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Organic farming at local and landscape scales fosters biological pest control in vineyards

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Abstract. While organic farming practices, which are often promoted as models of ecological intensification, generally enhance biodiversity, their effects on the delivery of ecosystem services, such as biological pest control, are still unknown. Here, using a multi-scale hierarchical design in southwestern France, we examined the effects of organic farming and seminatural habitats at the local and landscape scales on biological control services of three pests, including weeds and insects, in 42 vineyards. Organic farming at the local and landscape scales was beneficial to the mean and temporal stability of biological control services, while the proportion of seminatural habitats in the landscape reduced the level of biological pest control potential. The effects of organic farming and seminatural habitats across spatial scales varied with the type of prey considered and with time. Egg moth removal rates were higher in fields under organic management compared to conventional management while weed seed removal rates increased with the proportion of organic farming in the landscape. Larval removal rates as well as seed removal rates were always more stable within time in organic fields than in conventional fields. Moreover, independently of farming system type, local variables describing the agricultural management intensity, such as pesticide use or crop productivity, were also found to be important variables explaining levels of biological control services. Pesticide use tended to reduce biological control potential, while crop productivity was associated with contrasting biological control responses depending on the pest type. Our study demonstrates the need to target multiple spatial scales and to consider farming practices, as well as the proportion of seminatural habitats, to design functional landscapes that optimize biological pest control services.

Key words: ecosystem services; landscape scale; natural pest control; organic farming; pesticide; seminatural habitats; vineyards; yield.

Introduction

Ecological intensification of agroecosystems, which consists of maximizing ecological functions that support ecosystem services, is a promising way to limit the environmental footprint of agriculture while maintaining productivity (Pretty 2008, Bommarco et al. 2013). However, its large expansion requires a deep understanding of the relationships among environmental variables and the ecological processes supported by biodiversity (Kremen and Ostfeld 2005, Bommarco et al. 2013). Within the set of ecosystem functions that support crop productivity, biological pest control is of major importance due to its strong potential to reduce pesticide use while limiting pest infestations and yield losses (Rusch et al. 2016*a*).

Several environmental variables operating at the field and landscape scales are key drivers of trophic interactions and biological pest control services in agroecosystems (Tscharntke et al. 2007, Rusch et al. 2017*a*). Organic farming at the field scale is among the main management options that support biodiversity and associated ecosystem services in agricultural landscapes (Gabriel et al. 2010, Tuck et al. 2014). Organic farming is, therefore, currently promoted worldwide as an agri-environmental scheme, but its performance in terms of biological pest control remains ambiguous. Organic farming increases diversity and the abundance levels of natural enemies of crop pests (Tuck et al. 2014, Lichtenberg et al. 2017). Moreover, the suppression of phytophagous species is generally greater in more diverse natural enemy communities than in species-poor communities, suggesting a higher level of biological pest control in organic fields (Letourneau et al. 2009). However, studies examining the relationships between organic management practices and the biological control level have produced inconsistent results, which suggests strong context dependencies (Roschewitz et al. 2005, Macfadyen et al. 2011, Maalouly et al. 2013).

Landscape context, and especially the proportion of seminatural habitats (defined here as landscape

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complexity) in the landscape, is also known as a key driver enhancing the abundance and diversity of natural enemies, as well as the levels of biological control services (Chaplin-Kramer et al. 2011, Rusch et al. 2016*a*). It has been proposed that landscape complexity may have a hump-shaped relationship with the beneficial effect of organic farming at the local scale (Tscharntke et al. 2005, Concepción et al. 2008). To date, the interactive effects of local management and landscape complexity on biological pest control have yielded contrasting results (Winqvist et al. 2011, Birkhofer et al. 2016). In addition, studies on biological pest control services did not explicitly consider the effect of farming practices within the landscape and how this may interact with other aspects of landscape structure on service provision. However, farming practices at the landscape scale could strongly affect population dynamics, species assemblages and trophic interactions. Few studies have empirically explored the effect of increasing the area under organic farming on natural enemies but not its cascading effect on biological control as well as its interactions with the proportion of seminatural habitats in the landscape (Inclan et al. 2015, Diekötter et al. 2016). However, assessing the relative performances of organic farming systems as the area cultivated under organic management increases is of crucial importance to guide land-use planning. We could hypothesize that increasing the area under organic farming will strengthen natural enemy communities, leading to a higher biological control potential. However, pest communities could also benefit from the greater area under organic farming owing to the lower efficiency levels of organic management options (Adl et al. 2011, Bianchi et al. 2013). Moreover, these effects might be affected by the proportion of seminatural habitats in the landscape, which affects the species pool of both natural enemies and pests (Tscharntke et al. 2007). Thus, examining the balance between biological control potential and pest infestation levels under different land-use regimes is required to determine the effects of organic farming expansion on pest communities and crop damage.

In most of the literature to date, biological control is often measured at one sampling date or by an aggregated measure over several sampling dates while the temporal dynamics in the delivery of biological control may affect crop productivity (Roschewitz et al. 2005, Thies et al. 2005). Landscape context and farming practices are expected to affect biological control services through the timing of the natural enemy's arrival (Thorbek and Bilde 2004, Costamagna et al. 2015). Fields located in landscapes having higher proportions of seminatural habitats are more likely to control pest populations earlier in the season than simple landscapes because of the greater and earlier levels of field colonization from source habitats (Raymond et al. 2015).

