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Semi-Natural Habitats Buffer the Effects of Crop Diversification on Arthropod Pest Control Services in Agricultural Landscapes

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ABSTRACT

Crop diversification is a promising strategy to strengthen pest control services in agricultural landscapes. Diversifying crops may limit pests through host crop dilution or by enhancing top-down control by their enemies. However, crop diversification may also benefit generalist pests through higher resource continuity. Using a large-scale dataset encompassing 742 landscapes across 13 countries, we assessed the impact of landscape-scale crop diversity on the abundance of natural enemies, the potential for biological control, and insect pest abundance. Crop diversification did not increase the overall abundance of natural enemies or the potential for biological pest control. Instead, crop diversity primarily favoured the abundance of specialist natural enemies and pests in highly simplified landscapes, an effect that was reduced in landscapes with high proportions of semi-natural habitats. Lastly, low proportions of host crops in the landscape were associated with higher abundances of natural enemies. Taken together, our results indicate that crop diversification is not a 'one size fits all' strategy to control agricultural pests, and that other landscape characteristics, such as high amounts of semi-natural habitats, must be considered to enhance biological pest control services.

1 | Introduction

Crop pests are a major threat to global food security (Oerke 2006; Savary et al. 2019). It is estimated that pests and pathogens reduce crop yield by an average of 20%–30%, resulting in substantial economic losses and high levels of pesticide use (Savary et al. 2019). While pesticides are currently the most common method for managing pests in agriculture, they also threaten biodiversity, human health and agricultural sustainability (Kim et al. 2017; Tang et al. 2021).

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As pest pressure is expected to intensify due to climate change (Deutsch et al. 2018), alternative pest management strategies are urgently needed to promote resilient and sustainable agricultural systems.

Harnessing biological pest control services provided by natural enemies of crop pests is a promising option for reducing pesticide use (Martin et al. 2019; Rusch et al. 2016). Many natural enemy species that control crop pests depend on key resources (e.g., pollen, nectar and overwintering sites) provided by semi-natural habitats, such as forests or permanent grasslands (Perrot et al. 2021). Conserving or restoring semi-natural habitats in agricultural landscapes may therefore enhance biological pest control services and limit the need for pesticide use (Etienne et al. 2023; Gagic et al. 2021; Meehan et al. 2011). However, several syntheses have revealed significant variability in the effects of semi-natural habitats on pest control services (Karp et al. 2018; Martin et al. 2019), suggesting that other aspects of agricultural landscapes, such as the spatial arrangement of habitats or specific farming practices, may also be important for shaping the relationships between pest control and habitat characteristics (Martin et al. 2019; Muneret et al. 2018). Moreover, enhancing semi-natural habitats around farms usually requires taking land out of production. This relies on collective and coordinated action at a larger spatial scale, which complicates efforts to diversify agricultural landscapes (Kleijn et al. 2019).

Planting multiple crop species across space (i.e., from the field to the landscape) and time (i.e., at the same time during the cropping season or over time to increase resource continuity) has been proposed as a viable additional or alternative strategy for limiting pest populations (Perrot et al. 2023; Vialatte et al. 2025). Farmers may be more willing to adopt crop diversification than to enlarge the amounts of semi-natural habitats on their farms, because the former might limit pest populations without reducing productive land area (Larsen et al. 2021; Martin et al. 2016; Sirami et al. 2019). Additionally, crop diversification has been demonstrated to buffer the impacts of climate change and increase the stability of food production (Renard and Tilman 2019; Renard et al. 2023).

Diversifying crops at the landscape scale may limit pest abundance via two complementary mechanisms. First, landscapes with more crop diversity may host larger natural enemy populations because of enhanced food resource complementarity, leading to better top-down control of pests (i.e., the natural enemy hypothesis; Root 1973). Second, landscapes with a high crop diversity may limit specialist pest populations by reducing the amounts of host crop in the landscape (host-crop dilution) and through physico-chemical barrier effects (i.e., the resource concentration hypothesis; Root 1973; O'Rourke and Petersen 2017; Rusch et al. 2013; Delaune et al. 2021). The proportion of pest host crops in the landscape could thus mediate the effects of crop diversity on pest populations (Kheirodin et al. 2020). However, crop diversification may also have positive bottom-up effects on pests by enhancing resource continuity across space and time for generalist pests (Li et al. 2020). Finally, the net effects of crop diversification on biological pest control may depend on the functional groups involved (Martin et al. 2019). Traits such as diet breadth, mobility and life-cycle complexity may ultimately affect the response of pests and their natural enemies to crop diversification (Tamburini et al. 2020). As a result, the effects of crop diversification on biological pest control services remain largely unclear, with the few existing studies reporting inconsistent findings (Aguilera et al. 2020; Priyadarshana et al. 2024; Redlich et al. 2018; Thomine et al. 2023).

Idiosyncratic effects of crop diversity on biological pest control services could further result from interactions with several aspects related to landscape structure, such as landscape composition or configuration (Martin et al. 2019). The proportion of semi-natural habitats in the landscape strongly shapes the natural enemy species pool and the spatiotemporal distribution of resources for arthropods (Martin et al. 2019; Rusch et al. 2016). Natural enemies and pests may need to move between crop and semi-natural habitats to exploit resources in both habitat types (Boetzl et al. 2024; Rand et al. 2006). Thus, the proportion of semi-natural habitats may modulate the effects of crop diversification on natural enemies and pest abundances, depending on processes of complementation or supplementation of resources. If the spatiotemporal distribution of organisms depends on complementary resources between crop and non-crop habitats (i.e., resources are non-substitutable), then high proportions of semi-natural habitats would be expected to magnify the positive effects of crop diversification on pests or natural enemies, whereas low proportions of semi-natural habitats would cancel these effects. Conversely, if spatiotemporal distributions of organisms are mainly driven by supplementation of resources between crop and non-crop habitats (i.e., resources are substitutable), then no synergistic effects between the proportions of semi-natural habitats and crop diversification would be expected. Very few studies have tested these hypotheses and explored these potential mechanisms (Perrot et al. 2023; Thomine et al. 2023), although producing such knowledge could greatly improve the design of pest-suppressive agricultural landscapes.

