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NATURE-BASED SOLUTIONS FOR A CHANGING WORLD

Research Article

Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context

Léa Beaumelle | Arthur Auriol | Marie Grasset | Alice Pavy | Denis Thiéry | Adrien Rusch

INRAE, Bordeaux Sciences Agro, ISVV, SAVE, Villenave d'Ornon, France

Correspondence
Léa Beaumelle, INRAE, Bordeaux Sciences Agro, ISVV, SAVE, Villenave d'Ornon F-33140, France.
Email: lea.beaumelle@gmail.com

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Abstract

1. Increasing plant diversity in agricultural systems is a promising way to balance food production and biodiversity conservation. Biological pest control, a crucial ecosystem service delivered by natural enemies, could particularly benefit from increased plant diversity at the local scale. Such positive effects however often depend on the landscape context that shapes the pool of natural enemy species available and their ability to colonize newly created habitats. However, how the landscape context modulates the local effect of plant diversity on natural enemies and pest control services remains unclear.
2. Here, we manipulated the diversity of cover crops (2 versus 20 plant species) in nine pairs of vineyards located along a landscape gradient ranging from 20 to 60% of semi-natural habitats. We sampled natural enemy communities in the soil and foliage and measured the predation rate of an important moth pest in European vineyards (*Lobesia botrana*).
3. Diverse cover crops enhanced the abundance of natural enemies by 140% across the experiment, but without changing their taxonomic richness and composition. We further found a distance-decay effect of cover crops on natural enemy abundance across cover crop types.
4. The landscape context remarkably modulated the effects of local plant diversity on natural enemy abundance and predation rates. While predation rates were on average similar in the low and high cover crop diversity treatments across the experiment, diverse cover crops had higher positive effects on predation and natural enemies in simple (<50% semi-natural habitats) than complex landscapes. Predation rates increased from 11 to 42% in the high compared with low cover crop diversity treatments in simple landscapes.
5. *Synthesis and applications*: Our study demonstrates the benefits of increasing plant diversity at the local scale to enhance the abundance of natural enemies as well as the level of biological pest control services in vineyard agroecosystems. Diverse cover crops mostly benefit natural enemies and biological pest control in simplified

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landscapes, highlighting that the success of local agroecological practices in improving biodiversity and ecosystem services depends on the landscape context. Thus, we suggest that a strategic spatial arrangement of agricultural practices increasing local plant diversity is necessary to maximize beneficial effects on biodiversity and ecosystem services.

KEYWORDS
agroecology, arthropods, biodiversity, biological pest control, ecosystem services, landscape ecology, vineyards

1 | INTRODUCTION

Agricultural intensification is the main cause of biodiversity loss in terrestrial ecosystems (IPBES, 2019). By harnessing ecosystem functions supported by biodiversity, agroecology aims to design agricultural landscapes that can maintain commodity production while preserving the environment (Bommarco et al., 2013). Biological control of crop pests by their natural enemies is a major ecosystem service that can increase the sustainability of agroecosystems (Lewis et al., 1997; Rusch et al., 2017). It can contribute to reducing the use of pesticides and their harmful effects on the environment while maintaining crop productivity (Geiger et al., 2010; Rusch et al., 2010). Identifying agroecological practices beneficial to biological pest control services by enhancing natural enemies and their diversity is therefore crucial for future agriculture.

Multiple studies have demonstrated a positive relationship between biodiversity and ecosystem functioning across ecosystem types (Cardinale et al., 2012). In agroecosystems, biodiversity can strengthen the delivery of key ecosystem services such as biological pest control (Dainese et al., 2019; Ostandie et al., 2021). Plant diversity is particularly crucial to maintain multiple ecosystem services as plants shape trophic interactions across several levels (Andow, 1991; Isbell et al., 2011; Scherber et al., 2010). Increasing plant diversity is therefore often suggested as a key management option to harness biodiversity-based ecosystem services (Aguilera et al., 2020; Kremen & Merenlender, 2018). Plant diversification encompasses crop and non-crop diversity as well as various management practices that can be implemented at multiple scales from field-scale diversification (e.g., cover cropping, intercropping) to landscape-scale diversification (e.g., diversifying crop rotation, semi-natural habitats) (Letourneau et al., 2011; Rusch et al., 2010). While the separate effects of local and landscape plant diversification on biodiversity and ecosystem services have been extensively studied, the relative and joint effects of plant diversification practices across spatial scales on pest control services remain poorly explored.

At the field scale, increasing plant diversity can limit the density of insect pests as well as plant damage (Barnes et al., 2020; Letourneau et al., 2011; Wan et al., 2020). It has been estimated that crop diversification reduced pest abundance and crop damage by 23% compared with monocultures (Letourneau et al., 2011). The effects of plant diversity on insect pests are mediated by direct bottom-up effects (the resource concentration hypothesis) and indirect top-down effects (the natural enemies hypothesis) (Letourneau et al., 2011; Wan et al., 2020). According to the resource concentration hypothesis, insect pests are more likely to find and remain on their host plant in monospecific plant communities due to the high density of resource that increases immigration to and decreases emigration from monospecific communities (Root, 1973). The mechanisms behind these bottom-up effects involve disruption of host localization due to chemical or physical perturbations, as well as changes in host plant quality (Andow, 1991; Castagneyrol & Jactel, 2012; Finch & Collier, 2000; Thiery & Visser, 1986). The natural enemies hypothesis suggests that natural enemies are more abundant, diverse and efficient in more diverse plant communities leading to lower pest densities (Russell, 1989). These indirect top-down effects are mediated by the higher abundances of alternative prey or hosts, pollen, nectar, as well as microhabitats in diverse than monospecific plant communities. Evidence supporting these two non-exclusive hypotheses exists in the literature (Moreira et al., 2016), but the extent to which the landscape context modulates their prevalence remains to be explored.