In this study, we investigated the relative effects of farming systems (organic and conventional) and seminatural habitats at local and landscape scales on the level and the temporal variability of biological pest control potential in vineyards in southwestern France. Using an experimental design based on 42 paired vineyards (organic and conventional pairs) located in 21 contrasting landscapes, we evaluated the levels of biological control by measuring the predation of three different pest types, grape moth eggs, grape moth larvae, and weed seeds, throughout the season.

We hypothesized positive effects of organic farming at the local scale on the level and the temporal stability of biological control services. We expected that increasing the proportion of organic farming in the landscape would also benefit biological control services, but that this positive effect would only be detected in conventional fields owing to spillover between organic and conventional vineyards (Fig. 1). We therefore expected the same level of biological control services among organic fields but an increasing level of biological control services commensurate with the proportion of organic farming among conventional fields (Fig. 1). Furthermore, we hypothesized a positive effect of the proportion of seminatural habitats in the landscape on biological control services but we expected a higher effect of seminatural habitats on conventional fields (i.e., a higher slope between seminatural habitats and the biological control in conventional fields) than on organic fields (Fig. 1). Moreover, we hypothesized that organic farming in the landscape could partly compensate for lower proportions of seminatural habitats in the landscape (i.e., similar levels of biological control are expected in very complex landscapes compared to landscapes of intermediate level of complexity but with higher proportion of organic farming). This effect was expected because we assumed that organic fields might support a set of natural enemies different from those supplied with seminatural habitats, both of them should provide biological control. Because we assumed a major role for seminatural habitats in shaping the pool of natural enemy species in the landscape, we predicted that biological control services could not be maximized in landscapes with very low proportions of seminatural habitats and very high proportions of organic farming.

METHODS

Study sites and design

Our study design consisted of 21 pairs of organic and conventional vineyards (42 plots in total) located in southwestern France, near Bordeaux, within the largest French wine-growing region (44°81′ N, 0°14′ W; Fig. 2). Pairs of vineyards were on average 125 m apart to limit differences in soil types or climatic conditions and were selected along two orthogonal landscape gradients: a gradient of the proportion of seminatural habitats and a gradient of the proportion of organic farming. The landscape gradients were established based on landscape composition calculated at a 1-km radius around each focal vineyard. At this scale,

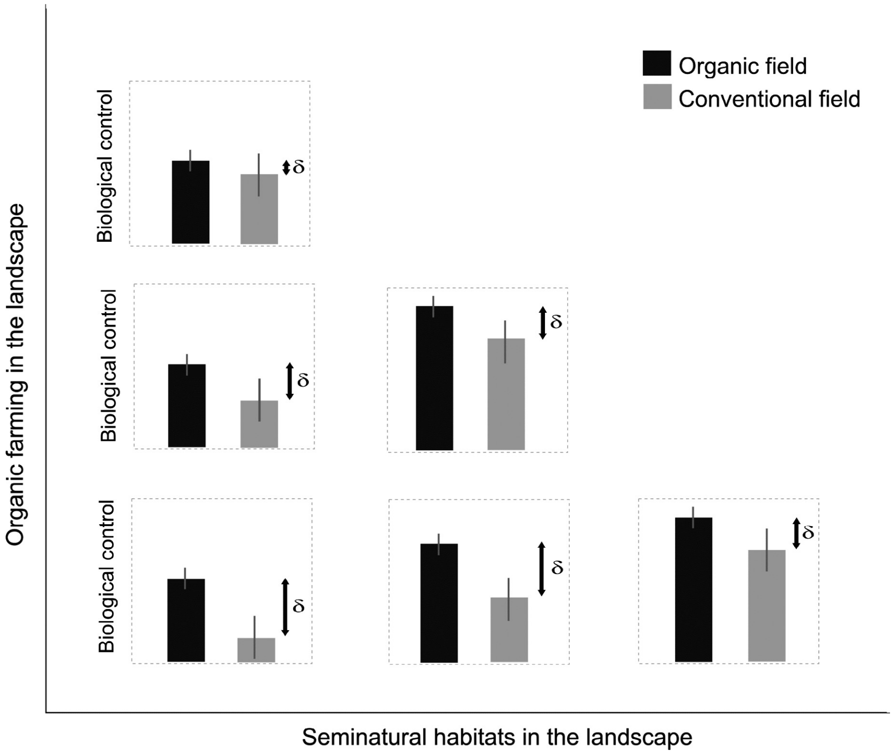

FIG. 1. Schematic representation of the expected effects of organic farming at local and landscape scales on the mean and stability of biological pest control services. Our hypothesis suggested that the beneficial effects of organic farming applied at a field scale on biological control services (or biodiversity) are dependent on the landscape composition in terms of seminatural habitats and organic farming. Specifically, increasing the proportion of organic farming in the landscape would be more beneficial to biological control services in conventional fields than in organic fields because of the spillover between organic and conventional fields. In addition, seminatural habitats were expected to provide more natural enemies than agrosystems; thus, fields located in landscapes having a high proportion of seminatural habitats should have higher levels of biological control. The beneficial effect of seminatural habitats would be higher than conventional fields because they support less biodiversity with all other things being equal (Tscharntke et al. 2005, Concepción et al. 2008). The variable δ represents the difference of biological control levels between organic and conventional fields that varies according to the landscape context. Values shown are expected means and their expected standard deviations.

the proportion of seminatural habitats ranged from 1% to 75%, and the proportion of organic farming ranged from 2% to 25% of the total land area. This study design allowed for the unraveling of farming system effects at the local scale as well as the relative effects of the proportions of seminatural habitats and organic farming at the landscape scale on biological control services. All organic vineyards had been converted to organic farming for at least five years. Landscape variables were also calculated at three other spatial scales: 250, 500, and 750 m radii around each vineyard using ArcGIS 10.1 (ESRI, Redlands, California, USA). Orthogonality among landscape gradients was maintained at all scales.