In this study, we used a large-scale dataset of 27 studies encompassing 742 fields across 13 countries to assess how crop diversity and the proportion of host crops in the landscape affect pest control services, and how the proportion of semi-natural habitats modulates both relationships. We evaluated biological pest control services using three complementary metrics: natural enemy abundance, biological pest control potential (i.e., pest parasitism rates or predation rates), and pest abundance. We hypothesized that increasing crop diversity and the proportion of semi-natural habitats has (H1) synergistic positive effects on natural enemy abundance and biological pest control due to resource complementarity (Schellhorn et al. 2015; Sirami et al. 2019). We further hypothesized that increasing crop diversity has negative effects on the abundance of specialist pests, mediated by (H2) enhanced top-down control (Redlich et al. 2018) and/or (H3) host-crop dilution (Delaune et al. 2021; Schneider et al. 2015). We therefore expected that increasing crop diversity would lead to higher predation and parasitism rates (H2), and that decreasing the proportion of a pest's host crop in the landscape would reduce pest abundance by limiting access to key resources, with no apparent effect on natural enemy communities (H3). Finally, we expected different responses of functional groups to crop diversification depending on their diet breadth, with (H4) an expected positive effect of crop diversification for generalist natural enemies and pests due to enhanced resource continuity in space and time, but a negative effect on specialists due to dilution processes.

2 | Materials and Methods

2.1 | Data Collection

To test the effects of crop diversification, the proportion of host crops and the proportion of semi-natural habitats on natural enemies, pests and pest control services, we collated datasets from studies investigating landscape effects on at least one of three metrics for pest control: abundance of natural enemies (Natural enemies), pest parasitism or predation rates (Biological pest control potential) or abundance of pests (Pests). Natural enemy abundance and biological pest control reflected the top-down control potential, while pest abundance reflected top-down and bottom-up forces on pest populations. We took advantage of an existing worldwide database of pest control in agricultural landscapes that included studies with at least five distinct sampling locations across a gradient of landscape composition (Karp et al. 2018) that we complemented with other relevant published datasets provided by our consortium of co-authors (Tables S1 and S3). As the proportion of pests' host crop was quantified using the proportion of a study's focal crop as a proxy (see section «Landscape composition metrics»), we refer to pests' host crop proportion as 'focal crop' hereafter. We excluded studies that lacked precise land-use data or landscape-scale gradients, for which we could not analyse landscape composition metrics related to crop diversification, focal crop area and proportion of semi-natural habitats. The final dataset included 27 studies, conducted between 2001 and 2020, encompassing 742 field sites across 13 countries in which one or several metrics of biological pest control were reported (Table S1). Most of the selected studies were located in Europe (Figure S1), but there was at least some representation from Asia, the Americas and Australia (none in Africa).

2.2 | Natural Pest Control Metrics

Overall, nineteen studies measured the abundance of natural enemies across a total of 481 field sites, 17 studies measured biological control potential across a total of 410 field sites, and 18 studies measured pest abundance across a total of 509 field sites. Eight studies had simultaneous measures of all three types of metrics, while four, two and two studies measured only natural enemy abundance, biological control potential or pest abundance, respectively (Figure S2).

Our dataset encompassed 23 different arthropod taxa identified as potential natural enemies of crop pests by the authors of the primary studies. Natural enemies were mainly sampled using pitfall traps ($n = 9$ studies), visual counting ($n = 8$) and sweep netting ($n = 4$). Other methods involved sticky traps, beat-sheets, vacuum sampling, malaise traps and/or pan traps. Each study reported data for an average of 4.7 (min–max: 1–11) natural enemy families. Araneae and Carabidae were the most studied natural enemy taxa (sampled in 11 out of 27 studies), followed by Coccinellidae ($n = 10$), Syrphidae ($n = 9$), Parasitoids ($n = 9$) and Chrysopidae ($n = 7$). Regarding pest abundances, the database covered a total of 24 families of pests (32 pests were identified at the species level) with an average of 2.8 (min–max: 1–12) pest families per study. Pest abundance was mostly assessed by visual counting ($n = 13$) and sweep netting ($n = 3$), with the other studies using sticky traps, beat-sheets, or vacuum sampling. The most studied pest family was Aphididae ($n = 12$), followed by Chrysomelidae ($n = 8$). Finally, the biological control studies estimated predation and parasitism rates from sentinel cards ($n = 4$ and 12, respectively). Only 4 studies using sentinel cards investigated pest parasitism and predation simultaneously. For predator exclusion experiments, predation rates were calculated following Gardiner et al. (2009). Briefly, the relative pest suppression per field site was expressed as the change in pest numbers between open versus caged plants, as a proportion of pest abundance in the absence of predators.

We analysed the abundance of natural enemies and pests and the biological pest control potential at the field scale. To account for multiple measurements per field site and per year, we summed the total abundance of natural enemies or pests per field, year and sampling method, and divided this abundance by the sampling effort that can vary within the same site. For a given field, a given year and a given sampling method, sampling effort corresponds to the total number of replicates (in space and/or time). For biological control measures, which were expressed as proportions, we averaged measurements conducted over different sampling occasions and locations within each field and year.

We compared the effects of crop diversity for generalist and specialist natural enemies and pests. To do so, we classified pest dietary specialization based on Poveda et al. (2025) and natural enemy dietary specialization based on Martin et al. (2019). Additional information was obtained through literature searches for taxa not covered by the previously mentioned studies. If a species group had a similar proportion of generalist and specialist species, then the diet was recorded as 'unknown'. Table S2 shows the assignment of diet breadth for the different species groups covered in our analysis.

2.3 | Landscape Composition Metrics

We calculated landscape composition metrics at a 500-m radius buffer around the centroid of the experimental study area. We selected this spatial extent as it is known to adequately explain landscape-scale effects on natural enemy or pest communities (Perrot et al. 2021), while allowing us to maximize the number of datasets that could be included in our analyses. Data from primary studies consisted of either shapefile data or attribute tables with the proportions of each land-use class in the landscape. All primary shapefile data (except for one study) were based on national land-cover datasets or on manually digitalized land-cover and were ground-truthed using intensive field surveys (Table S3). Landscape metrics were calculated with the 'sf' package in R (version 4.2.1). Using the habitat classification derived from the primary studies, we quantified, for each landscape, the proportion of semi-natural habitats (i.e., forests, hedgerows, fallows, field margins, woodlands, grasslands) and the proportion of each crop type separately to be able to compute crop diversity metrics (Table S1). We also quantified the proportion of the studied focal crop in each landscape.

