, eggs were glued within a circle of 1 cm diameter and set during four days in crops, and the number of cards entirely or partially without eggs at the end of the 4 d was counted (*SI Appendix*, Fig. S8). Aphids, weeds, and eggs were purchased from Monster-Souris (Nantes, France), Herbiseed (Reading, United Kingdom), and Bioline (Paris, France), respectively. Cards were frozen at −20 °C for 24 h before the experiment to avoid an attractant or deterrent effect on predators from glue evaporation (54).

In each field, we selected two parallel transects of length 21 m and separated by at least 10 m, to ensure independence between transects, and at least c. 30 m from the field edge (*SI Appendix*, Fig. S8). Sentinel cards were placed in cereal on average 143.49 Julian days (±25.15 SD), oilseed rape 128.65 (±26.84), maize 190.12 (±19.53), sunflower 187.44 (±17.64), hay 159.67 (±33.89), and meadow 161.96 (±33.35). On each transect, four cards of each prey type (i.e., eight for each prey type per field) were set, each 7 m apart (*SI Appendix*, Fig. S8). Seed and ground-level aphid cards were placed on the ground in the same position and spaced 40 cm apart (*SI Appendix*, Fig. S8). Canopy-level aphid and egg cards were placed at the same position in the crop canopy secured by pins to crop plants (*SI Appendix*, Fig. S8). Cards located on the ground were folded in half to provide a tent-like shelter and limit deterioration of the glued prey caused by climatic factors (e.g., rain, sun, and wind; *SI Appendix*, Fig. S8). Each field was sampled twice to account for temporal variation of predation rates throughout the season (55), except in 2018 and 2019 with the aim to reduce the workload. Sampling bouts were spaced at least of 44.05 (±16.02 SD) days. Predation rates were averaged between the two sessions for 2013 to 2017 to account for variation in sampling effort among years. Mean predation rates per crop and prey type are provided in *SI Appendix*, Table S5.

Insect Pest and Weed Sampling. In the same fields, we estimated insect pest abundance using two complementary methods, i.e., pan traps and pitfall traps. These are two common methods for evaluating pest abundance (59, 60). Pitfall traps were placed at ground level to estimate ground-level insect pest abundance (61), whereas pan traps were placed at crop-canopy height to estimate canopy-level insect pest abundance (12). Both trap types were placed in winter cereal and oilseed rape fields during oilseed rape flowering, and in maize and sunflower fields during sunflower flowering. The date for setting the traps differed by 4.82 (±11.53 SD) days from setting the sentinel prey cards.

In 2013 and 2014, five pitfall traps were installed per field: two within the first 5 m of the field, one at 25 m, and two at 50 m into the field from the edge. In 2015 onward, the pitfall trap at 25 m was removed to reduce the workload (*SI Appendix*, Fig. S8). Pitfall sampling was repeated twice a year from 2013 to 2017, whereas only one sampling was performed in 2018 and 2019. In addition, in each field, six pan traps were set once during the cropping season, at the field edge and at 50 m from the edge, from 2013 to 2015 (*SI Appendix*, Fig. S8). Pan traps comprised bowls either white or sprayed yellow or blue to account for pest color preferences (62). From 2016, only three pan traps (one of each color) were set at the field center, twice per season (see ref. 11). Pitfall and pan traps were filled with water, salt, and organic soap and left in the field for 4 d. Pest abundance was determined by a professional entomologist. In each field, we computed pest abundance per method as the sum of the five most common pest groups by pan or pitfall, i.e., flea beetles, weevils, aphids, leafhoppers, and pollen beetles. The pest abundance was averaged per color at the same position (only for pan traps), then per position, then per field, and finally between the two sessions. Thus, only one value per field and per group was available.

Weed abundance was sampled in twenty 1-m^2 quadrats in each field in the field core. The 20 quadrats were spaced 10 m apart and placed along two transects separated by 40 m and orthogonal to crop rows (see ref. 52). Each 1-m^2 plot was georeferenced and divided into four 0.5 m × 0.5 m subplots (hence, 80 subplots per field) within which weed absence/presence per species was recorded (63). We estimated weed species abundance by the sum of occurrence of each plant species per field (from 0 to 80). Weed abundance per field was assessed by summing weed species abundance for all species present in the field. Weed and pest abundances per crop type are provided in *SI Appendix*, Table S5.

Landscape Metrics. All landscape metrics were calculated at five different radii ranging from 500 m to 2,000 m from the centroid of sampled fields (9, 39). We selected three landscape metrics: Shannon diversity of crop types as well as the amount of grassland and wood habitats (including forest and hedgerow). Grasslands included both meadows and hay. The two types of grasslands were separated based on plant composition (leguminous fields: alfalfa which accounted for >95% of cases and clover were automatically classified as hay). Meadows included only herbaceous or mixed (herbaceous with some legumes) grasslands. Both permanent meadows and hay were mainly mowed. Using our historical GIS database (land use is mapped annually at the field level, see ref. 42), we quantified ages of meadow and hay to test the effects of grassland age on pest or weed control. Meadows were aged on average in this study, 6.15 (±5.52 SD) years old, whereas hays were 2.06 (±1.28 SD) years old. Shannon crop diversity was calculated using seven crop categories: cereal, oilseed rape, maize, sunflower, pea, ryegrass, and "other crops" (which comprised all other crop types, representing less than 1.5% of the total area in the 2,000 m radius buffer). Pairwise Pearson correlation coefficients between field size, woody habitats, meadow, hay, and Shannon crop diversity were $|r| \leq 0.03$. See *SI Appendix*, Fig. S9 for all correlations between landscape metrics.