Biological control potential

In each vineyard, biological control potential was estimated using removal rates of sentinel prey species (Meehan et al. 2012). We measured multiple removal rates using different prey types: eggs and larvae of two grape moths (*Lobesia botrana* and *Eupoecilia ambiguella* belonging to the Tortricidae family) and weed seeds of three species (*Capsella bursa-pastoralis*, *Plantago lanceolata*, and *Chenopodium album*). We used eggs and larvae of Tortricidae because they are prominent grape pests worldwide, including in the study region, and they are potentially regulated by different taxa (van der Geest and Evenhuis 1991, Thiéry and Moreau 2005). We selected these weed species because they are common plant species within vineyards in our study region and because they differ in size and mass, which allows them to be potentially predated by different species throughout the season (Honek et al. 2006, Trichard et al. 2013). Thus, our assessment covered the services provided by predators as well as granivorous invertebrates and vertebrates. All of the sentinel preys were exposed three times over the growing season, from late May to early October in 2015, which is the period when they are naturally present and observed in the vineyards (see Muneret et al. 2018). Both species of Tortricidae have between two to four generations over the growing season under Bordeaux vineyard conditions (Thiéry et al. 2018). Note

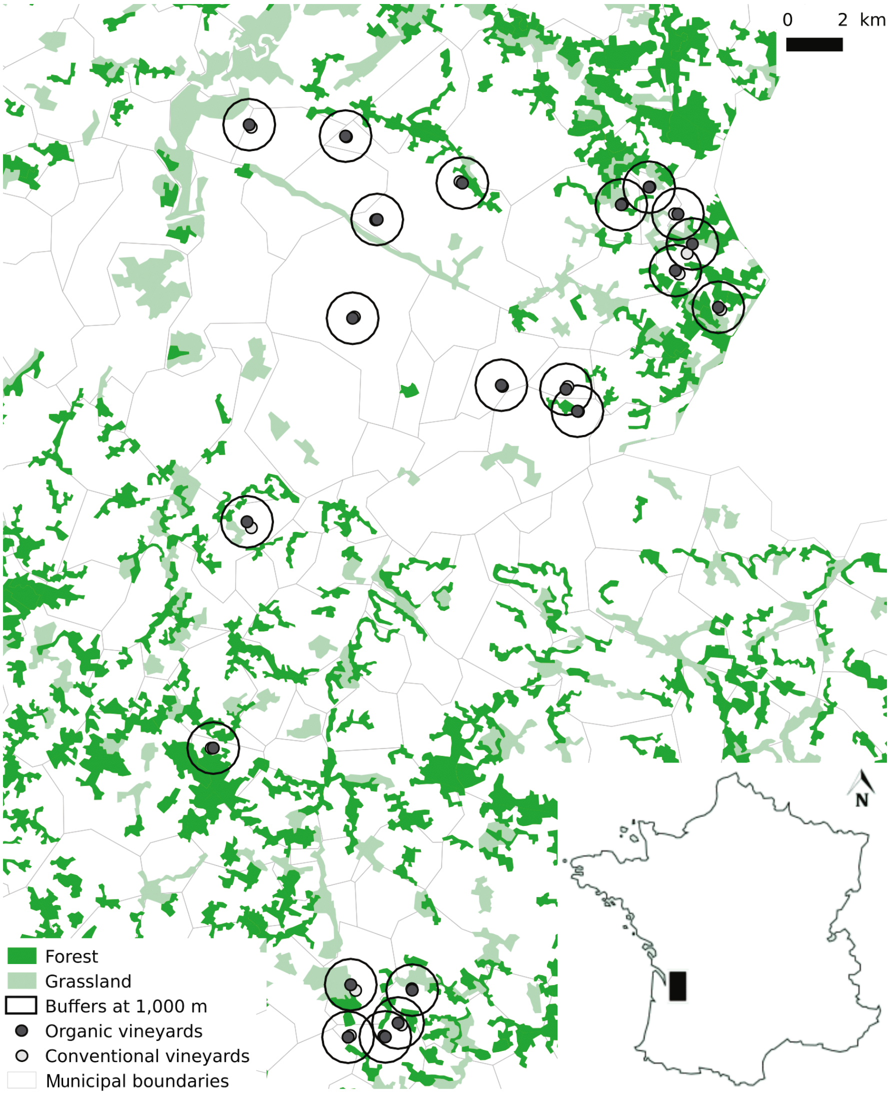

FIG. 2. Map of the study area in France with the 42 focal vineyards. The buffers, which have been calculated at a 1,000-m scale, were represented. For clarity, we only represented the buffers around organic vineyards.

that the third sampling date related to the seed predation occurred just after the grape harvest (in early October; Table 1).

The sentinels were exposed on (1) three vine rows for the eggs and larvae of grape moths and (2) under one vine row for the seeds, located between the 5th and 15th closest vine rows of the paired fields. All the sentinel cards were settled at least 10 m away from the edge or from any other sentinel card. Laboratory-reared eggs of *L. botrana* laid on parchment paper (which was previously glued on felt) were used to measure removal rate of eggs in vineyards. Parchment paper pieces (~1 × 3 cm) supporting 10 moth eggs were cut and glued on plastic cards (~1 × 8 cm). Ten cards were then exposed in each plot for five days at the first sampling date and four days at the following two sampling dates. Cards were attached to the vine stock as close as possible to the grapes. The removal rate of larvae was determined using laboratory-reared larvae of *E. ambiguella*. Five larvae were pinned on 10 cardboard cards and exposed to predation for 24 h at the three sampling dates. Larvae

TABLE 1. Sampling periods for measuring biological control services on each sentinel prey.