For each primary study, we calculated two indices that characterize complementary facets of crop diversity: crop richness, calculated as the total number of different crop taxa (species or family) in the landscape, and the Shannon index of crop diversity (H'), which weighs each crop by the proportion of total cropland it occupies. If p_i is the proportion of total cropland dedicated to crop i and N is the total number of crop taxa (species of family), $H' = -\sum_{i=1}^{N}\left(p_i \ln\left[p_i\right]\right)$. If certain crops were described at the family level, while other crops of the same family were described at the species level, then we considered them as additional crop species. There were 76 crop types in the database (Table S4), with most studies describing crops at the species (87% of crop types, 66 species) or at the family level (6.5% of crop types, 5 families). When the crop species or family could not be identified (because of insufficient description of the crops or broad categories such as aromatic, vegetable, or legume), we classified these patches as undescribed crops (mean = 2.5%, min–max: 0%–57.1% in the 500 m buffer) across all original studies. To limit bias in crop diversity estimates, we excluded sites with more than 10% of undescribed crops (natural enemies = 56 sites, pests = 40 sites, biological control = 20 sites). We kept 'undescribed crops'' as a crop type in the analysis; that is, we considered it to be an additional category, species or family for the calculation of crop diversity metrics.

Overall, landscapes were composed on average of 4.8 crop species (min–max: 0–16), and the Shannon index of crop diversity was on average 1.0 (min–max: 0–2.3). The proportion of semi-natural habitats as well as focal crops varied from 0% to 100% (mean SNH% = 28.5% and mean focal crop % = 25.1%; Table S1). The 100% value of semi-natural habitats in the landscape came from one study using phytometers (Table S1). All correlations between the crop diversity metrics and the proportion of focal crop or the proportion of semi-natural habitats were weak (ranging from $r = -0.08$ to -0.22, Figure S3).

2.4 | Statistical Analyses

We standardized all pest control variables using z-scores (i.e., each response variable was centered and scaled within a study) to ensure comparability between studies. When the study sampled natural enemy or pest abundance by multiple sampling methods, measured different types of biological control (parasitism and predation) or considered different crop species, we standardized pest control variables within biological control type, sampling method, or crop species. Count data (i.e., natural enemy or pest abundance) were $\log(x+1)$-transformed before computing z-scores to meet model assumptions and normality of model residuals (Morrissey and Ruxton 2020). Because our goal was to investigate the effect of increasing crop diversification in any given agricultural landscape, and to avoid comparing absolute crop diversification values from very contrasting regions across the globe, we used z-score transformed data of landscape features within studies (Figure S4). Landscape metrics were also $\log(x+1)$-transformed before to linearize relationships with natural pest control proxies.

Using linear mixed models (LMMs), we evaluated the effects of crop diversification, the proportion of semi-natural habitats, and the proportion of the focal crop, as well as their interactions, on natural enemy abundance, biological pest control potential and pest abundance. The structure of the fitted models was as follows:

$$Y \sim \text{Crop diversity index} \times \%\,\text{Semi} - \text{natural habitats} + \%\,\text{Focal crop} \times \%\,\text{Semi} - \text{natural habitats} + (1|\ \text{Study ID}\_\text{Year})$$

For each response variable, we fitted and compared two models, with crop diversity index being either crop richness or Shannon index (due to correlation between the two metrics) computed at the crop taxonomic level considered (either species or family level). The model included the study ID_Year as a random effect (combining study_ID with year for 9 studies out of 27 that spanned multiple years) to account for non-independence in the response variables.

We further compared the effects of explanatory variables on generalists and specialists, as well as across different taxonomic groups. For that, we ran the same models as described above on subsets of the overall database for generalists and specialists, and for the taxonomic groups where we had at least seven datasets. For natural enemies, we considered the abundance of Araneae ($n = 11$), Carabidae ($n = 11$), Coccinellidae ($n = 10$), Syrphidae ($n = 9$), Parasitoids ($n = 9$) and Chrysopidae ($n = 7$) independently. For pest abundance, we considered the abundances of Aphididae ($n = 12$) and Chrysomelidae ($n = 8$) independently. In addition, we explored the variability of the effects of landscape characteristics on biological pest control potential by running separate models for parasitism rates ($n = 12$) and predation rates ($n = 4$).

We performed two sensitivity analysis on our models. First, we investigated whether the effect of crop diversity on pest control depended on the taxonomic level at which crop diversity was evaluated (Figure S5). To do so, we compared our models based on crop diversity estimated at the species level, with similar models using crop family diversity (i.e., crop species were regrouped by family to compute crop family richness and the Shannon index of crop family diversity). Second, we investigated the impact of removing sites with extreme values in terms of proportions of semi-natural habitats or proportions of focal crop. To do so, we compared the original models with models refitted on a dataset excluding sites with very high proportions of semi-natural habitats ($\geq 95\%$) and/or low proportions of focal crops ($\leq 5\%$) (Figure S6).

To account for differences in the number of sites between studies (for natural enemies: mean = 26.6 sites, min-max = 11–51; pest: mean = 28.7 sites, min-max = 8–68; biological control: mean = 24.4 sites, min-max = 7–61), we used the inverse of the number of sites per year and per study as weights in LMMs. In all models, residuals were visually checked to ensure normality and homoscedasticity. Collinearity between variables was assessed with the variance inflation factor (VIF) and none was found (all VIFs < 1.1). For each model, we used stepwise selection with a both direction (forward/backward) method based on AIC to remove non-informative interactions (ΔAIC < 2), allowing a direct interpretation of simple terms. All analyses were performed in R 4.2.1. using the 'nlme' package

for linear mixed models and 'stats' for Akaike's Information Criterion comparisons.