At the landscape scale, habitat diversity shapes natural enemy communities as well as the level of biological pest control services they deliver (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Rusch et al., 2016). Semi-natural habitats, such as hedgerows, grasslands or forests, support crucial resources and habitats for natural enemies such as alternative preys, nectar, pollen or overwintering sites (Landis et al., 2000; Rusch et al., 2010; Sarthou et al., 2014; Tena et al., 2015). While several studies have demonstrated that natural enemies and trophic interactions are affected by landscape structure, the direction and magnitude of such effects on pest populations and crop damages remain highly variable (Karp et al., 2018). Such context-dependent effects of landscape structure on biological pest control could be due to interactive effects between landscape and local management. Indeed, according to the intermediate landscape complexity hypothesis, the landscape context might non-linearly modulate the effect of local management on biodiversity and ecosystem services (Tscharntke et al., 2012). According to this hypothesis, local management options (such as flower strip, reduced tillage or organic farming) have limited effects on biodiversity and ecosystem services in very simple and complex landscapes, while the highest positive effects are expected in landscapes

of intermediate complexity. In very simple landscapes (less than 20% of semi-natural habitats), the species pool is supposed to be too low to support an increase in species diversity in response to beneficial management options at the local scale. In very complex landscapes, high levels of biodiversity and ecosystem services are expected and might therefore limit any further positive effects of local management options aiming to improve biodiversity and ecosystem services. The interactive effect between local- and landscape-scale habitat diversity on biodiversity and ecosystem services has been the focus of a number of recent studies (Muneret et al., 2019a; Winqvist et al., 2011). However, few studies have specifically quantified such an effect on natural enemy communities and biological pest control, and they yielded inconsistent findings (Albrecht et al., 2020; Tschumi et al., 2015; Winqvist et al., 2011). Moreover, the interactive effects between local increase in plant diversity and landscape scale habitat diversity are expected to differ significantly in perennial compared with annual crops, due to different spillovers of organisms between crop and non-crop habitats (Rand et al., 2006; Tscharntke et al., 2016). Yet, in perennial crops such as vineyards, these interactive effects remain poorly understood.

In this study, we explored the effect of cover crop composition and diversity on natural enemy communities and pest control services along a wide gradient of proportion of semi-natural habitats in the landscape. We asked if more diverse cover crops enhanced the abundance and richness of natural enemies and biological pest control independently of the landscape context in vineyards. We focused on vineyards because they are intensively managed (e.g., in France, 20% of the total pesticide use while they cover only 3% of agricultural land (Sabatier et al., 2014)), and many efforts are currently undertaken to implement agroecological practices. Furthermore, vineyards are perennial crops in which increasing local-scale plant diversity is particularly challenging given that increasing crop diversity is not an option. The use of cover crops in vineyards inter-row is however a practice that is gaining attention due to their multiple beneficial effects on agroecosystem functioning (Daane et al., 2018; Winter et al., 2018). However, the interactive effects of cover crop diversity and landscape context on natural enemies and biological pest control remain unclear (Wilson et al., 2017).

We hypothesized that (1) diverse cover crops enhance natural enemy abundance and richness, as well as pest control potential compared with lowly diverse cover crop (Letourneau et al., 2011), (2) different guilds of natural enemies are affected differently by cover crop diversity (Muneret et al., 2019a) and (3) the positive effects of cover crop diversity are higher at intermediate landscape complexity than in simplified or complex landscapes (Tscharntke et al., 2012; Wilson et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study design

A field experiment was conducted in conventional vineyards located in the Bordeaux area, France (45°01′28″N, 0°21′13″W) in 2018. Nine sites were selected along a landscape gradient ranging from 22 to 63% of semi-natural habitats in a 1 km radius around each site. We selected semi-natural habitats as a measure of landscape complexity as this is highly correlated to other measures of landscape heterogeneity and because landscapes of our region are mainly composed of vineyards, forests and grasslands (Muneret et al., 2018; Roschewitz et al., 2005). We used a spatial extent of 1 km radius, in line with many studies on biological pest control studies, and because it explains the responses of predators and pests in vineyards landscapes (Muneret et al., 2019a; Petit et al., 2020). At each site, a treatment with high cover crop diversity (flower strips) and a control with low cover crop diversity (grassy strips) were applied each in one separate field within the same farm and soil type. This ensured that the arthropod communities in the different cover crop treatments were subjected to the exact same management practices and soil type within each landscape. The experimental design resulted in nine pairs of vineyards. All vineyards were planted with Merlot variety (*Vitis vinifera*) and cultivated without irrigation, under conventional management with regular pesticide use (mostly fungicides), soil tillage and mowing every other inter-row (Muneret et al., 2018; Papura et al., 2020). The high diversity treatment consisted in a mixture of 20 plant species designed specifically for vineyards' inter-row and containing a range of functionally different plants (such as Fabaceae, melliferous plants: see Supplementary Materials for the full list of plant species). The low diversity treatment consisted in a mixture of two Poaceae (*Lolium perenne* and *Festuca rubra*). Plants were sown manually after soil tillage on 24 April and 11 May 2018 in one out of two inter-rows, on a total of eight inter-rows per plot. Cover crops were sown along a distance of 20 m from the plot margin to the center of the plot (Figure S1).