Sentinel prey	Sampling date 1 Early season	Sampling date 2 Mid season	Sampling date 3 Late season
Egg	19–27 May	22–27 June	4–11 August
Larva	2–12 June	30 June–10 July	26–28 August
Weed seed	19–27 May	22 June–3 July	2–13 October

cards were also attached to the vine stock as close as possible to the grapes. Weed seed removal rate was examined by exposing 90 seeds per plot, belonging to three weed species, glued on three sandpaper cards (~10 × 10 cm) at each sampling date. We glued them on cards using a specific glue (Tangle-Trap; TangleFoot, Grand Rapids, Michigan, USA) so that granivorous species were able to remove them. We also covered the potential apparent glue with sand to prevent the adherence of granivorous arthropods. In fields, we nailed the cards to the ground under one vine row for seven days. A total of 50 larvae, 100 eggs, and 90 seeds were exposed in each plot at each sampling date. At the end of the exposure period, the number of remaining individuals was counted on each card.

Description of the vineyard management

All vineyards were managed as usual by 38 different farmers. To move beyond the traditional dichotomy between organic and conventional farming systems and analyze the relative impacts of specific practices or their combinations on biological pest control services, we collected data related to crop management by interviewing the farmers (see Appendix S1: Table S1). We collected data on crop density, field age (i.e., time since planting), soil tillage practices, and pesticide applications for each vineyard. For each field, we calculated the treatment frequency index (TFI; OECD 2001) as described in Muneret et al. (2018) to evaluate the pesticide-use intensity. We also built a unitless index of tillage intensity that corresponded to the number of tilling operations per year weighted by the area involved, as follows:

$$\text{Tillage intensity} = \frac{d_{\text{und}}}{d_{\text{tot}}} \times N_{\text{und}} \times p_{\text{und}} + \frac{d_{\text{bet}}}{d_{\text{tot}}} \times N_{\text{bet}} \times p_{\text{bet}}$$

where d_{tot} represents the total distance between two vine rows. This total distance is divided in two parts because they are managed in different ways to control weeds, while keeping the carrying capacity of the soil. The variable d_{und} represents the distance under the wine row (~60 cm) and d_{bet} represents the remaining total inter-row distance. N_{und} and N_{bet} represent the numbers of tilling operations for each type of distance. Finally, p_{und} and p_{bet} represent the proportion of the under- and between-row concerned with the operation, respectively, because often one-half, or even less, of the between-row areas are tilled in vineyards. Additionally, crop productivity was estimated a few days before harvest by counting the number of grapes on 20 randomly chosen vine stocks and by weighing 25 randomly chosen grapes from different vine stocks. We multiplied the average number of grapes per vine by the average grape mass and the vine-stock density per vineyard to calculate the crop productivity (Mg). The crop productivity in this study design did not significantly differ between local farming systems (organic and conventional), and we were not able to estimate crop productivity for 2 of the 42 vineyards (Muneret et al. 2018).

Data analyses

Generalized linear mixed models with binomial error distributions were used to examine the effects of farming systems and the landscape context on the average biological control for each type of pest. For each pest type, the response variable was defined as the number of individuals removed vs. the number of remaining individuals per card in all models. In total, our analyses included 1,176 larva cards, 1,169 egg cards, and 1,065 seed cards for the 40 vineyards included in this section. For each pest type, we fitted six models of increasing complexity (M0, M1, and M2 at the four landscape scales) and we used a multimodel inference approach to test our hypotheses. This approach makes it possible to first consider local covariates not controlled by our experimental design and to progressively include explanatory variables at the farming system and the landscape levels. This approach is therefore much more conservative than only analyzing the effect of the variables of our study design and limit potential bias related to uncontrolled covariates. Moreover, this modeling procedure allows us to identify the most important spatial scale for explaining pest removal rates. All the models fitted at each step had the same baseline structure containing the sampling date as a fixed term and three random terms, field nested in the field pairs effect to account for the study design, and the observation effect to correct for over dispersion.

The first model, M0, included five local covariates: field age and vine stock density, which were considered as potential confounding covariates, as well as total TFI, tillage intensity, and crop productivity, which were considered as descriptors of the local management performance. Covariates that were significant at the M0 step (i.e., with a confidence interval significantly different from zero) were conserved and included in the M1 models. Therefore, the explanatory variables included in M1 models were the selected local covariates and local farming systems and an interaction term between local farming system and sampling date in addition to the baseline structure. M1 models allow for the testing of the effects of local farming systems on biological control services after taking into account the potential confounding effects of specific local covariates. Finally, we fitted four different M2 models, one for each spatial scale (250, 500, 750 and 1,000 m) to test our hypotheses related to the effects of the landscape context and its interactions with local farming systems on biological control. M2 models included the same structure as M1 models, but also considered landscape variables at a given scale and interactions between (1) the sampling date and landscape variables, (2) the local farming system and landscape variables, and (3) landscape variables with each other (see Appendix S1: Table S2 to recap all of the terms included in these models).

At each step, all the possible models were ranked using the Akaike Information Criteria (AIC), and models with a ΔAIC < 2 were retained among the set of top models. This set of top models was then used to estimate the mean effects and confidence intervals of each explanatory variable using model averaging (Grueber et al. 2011). We calculated the marginal R^2 values and conditional R^2 values of the model having the lowest AIC at each step to evaluate the amount of variability explained for each level of model complexity (Nakagawa and Schielzeth 2013). Before modeling, we standardized all explanatory variables, with mean equal to 0 and standard deviation equal to 0.5 (Schielzeth 2010). If required, then we used the BOBYQA optimizer to assist with model convergence.