3 | Results

Our results indicate that crop diversification did not significantly enhance the overall abundance of natural enemies or the level of biological pest control. In contrast, the effect of crop diversification on pest abundance depended on the proportion of semi-natural habitats (Figures 1 and 2, Table S5). This interactive effect revealed that increasing crop diversity led to more abundant pest populations in landscapes with low proportions of semi-natural habitats, an effect that was less pronounced in more complex landscapes with relatively high proportions of semi-natural habitats (Figure 2, Table S5). No strong effect of the proportion of semi-natural habitats alone was detected on any pest control metrics, although

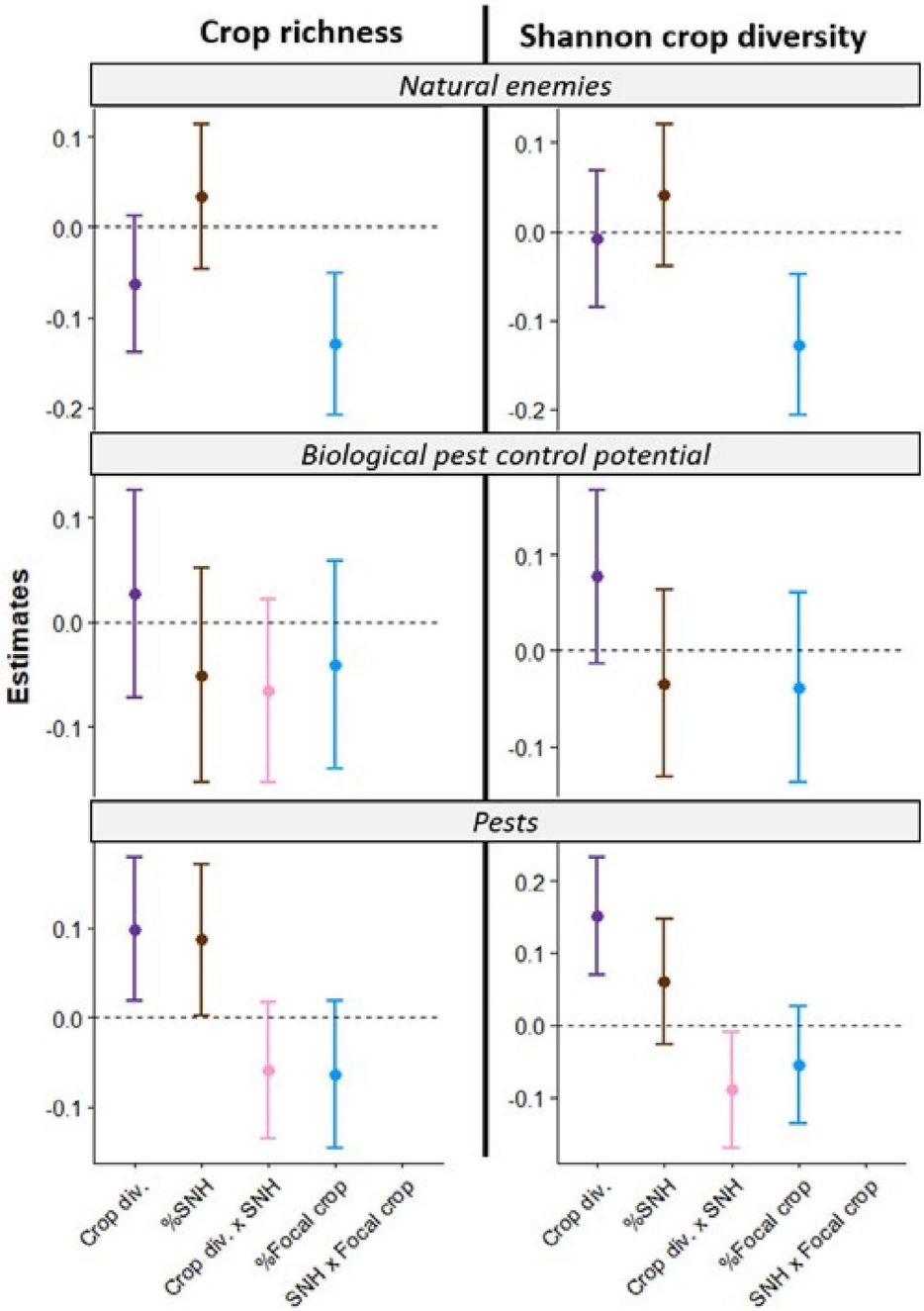

FIGURE 1 | Effects of crop species diversity, the proportion of semi-natural habitats and the proportion of the focal crop in the landscape on natural enemies, biological pest control potential and pest abundance. The figure shows estimates and 95% confidence intervals of the effects of crop species richness (left) or of the Shannon index of crop diversity (right), as well as the proportion of semi-natural habitats (%SNH), the interaction with crop diversity (Crop div. × SNH) and the proportion of studied focal crop in the landscape (%Focal crop) on three metrics of natural pest control: (1) the abundance of natural enemies (first row), (2) biological pest control potential (second row) and (3) pest abundances (third row). Estimates are based on linear mixed models after model selection. Natural enemies: $N = 19$ studies and 612 observations; Biological control: $N = 17$ and 445 observations; and Pests: $N = 18$ and 552 observations.

pest abundances tended to increase with the proportion of semi-natural habitats in the model including crop richness. We further found a significant negative effect of increasing the proportion of the study's focal crop in the landscape on the overall abundance of natural enemies (Figures 1 and 3, Table S5). We obtained similar results from models using either crop richness or the Shannon index of crop diversity as a metric of crop diversification, but the interactive effect of crop diversity and the proportion of semi-natural habitats on pest abundance was only significant with the Shannon index (Figure 1, Table S5). Model outputs were also similar when crop diversity was assessed at the family level (Figure S5) or when sites with extreme values were removed from the analysis (Figure S6).