2.2 | Natural enemy sampling

Two guilds of natural enemies (soil- and vine-dwelling) were sampled at increasing distance from the cover crop treatments in each field. Soil enemies were sampled using pitfall traps and vine enemies with beating nets. The samplings were conducted at three distances from the cover crop treatments: in the middle of the cover crop (0 m) and at 15 and 30 m away from the middle of the cover crops. Three sampling sessions were conducted (in June, August and September). For each sampling session and at each distance (0, 15 or 30 m) in each field, two pitfall traps filled with soap water were placed in the soil of different inter-rows for a week before being collected and individuals pooled before identification. Vine arthropods were pooled from beating 15 randomly located vines per distance per field at each sampling session. In the end, for each distance ($n = 3$), guild ($n = 2$), treatment ($n = 2$) and field ($n = 9$), the sample size was $n = 3$ (one pooled sample per session), yielding a total sample size of $N = 324$. Individuals belonging to natural enemy community (spiders, Carabidae, Opiliones, Neuroptera and Dermaptera) were identified to the nearest possible taxonomic level, but the high number of juvenile spiders limited species identification, and about 77% of all arthropod individuals were thus identified to the genus. We calculated taxonomic richness as the number of taxonomic groups in each sample. Rarefied richness could not be used due to a

number of samples where the abundance was zero. As the sampling effort was identical across the experiment, we focused on taxonomic richness instead of rarefied richness.

2.3 | Pest control measurements

We evaluated the biological pest control potential of one of the main vineyard pests, the European grapevine moth (*L. botrana* Fam. Tortricidae) (Thiéry et al., 2018), using sentinel cards (Muneret et al., 2019b). We focused on *L. botrana* which causes important damage in European vineyards by direct phytophagy on the grapes or by promoting the development of bunch rot that can cause serious qualitative and quantitative damage (Delbac & Thiéry, 2016). In heavily attacked vineyards, it is possible to have up to 10–30 larvae of *L. botrana* per bunch leading to the complete destruction of the bunch depending on the cultivar (Fermaud et al., 2016).

Each sentinel card consisted of 10 moth eggs laid on parchment paper in the laboratory and then glued on a plastic card of about 1 × 8 cm. Moth eggs were obtained from our own laboratory rearing (temperature: 22°C, hygrometry: 60%, photoperiod: 16D/8N). In each field, eight cards were attached to the vine stock, close to the grapes, at each distance from the cover crop treatment, and left for 3 days before being collected. Biological control potential was then measured based on the proportion of eggs removed from the card. Three measurement sessions were conducted (in July, August and September). During the last sampling session, only 4 egg cards were used due to low moth eggs availability in the laboratory and incompatibility with pesticide spraying programs. Across the experiment three egg cards were lost/destroyed yielding a total final sample size of 999 sentinel cards.

2.4 | Data analyses

We tested the main and interactive effects of the plant diversity treatment (low versus high diversity), the landscape context (proportion of semi-natural habitats), and the distance to the center of the cover crop treatment (0, 15, 30 m) on the abundance, richness and community composition of two guilds of natural enemies (soil and vine) and on pest predation rates. We used the proportion of semi-natural habitats as a proxy of landscape complexity (Muneret et al., 2018). The proportion of semi-natural habitats resulted from the sum of proportions of forests, meadows and fallows. We used the regional database PIGMA (http://portail.pigma.org) and calculated the proportion of different habitat types in a 1000 m radius around each site using ArcGIS 10.1 (ESRI).

We used generalized linear mixed effect models (GLMMs) to analyze abundance and taxonomic richness of natural enemies and biological pest control potential with the R package lme4 (Bates et al., 2015; R Core Team, 2019). We analyzed natural enemy communities by constrained ordination (partial Redundancy Analysis) using the R package vegan (Oksanen et al., 2019).