To determine the level of model complexity, and indirectly the spatial scale, that was the most important for explaining our response variables, we recalculated the Akaike weights among all of the models from the six different sets (i.e., M0, M1, and M2 at four spatial scales) obtained for each pest exposed. We, therefore, estimated the relative importance of each level of complexity for a given response variable. The sum of the Akaike weights (Sum W_i) of the models obtained at a given level of complexity provided the model's probability of being the top model across all of the scales.

In addition to the average level of biological control for each pest type, we calculated the temporal variation of the biological control. We first averaged raw data per field and sampling date. Then, we calculated the coefficient of variation of the biological control for each vineyard ([SD/mean] × 100) based on the three sampling dates for each pest type. We then used linear mixed models to evaluate the effects of farming systems and the landscape context on the temporal variation of biological controls (n = 38 for larvae, n = 40 for eggs, and n = 120 for seeds). For the mean biological control, we used the same modeling procedure (M0, M1, and M2 at the four landscape scales) but we included less covariates in the models at each step owing to the size of the dataset. In M0, we included field age, vine stock density, total TFI, and tillage intensity. We did not include crop productivity as an explanatory variable because it required the removal of two vineyards from the data set. In the M2 models, we included interactions between local farming systems and each landscape variable to test our hypothesis, but we removed the interaction between landscape variables to limit the number of predictors in our models. Because the response variables were calculated using the three sampling dates, we did not include sampling date as an explanatory variable. Note that we used the AIC$_c$ (AIC corrected for small sample sizes) to select the top models because of the size of the data set.

Diagnostic residual plots of all full models were confirmed using the DHARMa package (Hartig 2017). Using variograms, we detected no spatial autocorrelation among the residuals. Collinearity among explanatory variables was assessed using the variance inflation factor and no collinearity among predictors was detected (the highest value was 2.29 for the total TFI) (Appendix S1: Fig. S1). All analyses were performed using the R software (R Core Team 2016) and the packages lme4 (Bates et al. 2014) and MuMIn (Bartoń 2016).

RESULTS

On average, 88% ± 28% (mean ± SD) and 84% ± 32% of the exposed larvae were removed in organic and conventional vineyards, respectively. Egg removal rate was, on average, 45% ± 36% in organic and 39% ± 35% in conventional vineyards, and 20% ± 22% of the weed seeds were removed in both organic and conventional vineyards. Over the growing season, the overall level of biological control, calculated as the mean level of removal of all pest types, was higher in midseason (58% ± 39%) followed by late season (50% ± 41%) and early season (44% ± 40%).

Removal rates of pest eggs and larvae

For egg removal rates, models containing local covariates, local farming systems, sampling dates, landscape variables (i.e., proportions of organic farming and seminatural habitats), and interactions had the highest probabilities of being top models (Sum $W_{i\_250\mathrm{m}} = 0.33$, Sum $W_{i\_500\mathrm{m}} = 0.1$, Sum $W_{i\_750\mathrm{m}} = 0.35$, and Sum $W_{i\_1000\mathrm{m}} = 0.22$; Appendix S1: Fig. S2). Models fitted using local covariates or local farming systems had a probability close to zero of being selected as top models (Sum $W_{i\_\mathrm{local}} \approx 0$; Appendix S1: Fig. S2). None of the landscape scales were clearly identified as the most relevant to explain egg removal rates because no fitted model had a major probability of being selected as the best model.

Nonetheless, several variables were significantly related to egg removal across scales. First, among local covariates, the crop density was positively correlated with the proportion of egg removed, while crop productivity and total TFI were negatively correlated with the proportion of egg removed (Table 2; Fig. 3a, b). Egg removal rates also varied according to sampling dates, with the midseason sampling date exhibiting the highest level of egg removal (61% ± 32%) compared with the early and the late sampling dates (33% ± 27% and 31% ± 37%, respectively). Second, all models fitted using landscape variables showed two significant interactions: one between the sampling date and the local farming system and the second between the sampling date and the proportion of seminatural habitats (Table 2). Specifically, organic vineyards showed higher levels of egg removal than conventional ones in the late season, while they were similar in the early season (Table 2, Fig. 4a). At the same time, the effect of the proportion of seminatural habitats on egg removal was increasingly negative over the year (Table 2, Fig. 4b). The removal rate of

TABLE 2. Selection table for models explaining egg predation in vineyards.