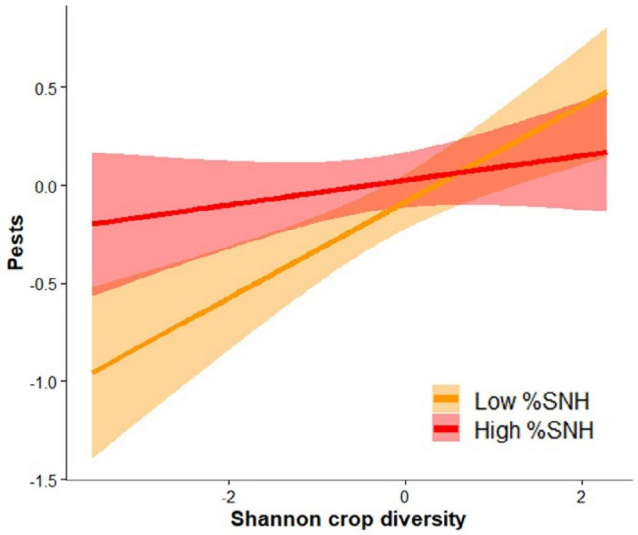

FIGURE 2 | Interactive effect between crop species diversity (Shannon index) and the proportion of semi-natural habitats on pest abundance. Lines are predictions of the linear mixed models based on standardized values (centered and scaled, see methods). Light colours represent relationships between crop diversity metrics and natural pest control metrics for low proportion of semi-natural habitats (−1SD), and dark colours represent the relationships for high proportion of semi-natural habitats (+1SD). Confidence bands are confidence intervals at 95%.

Diet breadth strongly modulated the responses of natural enemies and pests to crop diversification and the proportion of semi-natural habitats. While crop diversification had neutral to negative effects on the abundance of generalist natural enemies (Figure 4A), it increased the abundance of specialist natural enemies, but only in landscapes with low proportions of semi-natural habitats (Figure 4A, Table S6, Figure S7A). Crop diversity had positive effects on the abundance of both generalist and specialist pests, but the positive effect of crop diversity on the abundance of specialist pests was only observed in landscapes with low proportions of semi-natural habitats (Figure 4C, Table S6, Figure S7B). Increasing the proportion of the focal crop significantly reduced the abundance of generalist natural enemies while it had no effect on specialists (Figure 4A).

In addition, our analysis revealed substantial variation among taxonomic groups in their responses to crop diversity, the proportion of semi-natural habitats, and the proportion of focal crops in the landscape (Figure 5, Table S7). Among the natural enemy groups examined, only spiders (Araneae) showed a negative response to increasing crop diversity alone, while the abundance of all other groups remained unaffected (Figure 5A, Table S7). Ground beetles (Carabidae) were the only group that responded positively to the proportion of semi-natural habitats (Figure 5A, Table S7). Syrphidae were affected by the interaction between semi-natural habitats and crop diversity, indicating that crop diversity enhanced the abundance of Syrphidae only in landscapes with low proportions of semi-natural habitats, while it decreased their abundance in landscapes with high proportions of semi-natural habitats (Figure 5A, Figure S8, Table S7). The overall negative effect of an increasing proportion

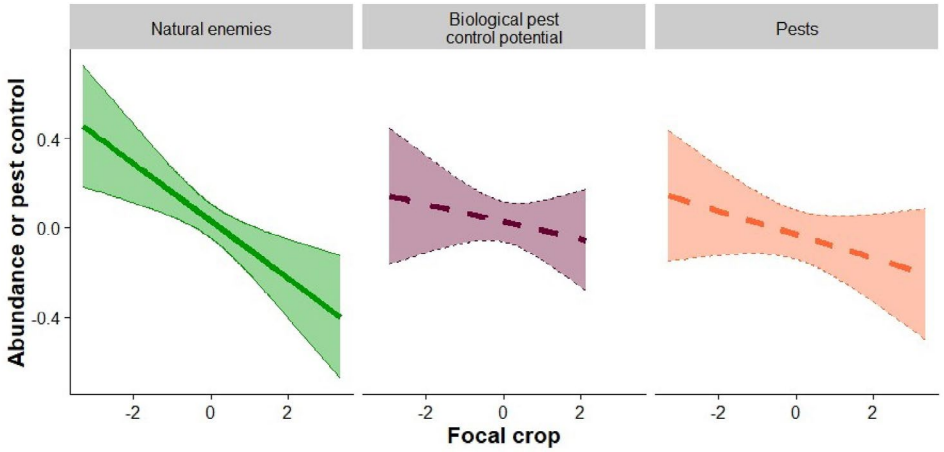

FIGURE 3 | Effect of the proportion of focal crop on natural enemy abundances, biological pest control potential, and pest abundances. Focal crop is the standardized proportion of studied focal crop in a 500 m radius in the landscape (centered and scaled, see methods). Lines represent predictions of the linear mixed models based on standardized values. Natural enemies are in green, biological pest control potential in purple, and pests in orange. Solid lines show significant relationships and non-significant relationships are dashed. Confidence bands are confidence intervals at 95%.

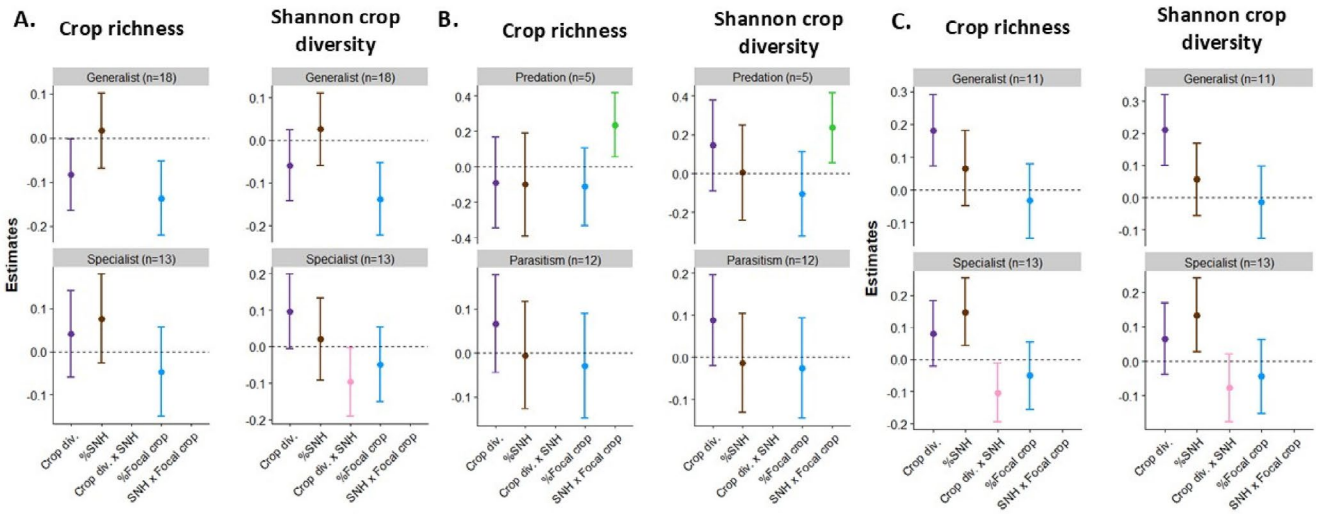

FIGURE 4 | Effects of crop species diversity on (A) the abundance of generalist or specialist natural enemies, (B) different aspects of biological control potential (predation and parasitism rates) and on (C) the abundance of generalist or specialist pests. For each response variable, the figure shows estimates and 95% confidence intervals from linear mixed-effects models of crop species richness (left) or the Shannon index of crop diversity (right), as well as the proportion of semi-natural habitats (%SNH), the interaction with crop diversity (Crop div. × SNH), and with the proportion of the studied focal crop (%Focal crop). Only estimates kept by model selection are shown.