2.4.1 | Abundance

GLMMs were fitted to natural enemy abundance with a negative binomial distribution to account for the nature of the data (counts and overdispersion). We tested the following full model:

$$\text{Abundance} \sim \text{Treatment} * \text{Guild} * \text{Landscape} + \text{Treatment} * \text{Guild} * \text{Distance} + (1|\text{site} : \text{session})$$

The model included the fixed effects of the Treatment (two-level factor: low plant diversity and high plant diversity); Guild (two-level factor: soil and vine guilds of natural enemies); Landscape (continuous variable: scaled percentage of semi-natural habitats in a 1000 m radius); and Distance (continuous variable: scaled distance to the center of the cover crop). The model also included a random effect of the session within each site on the intercept (factor with 27 levels) to account for non-independent observations conducted the same date at each site. We first tested the full model versus null model (Abundance ~ 1 + (1|site:session)) and verified the residuals of the full model using the R package DHARMa (Hartig and Lohse, 2020). Based on residuals patterns, we included a quadratic effect of landscape complexity that significantly improved model fit and residual plots, and was also biologically relevant (Tscharntke et al., 2012). We further evaluated spatial autocorrelation by inspecting the residuals versus spatial coordinates of each plot, and found no significant pattern. We tested the main effects of our variables and their interactions using Wald Chi-square tests and likelihood ratio tests, using the R function drop1 (Zuur et al., 2009), both approaches yielded the same results. Following Harrison et al. (2018) and Forstmeier and Schielzeth (2011) , we report the results of the full model instead of the optimal model.

2.4.2 | Diversity

We used a similar approach and model structure to investigate the response of the taxa richness of vine and soil natural enemies to the treatment, landscape and distance to cover crop treatment. The model was identical to the abundance model above. We fitted a negative binomial GLMMs that provided better fit than LMMs with gaussian distribution, even after log-transformation. We also included a quadratic effect of the landscape based on residual diagnostic plots, and followed the same protocol to model simplification and reporting (Harrison et al., 2018; Zuur et al., 2009).

2.4.3 | Biological pest control

We modelled the number of eggs predated per sentinel card using a GLMM with negative binomial distribution, after trying alternative distributions (binomial, Poisson) that provided poor fit to the

TABLE 1 Abundance of natural enemy groups in the high and low cover crop diversity treatments (High Div, Low Div, respectively) across the landscape gradient

Order	Treatment	Mean	SD	Total
Araneae	Low Div	1.92	2.07	1722
Araneae	High Div	2.15	3.04	2028
Coleoptera	Low Div	2.48	3.22	473
Coleoptera	High Div	3.13	6.7	532
Dermaptera	Low Div	0.0377	0.191	6
Dermaptera	High Div	0.0449	0.328	7
Neuroptera	Low Div	0.131	0.584	21
Neuroptera	High Div	0.18	0.523	29
Opiliones	Low Div	0.884	1.38	160
Opiliones	High Div	0.924	1.33	170

Mean abundance, standard deviation (SD) and total abundance are given for each order of natural enemy across soil and vine guilds ($n_{\text{high div}} = 156$, $n_{\text{low div}} = 159$).

data based on residual diagnostic plots. The following full model was tested:

Predation ~ Treatment * Landscape + Treatment * Distance + (1|site:session)

Again, we included a quadratic effect of the landscape based on the residual diagnostic plots of initial models that did not include such a non-linear effect.

2.4.4 | Community composition

We used RDA using the same model structure as above to analyse the effect of Treatment, Landscape, Guild and Distance on community composition of predators. We summed the abundance of each taxa across sampling sessions before analysis. The community matrix was Hellinger transformed prior to analysis. Permutation tests (using 999 permutations) were used to test the significance of all constrained axes.

3 | RESULTS

A total of 5148 natural enemy individuals belonging to 198 taxonomic groups were collected across the experiment (Table 1); 73% were spiders, 20% Coleoptera, 6% Opiliones, and a few Neuroptera (50 individuals) and Dermaptera (13 individuals). The soil guild was composed of 67% spiders, 28% Coleoptera and 5% Opiliones (with a total number of 156 taxa). The vine guild however was dominated by 86% spiders, no Coleoptera, and 10% Opiliones (with a total number of 82 taxa). In terms of biological pest control, the average predation rate was 0.30 (SD: 0.27, $n = 999$) across the experiment.

3.1 | Abundance

The cover crop treatment affected the abundance of natural enemies, with significantly higher abundances in the high than in the low diversity treatment overall (Figure 1(a), Chi-square = 5.82, df = 1, $p = 0.016$). The model predicted on average 140% more individuals in the diverse cover crop treatment. However, the landscape context modulated the response of natural enemies to plant diversity (significant interaction: Chi-square = 6.74, df = 2, $p = 0.034$). The model predicted lower abundances at intermediate landscape complexity (i.e., around 40% of semi-natural habitats), and higher abundances at low and high landscape complexities (Figure 2(a)). There was a slight negative effect of the distance to the cover crop (Chi-square = 4.92, df = 1, $p = 0.027$), indicating that the abundance of natural enemies progressively declined further away from the center of the cover crop treatments (on average 17% less individuals at 30 m versus at the center of the cover crop; Figure S2)). Finally, the abundance of natural enemies differed depending on the guild (Chi-square = 121.75, df = 1, $p < 0.0001$) with much higher densities of soil compared with vine arthropods, but the two guilds showed similar responses to the landscape context (interaction: Chi-square = 4.91, df = 2, $p = 0.086$) as well as the cover crop diversity treatment (Chi-square = 1.39, df = 1, $p = 0.239$).