Models and variables	Sum W_i	AIC	df	Estimates	CI	Relative variable importance	Variance	SD
M0 (R^2_m = 0.13; R^2_c = 0.17)	<0.01	5,210	9					
Intercept				−1.02	−1.36, −0.68			
Vine trunk density				0.6	0.06, 1.14	1		
Total TFI				−0.44	−0.74, −0.13	1		
Mid season				1.91	1.59, 2.23	1		
Late season				−0.29	−0.61, 0.03			
Crop productivity				−0.71	−1.15, −0.27	1		
Tillage intensity				0.02	−0.28, 0.43	0.22		
Field age				−0.01	−0.45, 0.34	0.21		
obs(field × pair)							*3.92*	*1.98*
field × pair							*0.00*	*0.00*
pair							*0.37*	*0.61*
M1 (R^2_m = 0.13; R^2_c = 0.17)	<0.01	5,210	9					
Intercept				−1.02	−1.38, −0.66			
Vine trunk density				0.59	0.06, 1.13	1		
Total TFI				−0.44	−0.79, −0.10	1		
Mid season				1.91	1.59, 2.23	1		
Late season				−0.29	−0.61, 0.03			
Crop productivity				−0.7	−1.14, −0.27	1		
Local farming systems (Conventional)				−0.01	−0.46, 0.38	0.27		
obs(field × pair)							*3.91*	*1.98*
field × pair							4.67×10^{-15}	6.83×10^{-8}
pair							*0.381*	*0.62*
M2 at the 750-m scale (R^2_m = 0.13; R^2_c = 0.17)	0.35	5,199	14					
Intercept				−1.08	−1.44, −0.72			
Vine trunk density				0.59	0.09, 1.09	1		
Total TFI				−0.44	−0.78, −0.11	1		
Proportion of organic farming				−0.46	−1.42, 0.30	0.83		
Proportion of seminatural habitats				−0.54	−1.46, 0.37	1		
Mid season				1.91	1.55, 2.28	1		
Late season				−0.14	−0.56, 0.27			
Crop productivity				−0.7	−1.18, −0.28	1		
Proportion of organic farming × Proportion of seminatural habitats				−0.86	−2.95, 0.21	0.63		
Proportion of seminatural habitats × Mid season				−0.03	−0.64, 0.57	1		
Proportion of seminatural habitats × Late season				−1.02	−1.63, −0.40			
Local farming systems (Conventional)				0.02	−0.48, 0.68	0.24		
Local farming systems × Mid season				−0.04	−0.91, 0.34	0.13		
Local farming systems × Late season				−0.09	−1.31, −0.04			
Proportion of organic farming × Mid season				−0.09	−1.85, 0.26	0.11		
Proportion of organic farming × Late season				−0.03	−1.36, 0.76		*3.87*	*1.97*
obs(field × pair)							9.81×10^{-16}	$3.13 \times 10_{-8}$
field × pair							*0.23*	*0.48*

Notes: The table reports the explanatory variables selected, estimates, confidence intervals (2.5–97.5%) and the relative importance of the best model (M2 at the 750-m scale, which had the highest sum of Akaike weights normalized across all spatial scales, see Appendix S1: Table S2). The sums of the Akaike weights normalized across each spatial scale (Sum W_i) provides the probability of a given level of complexity to appear among the top models. Relative variable importance gives the probability of the explanatory variable being in the set of top models at the given scale (a value of 1 means that the variables are in all the best model at this scale). R^2 marginal and R^2 conditional are reported (R^2_m and R^2_c, respectively). R^2, AIC, and degrees of freedom (df) values were calculated using the best models at this scale. Random terms were calculated using the full model at each scale. For each model, random terms are presented in italic. TFI, treatment frequency index.

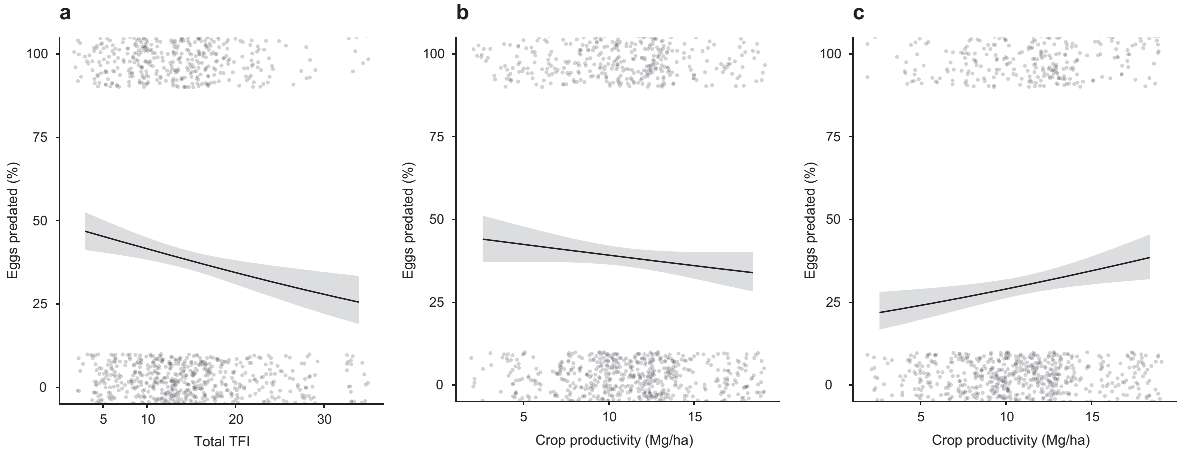

FIG. 3. Relationships between the local management intensity and predation rates of moth eggs and weed seeds. Relationships between (a) pesticide use, measured as the total treatment frequency index (TFI), and average egg predation, (b) crop productivity and average egg predation, and (c) crop productivity and seed predation. Note that the response variable has been dichotomized into a dummy variable (0/1) by median for plotting purposes only.