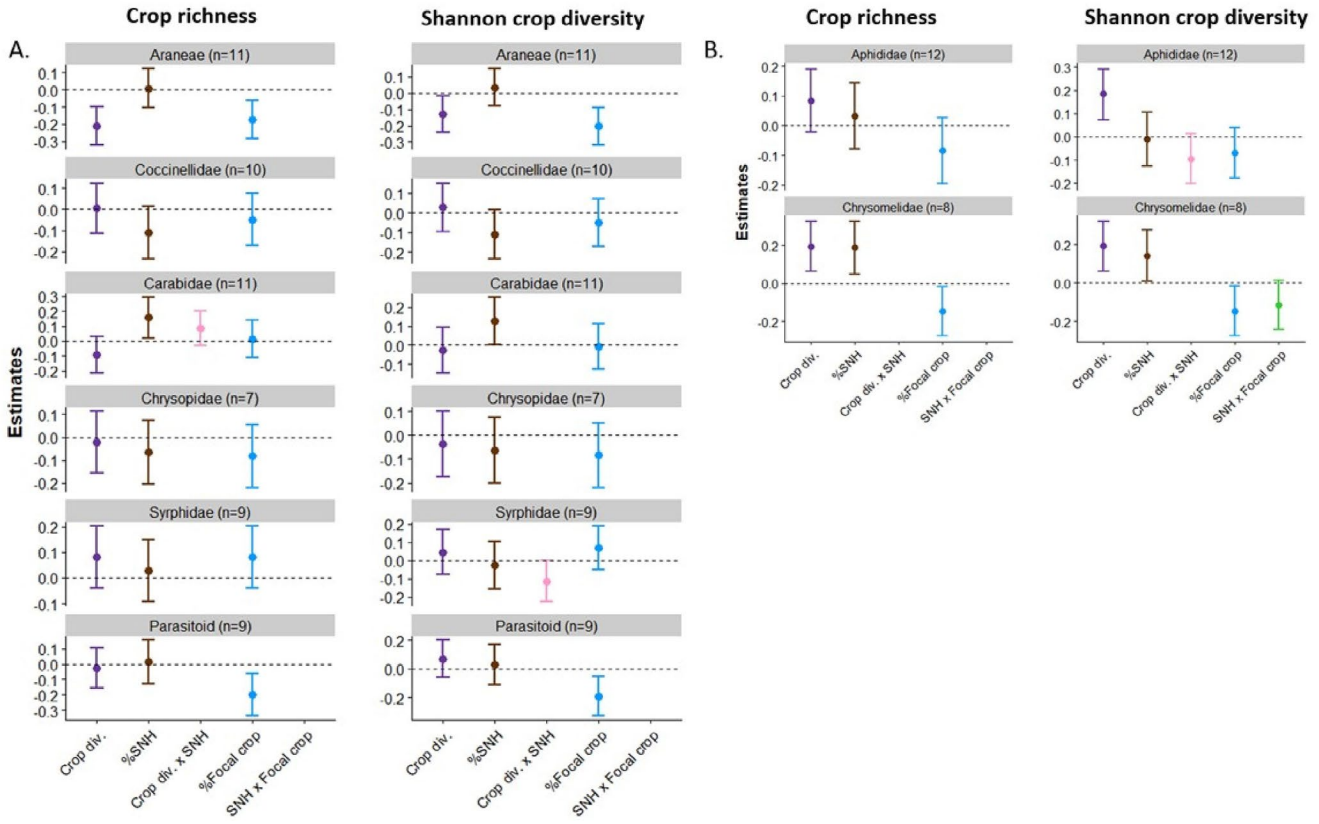

FIGURE 5 | Effects of crop species diversity on (A) the abundance of different families of natural enemies, and (B) the abundance of different pest families. For each response variable, the figure shows estimates and 95% confidence intervals from linear mixed-effects models of crop species richness (left) or the Shannon index of crop diversity (right), as well as the proportion of semi-natural habitats (%SNH), the interaction with crop diversity (Crop div. × SNH) and with the proportion of the studied focal crop (%Focal crop). Only estimates kept by model selection are shown.

of focal crop on natural enemies was mainly driven by spiders and parasitoids, with no significant responses observed for other groups (Figure 5A, Table S7).

Among pest taxa, both Aphididae and Chrysomelidae responded positively to crop diversification (Figure 5B, Table S7). In addition, the abundance of Chrysomelidae was significantly higher in

landscapes with a high proportion of semi-natural habitats and low amounts of patches of focal crops (Figure 5B; Figure S8, Table S7).

We found a significant interaction between the amounts of focal crop and the proportion of semi-natural habitats on pest predation rates, indicating that pest predation rates increased with the amounts of focal crop in the landscape only in landscapes supporting high proportions of semi-natural habitats (Figure 4B, Table S7).

4 | Discussion

Our study indicates that crop diversification is not a 'one size fits all' strategy for enhancing biological pest control. Although crop diversification increased overall pest populations, this effect was dampened in landscapes with a higher proportion of semi-natural habitats, particularly for specialist pests. In contrast, crop diversification alone did not significantly affect the overall abundance of natural enemies or biological pest control potential. Instead, its effect depended on the diet breadth of natural enemies, with neutral or negative impacts of crop diversity on generalists but positive effects on specialists in a context of low proportions of semi-natural habitats. Our results further indicate that the proportion of focal crop in the landscape may influence biological pest control services, as we found that a low proportion of focal crop was associated with higher abundances of natural enemies, especially of generalists. Taken together, our findings not only corroborate previous studies reporting variable effects of crop diversification on biological pest control services (Aguilera et al. 2020; Priyadarshana et al. 2024; Redlich et al. 2018; Thomine et al. 2023), but also provide new insights by identifying the contexts for which crop diversification can be beneficial to biological pest control.