3.2 | Diversity

There was no evidence that our cover crop treatment changed the number of taxa of natural enemies (Chi-square = 1.89, df = 1, $p = 0.169$). Taxonomic richness varied according to the guild (Chi-square = 125.63, df = 1, $p < 0.0001$). Soil predators were more diverse than vine predators (average predicted taxa richness of 8.37 (CI: 7.36–9.52) versus 5.16 (CI: 4.46–5.98) for the soil and vine guilds, respectively). Landscape complexity had no significant effect on taxonomic richness (Figure 2(b), Chi-square = 4.83, df = 2, $p = 0.090$), nor did the distance to the cover crop treatment (Chi-square = 2.13, df = 1, $p = 0.145$).

3.3 | Community composition

We further explored the response of natural enemy community composition and found no effect of the plant diversity treatment (Figure 3; $F = 0.76$, df = 1, $p = 0.676$). Taxa composition differed with the guild considered ($F = 49.3$, df = 1, $p = 0.001$, Figure 3), the proportion of semi-natural habitats in the landscape ($F = 3.02$, df = 1, $p = 0.009$) as well as the interaction between guild and landscape complexity ($F = 2.79$, df = 1, $p = 0.01$) (Figure 3). The distance to cover crop treatment did not modify the taxonomic composition of natural enemies ($F = 1.08$, df = 1, $p = 0.307$).

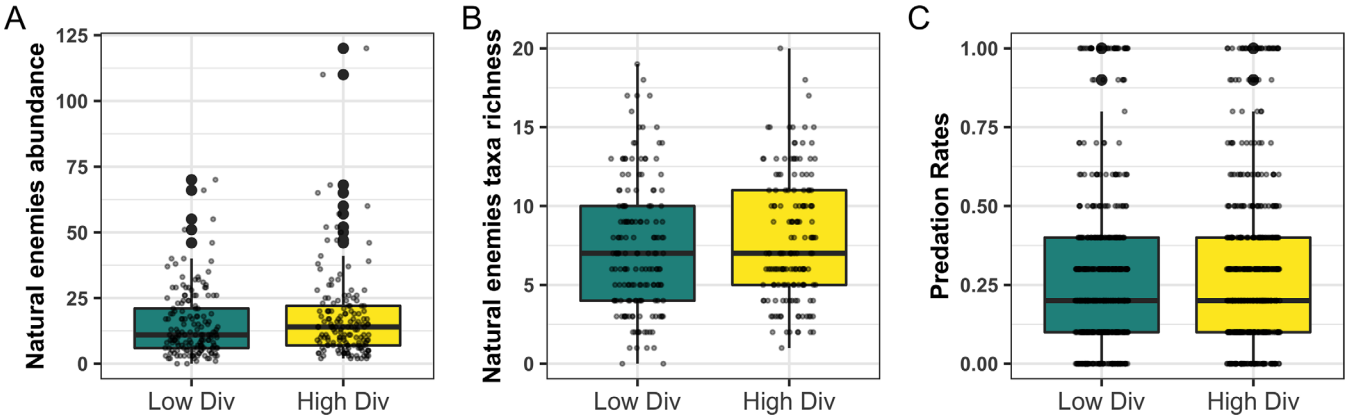

FIGURE 1 Cover crop diversity affects natural enemy abundance (a), but not richness (b) and pest predation rates (c) in vineyards. (a) Total abundance of natural enemies in high and low cover crop diversity treatments, across soil and vine guilds and landscapes ($n_{\text{high div}} = 156$, $n_{\text{low div}} = 159$). Total abundance was significantly higher in the high diversity treatment ($p < 0.05$). (b) Taxonomic richness of natural enemies across guilds and landscapes ($n_{\text{high div}} = 156$, $n_{\text{low div}} = 159$). (c) Proportion of sentinel grape moth eggs predated ($n_{\text{high div}} = 499$, $n_{\text{low div}} = 500$). Boxplots depict median values (horizontal bold lines), 25th and 75th percentiles (bottom and top of the boxes respectively), and vertical bars indicate 1.5 times the interquartile range