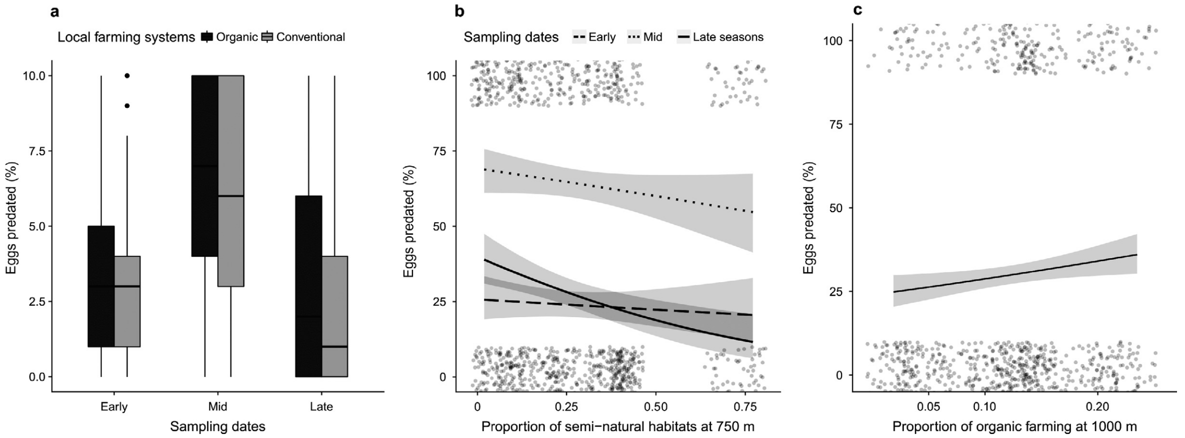

FIG. 4. Effects of organic farming and seminatural habitats on biological control services. Specifically, the relationships are between (a) the average egg predation and local farming systems, (b) the average egg predation and the proportion of seminatural habitats over the season, and (c) the average seed predation and the proportion of organic farming in the landscape. Note that the response variable has been dichotomized into a dummy variable (0/1) by median for plotting purposes only. In the boxplots, mid line represents the median, upper and lower edges represent the 75th and 25th quartiles of the data, whiskers extend to the largest values (until 1.5 times the interquartile range) and points are extreme values.

the grape moth larvae was never significantly explained by any local or landscape variables at any scale (Appendix S1: Table S3).

Removal rates of weed seeds

Models fitted using sampling dates, crop productivity, local farming systems, and landscape variables at the 1,000-m scale had the highest probabilities of being among the set of top models (Sum $W_{i\_1000\mathrm{m}} = 0.81$; Appendix S1: Fig. S2). Models fitted using local covariates and/or local farming systems had probability levels of near zero of being selected as top models (Appendix S1: Fig. S2). Models fitted at this spatial scale revealed that weed seed removal was positively related to crop productivity and to the proportion of organic farming in the landscape (Figs. 3c, 4c, Table 3). These models also indicated a significant effect of the sampling date on weed seed removal. Specifically, weed seed removal rates increased significantly throughout the growing season, with the percentage of removed seeds reaching 12.71% ± 16.26% in the early season, 23.39% ± 25.16% in the midseason, and 25.11% ± 22.30% in the late season. Finally, the interactions between sampling dates and the proportion of organic farming were also significant (Table 3). The effect of the proportion of organic farming was positive in the early and late seasons and negative in the midseason.

TABLE 3. Selection table for models explaining weed seed predation in vineyards.

Models and explanatory variables	Sum W_i	AIC	df	Estimates	CI	Relative variable importance	Variance	SD
M0 (R^2_{m} = 0.05; R^2_{c} = 0.07)	<0.01	3,998	7					
Intercept				−2.45	−2.68, −2.22			
Mid season				0.89	0.65, 1.13	1		
Late season				1.05	0.82, 1.29			
Crop productivity				0.3	0.01, 0.59	1		
Field age				−0.1	−0.51, 0.08	0.45		
Tillage intensity				−0.02	−0.37, 0.19	0.22		
Vine trunk density				−0.02	−0.49, 0.26	0.21		
Total TFI				−0.01	−0.30, 0.20	0.1		
obs(field × pair)							*1.41*	*1.19*
field × pair							*0.03*	*0.17*
pair							*0.09*	*0.31*
M1 (R^2_{m} = 0.05; R^2_{c} = 0.07)	<0.01	3,998	7					
Intercept				−2.44	−2.69, −2.20			
Mid season				0.89	0.65, 1.13	1		
Late season				1.05	0.82, 1.29			
Crop productivity				0.31	0.04, 0.58	1		
Local farming systems (Conventional)				−0.01	−0.27, 0.18	0.28		
obs(field × pair)							*1.41*	*1.19*
field × pair							*0.04*	*0.20*
pair							*0.010*	*0.31*
M2 at the 1,000-m scale (R^2_{m} = 0.06; R^2_{c} = 0.08)	0.81	3,982	10					
Intercept				−2.22	−2.50, −1.94			
Proportion of organic farming				0.96	0.19, 1.74	1		
Mid season				0.6	0.30, 0.90	1		
Late season				1.11	0.82, 1.41			
Crop productivity				0.32	0.06, 0.58	1		
Proportion of organic farming × Mid season				−1.29	−2.13, −0.46	1		
Proportion of organic farming × Late season				0.28	−0.55, 1.11			
Local farming systems (Conventional)				−0.01	−0.25, 0.19	0.22		
Proportion of seminatural habitats				0.01	−0.27, 0.35	0.22		
obs(field × pair)							*1.36*	*1.17*
field × pair							*0.03*	*0.18*
pair							*0.07*	*0.26*

Notes: The table reports the explanatory variables selected, estimates, confidence intervals (2.5–97.5%) and the relative importance of the best model (M2 at the 1,000-m scale, which had the highest sum of Akaike weights normalized across all spatial scales, see Appendix S1: Table S2). The sum of the Akaike weight normalized across each spatial scale (Sum W_i) provides the probability of a given level of complexity to appear among the top models. Relative variable importance gives the probability of the explanatory variable being in the set of top models at the given scale (a value of 1 means that the variables is in all the best model at this scale). R^2 marginal and R^2 conditional are reported. R^2, AIC, and degrees of freedom (df) values were calculated using the best models at this scale. Random terms were calculated using the full model at each scale. Random terms were calculated using the full model at each scale. For each model, random terms are written in italic. TFI, treatment frequency index.