We hypothesized that increasing crop diversity would have positive effects on natural enemy abundances and the level of biological pest control in the landscape (H1) and that these effects would limit the abundance of specialist pests (H2) (Perrot et al. 2023; Vialatte et al. 2025). Our results do not support these hypotheses, as increased crop diversity did not correlate with an increase in overall abundances of natural enemies (only valid for specialist natural enemies) or biological pest control potential. Moreover, crop diversification actually favoured specialist pest abundances in highly simplified landscapes. Our results therefore suggest that specialist pests can benefit from the higher spatiotemporal continuity in resources provided by crop diversity, especially in intensive landscapes supporting low amounts of semi-natural habitats (Schellhorn et al. 2015; Iuliano and Gratton 2020; Tscharntke et al. 2016). Moreover, pests may also benefit from the decrease in generalist predator abundance associated with increased crop richness observed in this study. However, other mechanisms might also explain these results, such as increased intra-guild predation, which could limit the top-down control on pests (Martin et al. 2013).

We hypothesized that diet breadth would significantly modulate the effect of crop diversification on the abundance of natural enemies and pests (H4). While our results corroborated this hypothesis, they were not totally in line with our theoretical expectations. Indeed, generalist natural enemies tended to decrease with increasing crop diversity, whereas specialists increased with increasing crop diversity, but only in landscapes with low proportions of semi-natural habitats. These results suggest that specialist natural enemies may have benefited from the positive bottom-up effects of crop diversity on pest abundance, whereas generalist natural enemies might have been more diluted across the crop matrix as landscape-level crop diversity increased. Overall, the interactive effect between the proportion of semi-natural habitats and crop diversity highlights that crop diversification benefits specialist natural enemies and specialist pests only when alternative resources provided by semi-natural habitats are lacking. This suggests that resource supplementation between crop and non-crop habitats drives the response of specialist natural enemies and specialist pests (see below). Our results also indicate a strong variability in the effect of crop diversity on different groups of natural enemies, suggesting that other environmental factors unrelated to crop diversity itself, such as the spatiotemporal distribution of prey, alternative hosts (non-pest) preys, nectar sources or overwintering sites, may drive their individual responses (Landis et al. 2000; Iuliano and Gratton 2020).

The interactive effects between semi-natural habitats and crop diversity on pest abundances and some natural enemies confirm recent empirical results obtained on different functional groups (Sirami et al. 2019; Frank et al. 2024). The buffering effect provided by semi-natural habitats may result from several non-exclusive mechanisms (Tamburini et al. 2020; Perrot et al. 2023). The weak effect of crop diversity on pest abundance in landscapes with a high proportion of semi-natural habitats may result from limited pest dispersal and population build-up due to barrier effects (Bhar and Fahrig 1998; Akter et al. 2023), spatial dilution of the pest pool on alternative host plants (Rusch et al. 2010; Tscharntke et al. 2016), or enhanced top-down control by specific natural enemy groups (Bianchi et al. 2006; Martin et al. 2019). However, semi-natural habitats may provide important alternative resources for pests in landscapes supporting low crop diversity, allowing populations to maintain in the surrounding environment (Bianchi et al. 2006; Rusch et al. 2013; Tscharntke et al. 2016). In addition, crop diversity may provide alternative resources for both pests and natural enemies in simple landscapes supporting low proportions of semi-natural habitats, which seems to be particularly the case for specialists (Vialatte et al. 2025; Landis et al. 2000). As expected, the lowest pest pressures were found in highly intensive contexts, combining low crop diversity and low proportion of semi-natural habitats, in which pest management strongly relies on the use of chemical insecticides (Nicholson and Williams 2021; Etienne et al. 2023). Although we could not test all these potential mechanisms, our analysis provides evidence for complementation and supplementation of resources between habitats for important functional groups of natural enemies (Thies et al. 2011). Combining crop diversification with high amounts of semi-natural habitats tended to enhance ground beetle abundance, suggesting resource complementarity. In contrast, crop diversification increased the abundance of specialist natural enemies, such as Syrphidae, only in simple landscapes, which suggests supplementation of resources between habitats (Figure S8). Complementarity effects may emerge for generalist predators such as ground beetles as semi-natural habitats provide overwintering sites (Pfiffner and Luka 2000; Sarthou et al. 2014), while increasing crop diversity supports multiple prey

over space and time (Dassou and Tixier 2016). Supplementation effects for specialist natural enemies may occur in highly simplified landscapes, where crop diversification can supply diverse prey, pollen and sugar resources, which are essential for these organisms (van Rijn and Wäckers 2016).

Contrary to our expectations and those of the resource concentration hypothesis (O'Rourke and Petersen 2017), we found that increasing the proportion of the focal crop in the landscape reduced the abundance of natural enemies without affecting the overall abundances of pests (H3). Spatial dilution of natural enemies among patches of focal crops in the landscape was mainly driven by the response of generalists, such as spiders. Our results suggest that these communities may be more closely associated with a given crop type than previously expected, and that the natural enemy species pool may be non-randomly distributed across the habitat mosaic in the landscape (Michalko and Birkhofer 2021). Overall strong habitat filtering or potential density-dependence effects may drive the spatial dilution effects observed for these groups (Thies et al. 2008; Marrec et al. 2017). In addition, our results indicate that despite no overall effect on pest abundances, some pests (Aphididae) were indeed unaffected by an increasing proportion of focal crop in the landscape, while others (Chrysomelidae) were reduced, also suggesting a crop resource dilution effect. Contrary to our results, long-term studies have demonstrated that landscape homogenization through increased proportions of similar crops benefits herbivorous insects over time, which in turn is associated with higher pesticide use (Meehan et al. 2011; Nicholson and Williams 2021). These contrasting results may be due to significant differences in the life-cycle and ecological traits of the species studied (e.g., overwintering in crop or non-crop habitats) (Martin et al. 2019). It may also come from the fact that in our study we could only consider the focal crop of the primary studies as a proxy for the amounts of host crop in the landscape while a clear description of the range of host crops in the landscape may have provided different results. Further research is needed to investigate whether the dilution effect, as observed in our study, is valid over time, from 1 year to the next (Schneider et al. 2015), or whether positive resource-mediated effects on pest populations emerge over time considering the whole range of host crop (Delaune et al. 2021). Addressing the temporal dynamics of such effects will be crucial to provide robust information to farmers about the long-term dynamics of natural enemies and pest populations with varying host crop proportion.