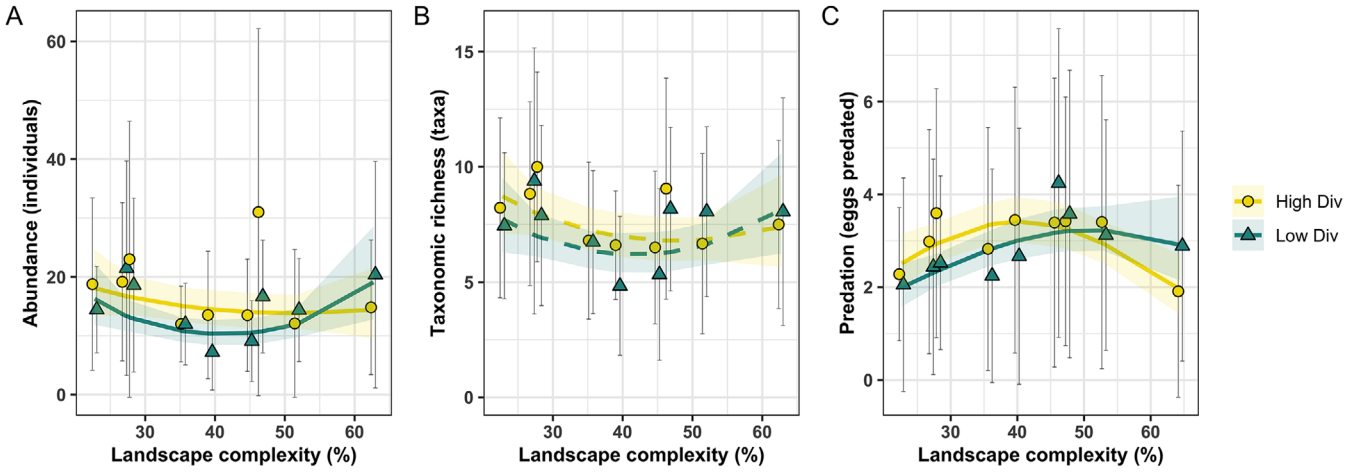

FIGURE 2 Landscape context modulates the effect of cover crop diversity on natural enemy abundance and pest predation. Relationships between landscape complexity (% of semi-natural habitats) and (a) the abundance of natural enemies across soil and vine guilds, (b) their taxonomic richness and (c) predation rates estimated by the number of sentinel eggs predated in the high versus low cover crop diversity treatments (High Div and Low Div, respectively). Slopes and 95% CI from GLMMs : solid lines ($p < 0.05$); dashed lines ($p > 0.05$). Coloured points indicate mean values across sampling distances and guilds and error bars are standard deviations (a and b: $N = 315$, $n = 18$ ($n = 15$ for landscape 36%, and High Div treatment in landscape 39%); c: $N = 999$, i = 57 ($n = 45$ for landscape 62%))

3.4 | Biological pest control

The effect of cover crop diversity on predation rates depended on the landscape context (interaction: Chi-square = 10.46, df = 2, $p = 0.005$; Figure 2). Overall, the proportion of semi-natural habitats affected predation rates non-linearly (Chi-square = 8.46, df = 2, $p = 0.015$), with higher pest predation at intermediate landscape complexity and lower rates at low and high landscape complexities. As shown in Figure 2(c), we found from 11 to 42% higher predation rates under high cover crop diversity than under low cover crop diversity at low landscape complexity (between 23 and 45% of semi-natural habitats), but similar or even lower predation rates under high compared with low cover crop diversity at high landscape complexity. There was no significant distance-decay effect of cover crops on predation rates (Chi-square = 0.03, df = 1, $p = 0.86$).

4 | DISCUSSION

The present study sheds new light on the effect of cover crop diversity and composition on biodiversity and ecosystem services in perennial agroecosystems. Our results reveal that locally increasing plant

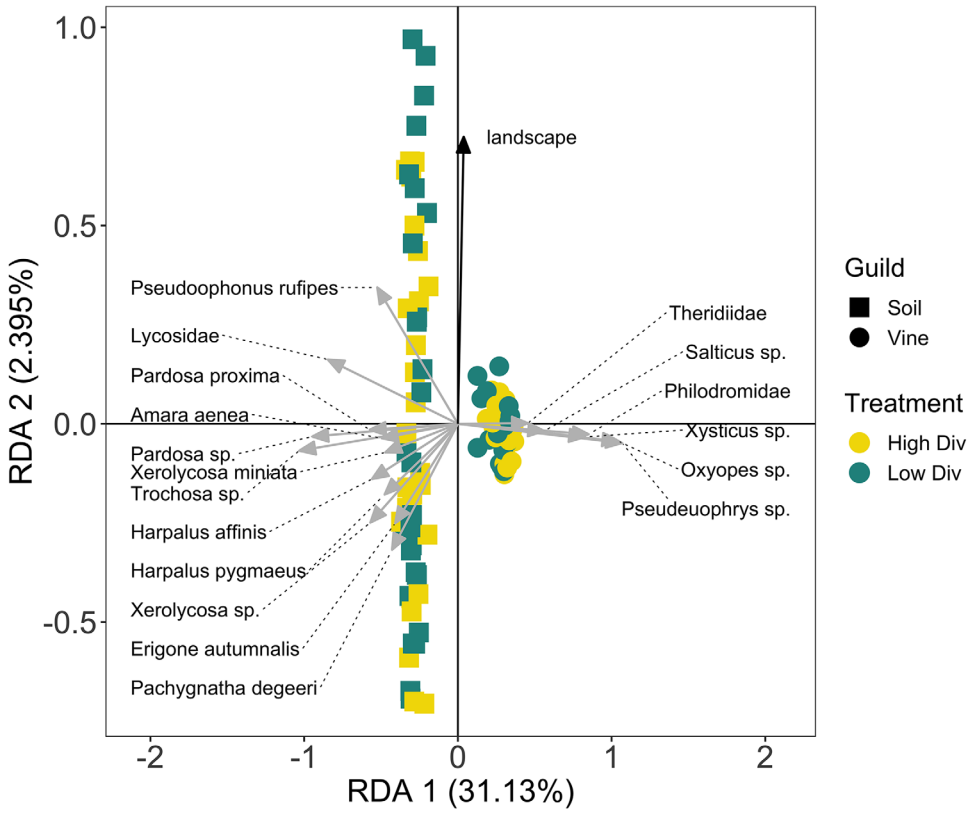

FIGURE 3 Cover crop diversity does not change natural enemy community composition. Redundancy analysis (RDA) plot of taxonomic groups and landscape complexity (% semi-natural habitats) according to the guild of natural enemies (soil and vine) and to the cover crop diversity treatment (High Div: high plant diversity, Low Div: low plant diversity). Grey arrows depict taxonomic groups that are the most correlated with each axis of the RDA