Statistical Analyses. First, we used four linear models, one for each prey type (ground-level and crop-level insect pests, weed seeds, and pest eggs) to investigate how seminatural habitats and crop diversity at a given spatial extent affected predation rates. The models included predation rate as the response variable, and Shannon crop diversity, amount of grasslands undifferentiated, and amount of woody habitats as explanatory variables. We also included two-way interactions between the explanatory variables. Because crop identity of the sampled field may affect natural enemy communities, it was included in the model as well as its interaction with each landscape variable. To take into account the variation of field size between focal fields, field size was also included in the models. We report full model estimates rather than using a model-selection approach because our aim here was to test specific hypotheses and not fitting the most parsimonious models. In addition, landscape metrics used as explanatory variables in the models were not correlated to each other by design (see above), allowing straightforward comparisons as well as the use of interactions between explanatory variables. Models for each prey were fitted using the three landscape variables calculated in each of the explored buffer radius size, i.e., one model per buffer size with all landscape features calculated at this given buffer size. Relevant spatial scales for landscape variables among those explored were selected based on the Akaike information criterion for each model and the model with the lowest AIC score was retained as the best model (64). Respectively, for ground-level insect pest, canopy-level insect pest, weed seed, and pest egg predation rates, the models with the lowest AIC values were for buffer sizes of 1,250 m, 750 m, 1,500 m, and 2,000 m (see *SI Appendix*, Fig. S10 for model comparisons).

Second, to investigate the effect of grassland type (hay or meadows), we fitted two alternative models to compare with the previous models, retaining the same spatial scales as for each prey type. The first model considered hay as a crop, hence increasing crop diversity in the landscape by including hay in the calculation of the Shannon crop diversity index. The grassland category therefore only included meadows. The alternative model considered hay as a subsidiary of meadows. In this model, only the amount of hay was considered as grassland, and meadows were not included at all. These two models were then compared with the model including meadows and hay in the grassland category, based on the AIC and R^2 values. An ANOVA was performed to estimate the variance explained by (i.e., the relative contribution of) meadow, hay, and crop diversity on different prey predation rates. A type II ANOVA was used because the sample size was unbalanced between crops (*SI Appendix*, Table S5 and ref. 65). In order to test the effect of age of meadow and hay on predation rates, models with only the amount of meadows or only the amount of hay in the landscape were ran again but using different subsets of meadows or hay, i.e., all meadows or hay irrespective of age, of more than 2 y old, of more than 5 y old, and finally, of more than 10 y old (only for meadow as hay of more than 10 y old did not exist in our study site). The slopes of effect of meadows, according to the age considered, on predation rates were compared between the models, with an increase in slope being interpreted as a stronger effect of meadow or hay with age.

Third, we investigated how predation rate of the given prey affected the abundances of weed seeds, and ground-level or canopy-level insect pests (the lepidopteran, *E. kuehniella* was not found in crop fields so no comparison could be made). For each of the three pest types, their abundance was the response variable and we considered the predation rates of either weed seeds, ground-level or canopy-level insect pests in addition of field size as explanatory variables. Interactions between crop identity and each landscape variable or the predation rate of each prey type were also included in additional models. For spatial scale of influence of landscape variables, we used the same buffer size estimated for predation rate, i.e., 1,250 m for ground-level insect pests, 750 m for canopy-level insect pests, and 1,500 m for weed abundance. We also ran models to investigate the effects of seminatural habitats (meadows and woody habitats) as well as crop diversity on pest/weed abundance, as well as more general models including the interactive term between meadows and predation rate.

All analyses were performed with R 3.6.2 (66) Data was available here (https://zenodo.org/records/10018232) (67). Because predation rates, pest and weed abundances showed skewed distributions with a year-nested structure, we ran a preliminary analysis to identify the best type of models, error distributions, and data transformation for the analysis. We compared four modeling options (see *SI Appendix*, *Appendix A* for details). We found that a linear model in which the dependent variable was centered and scaled and then log(x+abs(min)+1) satisfied the linear model assumptions (residuals distribution and homoscedasticity). Such model was the best option for modeling insects' response variables, whether dealing with predation rates or abundances. However, for plants (i.e., weed abundance and seed predation rate), we found that a generalized linear mixed model (GLMM) with year as a random variable and a Tweedie distribution performed better than other options. In addition, to reduce potential type I errors associated with multiple testing while minimizing type II errors, we controlled for false discovery rates using a Benjamini–Hochberg procedure with a threshold of 0.1 (68) to balance between error type I and error type II. We also checked for spatial autocorrelation in the residuals of the best models using Moran's index for predation rate and pest abundance models. No spatial correlation was observed for the models (all $P > 0.12$) except for the model using weed abundance as response variable (Moran $I = 0.077$, $P = 0.028$). However, taking into account the spatial autocorrelation for weed abundance did not modify any of the results (*SI Appendix*, Table S6).

The R packages "stats" was used for fitting linear models and to perform AIC-based model selection (for spatial scale selection only), "spdep" for calculation of Moran's index, "glmmTMB" for LMM and GLMM with Tweedie distribution, and "car" for variance analysis.

Data, Materials, and Software Availability. Original data and codes data have been deposited in Zenodo repository (https://zenodo.org/records/10018232) (67).

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