A few limitations of our study warrant further analyses. First, our database is dominated by invertebrates, while other natural enemies, such as entomopathogens, birds and bats, as well as other pests, such as weeds or crop pathogens, may respond differently to crop diversity and at other spatio-temporal scales (Sirami et al. 2019; Delaune et al. 2021; Priyadarshana et al. 2024). Future studies should therefore investigate whether similar effects of crop diversity, semi-natural habitats or host crop proportions also shape the distribution of an extended taxonomic range of natural enemy and pest organisms. Second, our analysis of the responses of natural enemies and pests is based on simple classifications, mainly considering diet breadth as well as taxonomic groups. For a large majority of species involved, key trait information, such as overwintering strategies or life-cycle complexity, is currently lacking. Characterizing natural enemies or pest communities as well as crops based on other functional traits could provide important additional insights into the mechanisms driving the effects of crop diversification on top-down control of pests (Bartual et al. 2019; McHugh et al. 2020; Perrot et al. 2023). Third, our study is based on the analysis of the effect of landscape composition at a 500 m spatial extent due to datasets limitations, and we cannot rule out the possibility that crop diversification effects might be modulated by unexplored landscape facets such as configurational heterogeneity or over larger spatiotemporal scales (Priyadarshana et al. 2024). Finally, we could not include the effect of farming practices (e.g., pesticide use, nitrogen fertilization) across scales in our analysis due to the lack of information in primary studies, and this hidden-heterogeneity may significantly impact population and metapopulation dynamics (Muneret et al. 2018). Future research should therefore investigate how key farming practices at the landscape scale modulate the detected relationships between crop diversity and pest populations.

Despite these limitations, our study provides important insights into the management of agricultural landscapes at the global scale. Our findings indicate that diversifying crops in highly simplified landscapes can benefit specialist natural enemies and pests while increasing the proportion of semi-natural habitats reduces this effect. In addition, our study highlights the importance of considering the proportion of focal crops, an overlooked facet of crop diversification, for understanding pest control services in agricultural landscapes. Reducing the proportion of focal crops in the landscape favours natural enemy abundance, which might have beneficial effects for limiting pest population levels over time. Further research should particularly investigate how other traits of crops, pests and natural enemies, such as crop phenology, life-cycle complexity or natural enemy mobility, modulate the effects of landscape composition on predator-pest dynamics.

Author Contributions

Thomas Perrot, Léa Beaumelle, Eva Thomine, Yann Tricault, Nicolas Desneux and Adrien Rusch conceived the study. Eva Thomine, Yann Tricault, Nicolas Desneux and Adrien Rusch collected the primary datasets and constructed the overall database. Thomas Perrot, Léa Beaumelle and Adrien Rusch conducted the data analysis and wrote the first draft of the manuscript. All co-authors contributed to the interpretation of the results and to writing the final version of the manuscript.

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Data Availability Statement

Data and code related to the paper are available here: https://doi.org/10.5281/zenodo.17379612.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Locations of study sites. Dot size increases with the number of sites per study. Dots are filled with colours according to study ID. **Figure S2:** Venn Diagram describing the number of studies for each of the three metrics of pest control services investigated here, and number of studies reporting several metrics simultaneously. **Figure S3:** Pearson correlations between different landscape variables in the dataset. **Figure S4:** Linear relationships between Shannon index of crop diversity and each of the three response variables (natural enemy abundance, biological control potential, and pest abundance) for the whole dataset. **Figure S5:** Effects of crop diversity at the family level, the proportion of semi-natural habitats and the proportion of the focal crop in the landscape on natural enemies, biological pest control potential and pest abundance. **Figure S6:** Sensitivity analysis showing the outputs of the main models presented in Figure 1 when excluding sites with high proportions of semi-natural habitats ($\geq 95\%$) and/or low proportions of focal crops ($\leq 5\%$). NE = natural enemies, BC = biological pest control potential. **Figure S7:** Interactive effect between crop diversity (Shannon index or Crop Species richness) and the proportion of semi-natural habitats in a 500 m radius on the abundance of specialist (A) natural enemies or (B) pests. **Figure S8:** Interactive effect of crop diversity, the proportion of the focal crop and semi-natural habitats in a 500 m radius on (A, B) different groups of natural enemies, (C) biological control measures and (D, E) pest groups. **Table S1:** Description of studies included in the analysis. **Table S2:** Lists of the dietary specialization of natural enemies and pests based on Poveda et al. (2025) and Martin et al. (2019). **Table S3:** Source and nature of the land-cover data from each study. **Table S4:** List of crop species present in the landscapes of the studies included in our analysis. **Table S5:** Effect of different crop diversity indices (crop richness, Shannon index of crop diversity), the proportion of the focal crop (%Focal crop) and the proportion of semi-natural habitats (%SNH) including interactions between %SNH and crop diversity or between %SNH and %focal crop on each response variable: abundance of natural enemies, biological pest control potential or pest abundance. **Table S6:** Effect of different crop diversity indices (crop richness, Shannon index of crop diversity), the proportion of the focal crop (%Focal crop) and the proportion of semi-natural habitats (%SNH) including interactions between %SNH and crop diversity or between %SNH and %focal crop on abundance of natural enemies or pests according to their diet, generalist or specialist. Estimates, z-values and p-values are given. "–" indicates variables that were not kept by stepwise selection. Significant results are in bold. **Table S7:** Effect of different crop diversity indices (crop richness, Shannon index of crop diversity), the proportion of the focal crop (%Focal crop) and the proportion of semi-natural habitats (%SNH) including interactions between %SNH and crop diversity or between %SNH and %focal crop on each response variable: the abundance of different families of natural enemies, different aspects of biological control (predation and parasitism rates) and the abundance of different pest families.