diversity using cover crops enhanced the abundance of natural enemies with positive cascading effect for biological pest control. However, locally increasing plant diversity did not influence taxonomic richness and community composition of natural enemies. Importantly, our study highlights clear interactive effects between plant community at the local scale and landscape complexity on biological pest control. We find that our cover crop treatment had the most positive effects on natural enemy abundance and biological pest control at intermediate landscape complexities, confirming that the landscape context is a key moderator of the success of local management options aiming to improve biodiversity and ecosystem services in agroecosystems.

4.1 | Cover crop diversity affected the abundance but not the taxonomic richness of natural enemies

We found that increasing the diversity of cover crops resulted in higher abundances of natural enemies in vineyards. Our findings are in line with the natural enemies hypothesis (Letourneau et al., 2011; Russell, 1989), and extend previous reports of the positive response of natural enemy abundance to flower strips adjacent to crops or to higher plant diversity within-field in agroecosystems (Sáenz-Romo et al., 2019; Tschumi et al., 2015 , 2016). The high diversity treatment included a mixture of 20 plant species belonging to different functional groups that offered a wider range of habitats, refuges and additional food sources for arthropods than the low diversity treatment, probably explaining the higher abundances of natural enemies (Balzan et al., 2014; Frank & Reichhart, 2004; Koricheva & Hayes, 2018; Langellotto & Denno, 2004; Wäckers et al., 2007). This is particularly true for spiders that dominated communities sampled in our study and that are very sensitive to habitat structure and plant diversity (Bruggisser et al., 2012; Daane et al., 2018; Langellotto & Denno, 2004). Spiders are known to respond positively to more diverse vegetation structure due to higher availability of retreats, improved microclimatic conditions and enhanced food availability (Entling et al., 2007; Kolb et al., 2020). The abundance of natural enemies decreased with the distance to the cover crop treatment across plant diversity treatments, confirming the positive effect of cover crops on natural enemies in our experiment (Figure S2). Indeed, the unsown parts of vineyards' inter-rows were covered by spontaneous, sparse vegetation across the experiment and for both treatments. These results further indicate that the positive effect of cover crops in vineyards remain localized in the sown area. The absence of significant interaction between diversity treatment and distance effects indicates that diverse cover crops also increased the abundance of natural enemies outside of the sown area.

Contrary to our hypothesis, cover crop diversity did not change the diversity nor the community composition of natural enemies. Our experiment involved a mixture of plants selected to improve not only arthropods in general, but also soil quality. It is possible that plant species mixtures specifically designed to benefit natural enemies would have yielded different results (Tschumi et al., 2016). Furthermore, one of the mechanisms by which diverse cover crops or flower strips enhance the diversity of arthropods on the relatively long term is by providing more overwintering sites (Frank & Reichhart, 2004; Ganser et al., 2019; Holland et al., 2016). Here, cover crops were sown in spring and arthropods were sampled during the following summer and early autumn. The treatment probably increased the abundance of species or taxa that were already present at these sites, but was not long enough to promote the establishment of new taxa. The low and high cover crop diversity treatments were under similar agricultural practices (pesticide use, tillage) in our experiment. Such practices probably filtered similar assemblages of arthropod species from the available species pool, but the high diversity treatment may have provided some of those species with more resources, allowing their abundance to increase. Indeed, the composition of arthropod communities was not affected by the treatment. Thus, our study reveals limited benefits of occasionally planting diverse cover crops to promote natural enemy diversity in vineyards. Future studies should address the temporal effects of cover crop diversity effects on natural enemy diversity, as well as the effects of functional plant diversity (Gardarin et al., 2018).

4.2 | The landscape context modulated cover crop diversity effects on natural enemies and biological pest control

Our results indicate that the proportion of semi-natural habitats in the landscape modulates local plant diversity effects on biological pest control services. Indeed, increasing cover crop diversity had higher relative effect on predation rates and on natural enemy abundances in simplified landscapes than in more complex ones. However, this pattern was the opposite in more complex landscapes, where high cover crop diversity treatments had lower predation rates than low cover crop diversity treatments overall. Overall, diverse cover crops had positive effects on natural enemy abundance and predation rates below 50% of semi-natural habitats, but above, the effects were inconsistent. These results are in line with the intermediate landscape-complexity hypothesis (Tscharntke et al., 2012) and may reflect higher spillover in complex landscapes, where natural enemies do find resources and refuges in semi-natural habitats around vineyards, and are thus less affected by local management practices (Landis et al., 2000; Rusch et al., 2010). Semi-natural habitats are known to benefit natural enemies (including spiders that largely dominated communities in our study) by providing refuges against disturbance, overwintering habitats, food resources and suitable microhabitats (Kolb et al., 2020; Mestre et al., 2018; Schmidt & Tscharntke, 2005). More complex landscapes therefore harbour more potential sources of early-season spillover into vineyards that may explain our findings (Hogg & Daane, 2010; Mestre et al., 2018). In simplified landscapes however, natural enemies may have benefited more from highly diverse cover crops at the local scale, as refuges and habitats around vineyards are more limited. Several studies have explored the interactive effect of local increase in plant diversity and landscape context on biodiversity or pest control services and found inconsistent results (Albrecht et al., 2020; Haenke et al., 2009; Jönsson et al., 2015; Tschumi et al., 2015; Woltz et al., 2012). Evidently, the extent to which the landscape context modulates the local effect of increased plant diversity on natural enemies and biological pest control depends on multiple factors including farming practices, species pool composition or pedoclimatic conditions that may explain the contrasted effects found in the literature (Karp et al., 2018; Muneret et al., 2019a; Woltz et al., 2012). By modifying cover crop treatments in pairs of fields within the same farm, soil type and cultivar, our study design tends to limit such confounding effects, and might explain our ability to detect significant interactive effects between local and landscape-scale context. Moreover, our findings are in line with the results of a recent study in Californian vineyards showing that flowering cover crops increase the abundance of natural enemies as well as parasitism rate of leafhoppers in landscapes with intermediate levels of diversity (Wilson et al., 2017). The hypothesis of a non-linear interactive effect between local plant diversity and landscape complexity on natural enemies and biological pest control could thus be particularly relevant in vineyard landscapes (Tscharntke et al., 2012). Here, we focused on the proportion of semi-natural habitats as a proxy of landscape complexity, as it is highly correlated with more specific measures of landscape complexity such as Shannon diversity and evenness indices in our systems (Muneret et al., 2018). Future studies could address the specific influence of other aspects of landscape complexity by accounting for the spatial arrangement of natural cover in the landscape, or the diversity of habitat patches.

Our results further highlight the complex relationships between the structure of natural enemy communities and the level of biological control services in agricultural landscapes. Indeed, high predation rates observed at intermediate landscape complexity were not associated with highest abundance or richness of natural enemies. Instead, the abundance of natural enemies (and to a lesser extent their richness) was lower at intermediate landscape complexity in our experiment. These results suggest that negative interactions between natural enemies may limit the top-down control of insect pests or that the subset of species involved in the top-down control of grape moth might respond differently than the overall predator communities. Our results may reflect lower levels of intra-guild predation or negative behavioural interactions between predators at intermediate landscape complexity where predators were overall less abundant. Furthermore, only a subset of the natural enemy community is responsible for the predation of grape moth eggs, and recent evidence indicates that small predator species are particularly important for the regulation of grape moth in vineyards (Ostandie et al., 2021). Ostandie et al. (2021) suggests that spider individuals with small biomass belonging to juveniles of the families Thomisidae and Araneidae and juveniles of *Oxyopes* sp. represented the bulk of the predator communities associated with high predation

rates of grape moth eggs in vineyards. Larger biomass species like harvestmen and earwigs that are known to benefit from semi-natural habitats in the landscape may have acted as intraguild predators feeding on intermediate predators or may have disturbed predators actually feeding on eggs of grape moth (Papura et al., 2020; Pinto Da Rocha et al., 2007).

5 | CONCLUSIONS AND RECOMMENDATIONS

Nature-based solutions are increasingly applied in agricultural systems to promote biodiversity and ecosystem services but evidence of their efficiency in real world systems remains scarce. Despite being limited in temporal and spatial scope, our study reveals important insights for managing vineyards inter-rows in ways that benefits both biodiversity conservation and grape production. We show that diverse, flowering cover crops enhance the abundance of natural enemies, which in turn increase predation rates of one of the most damaging insect pests of grape in Europe, even in the relatively short term (one season). This beneficial effect of cover crops on pest predation was mainly detected in simple landscapes (22–50% of semi-natural habitats in a 1 km radius), where it ranged from 11 to 42% higher predation rates. Such an increase could have important implications in terms of insecticide use as well as grape production. We therefore suggest that vine growers prioritize local increase in cover crop diversity in simple landscapes if they want to maximize the beneficial effects on biological pest control services. Our study provides clear recommendations for farmers and policy-makers involved in the development of agroecology in vineyards: the landscape context is a key driver of the success of practices aiming to improve biodiversity and ecosystem services by increasing within-field plant diversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A. R., D. T. and A. A. conceived the ideas and designed methodology. A. A., M. G. and A. P. collected the data. L. B. performed the analyses and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data and R codes associated with the analyses can be accessed from GitHub (https://github.com/leabeaumelle/EUCLID) and are archived in Zenodo: https://zenodo.org/record/4916881#.YMOivahKg2w (Beaumelle et al., 2021).

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ORCID

Léa Beaumelle https://orcid.org/0000-0002-7836-8767
Denis Thiéry https://orcid.org/0000-0002-9510-5651
Adrien Rusch https://orcid.org/0000-0002-3921-9750

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SUPPORTING INFORMATION

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

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