Temporal variation of removal rates over the growing season

Removal rates variability of eggs and larvae.—For removal rates of larvae, model fitted using local farming systems and landscape variables at 250-m scale had the highest probability of being among the set of top models (Sum $W_{i\_250\mathrm{m}} = 0.74$; Appendix S1: Fig. S3). At this scale, conventional vineyards had a higher level of temporal variation of level of removal than organic vineyards, and this effect was modulated by landscape complexity (Fig. 5a, Table 4). The temporal variation of removal rate of larvae was even higher in conventional vineyards embedded in complex landscapes than in simple landscapes. The temporal variation of egg removal was never significantly explained by any local or landscape variables at any scale (Table 4).

Weed seed removal variability.—Model fitted using local farming systems and landscape variables at the 750-m scale had the highest probability of being among the set of top models (Sum $W_{i\_750\mathrm{m}} = 0.33$; Appendix S1: Fig. S3). At this scale, as well as at the other scales, conventional system increased the temporal variation of seed removal over the year (Table 4; Fig. 5b).

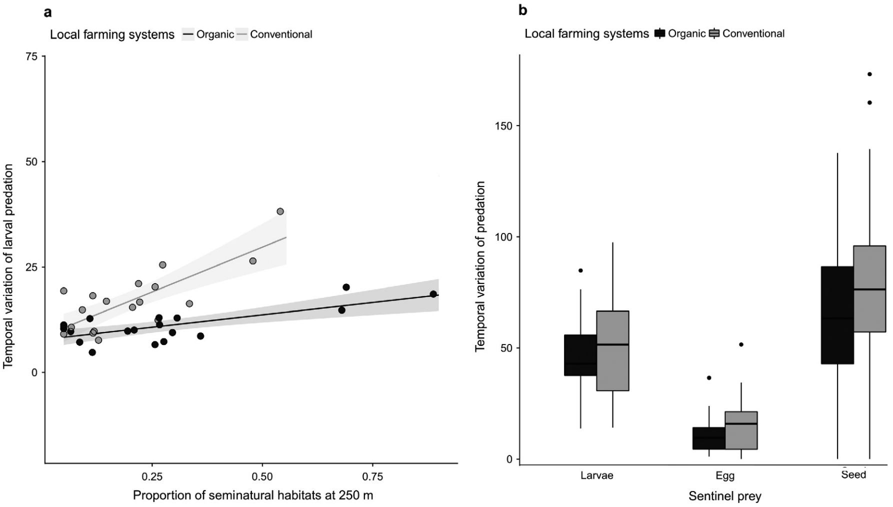

FIG. 5. Effects of local farming systems and seminatural habitats on the temporal variability of biological control services. (a) Landscape complexity-dependency effect of local farming systems on temporal variability of larval predation and (b) effect of sentinel prey types and local farming systems on the temporal variability of biological control over the year.

DISCUSSION

This is the first study examining the independent and joint effects of the proportions of organic farming and seminatural habitats at multiple spatial scales on biological pest control potential in agricultural landscapes. Our study shows that the effects of organic farming and seminatural habitats across spatial scales vary with the type of prey considered and with time. However, organic farming considered at either the local or the landscape scale was an important predictor explaining the average and the variability of biological control in vineyards. When significant, organic farming always enhanced biological control potential in comparison to conventional farming. In addition, and contrary to our hypotheses, increasing the proportion of seminatural habitats had no or negative effects on biological control potential. Our results therefore suggest that biological control services may be supplied more by agrobiont species than by species colonizing vineyards from seminatural habitats. Our analyses also highlighted that, despite local or landscape effects of organic farming and seminatural habitats, key local variables related to crop management, such as pesticide use and crop productivity, were important to consider when studying biological pest control.

Positive effects of organic farming on biological control at multiple scales

At the field scale.—This study revealed positive effects of organic farming at the field scale on biological control potential but mostly in interaction with either time or the landscape context. First, organic fields had higher levels of eggs removal rates at the end of the growing season compared with conventional fields, while the levels were similar at the beginning. Second, the temporal variability of removal rates was lower in organic fields for all three sentinel prey species, although this positive effect was only significant for seed removal and for larval removal when interacting with the proportion of seminatural habitats at the 250-m scale. Thus, organic farming at the field scale enhanced the biological control of eggs within a time period and showed a lower temporal variability level of larval removal rates relative to conventional farming. Such beneficial effects of organic farming could be attributed to differences in management practices between the two farming systems. Since total TFI had only one single significant negative effect and tillage intensity was never important, we assumed that a combination of practices more than specific farming practices could explain positive effects of organic farming on biological control. Moreover, weed cover can be more diversified in organic than in conventional systems (Nascimbene et al. 2012), which could benefit natural enemies and biological pest control through bottom-up effects (Langellotto and Denno 2004, Rusch et al. 2017*b*). Our results corroborate those of several studies that showed positive effects of organic farming at the local scale on some aspects of biological control services (Winqvist et al. 2011, Gagic et al. 2012, Lohaus et al. 2013). Lohaus et al. (2013), in cereal fields, found a positive effect of organic farming on aphid parasitism rates later in the season. Moreover, Gagic et al. (2012) found that organic fields had lower temporal variability levels in aphid–parasitoid food webs than in conventional fields. Our results also highlight that the effect of organic farming depends on the pest species, which could explain the variable results found in the literature (Macfadyen et al. 2009, Birkhofer et al. 2016).

At the landscape scale.—This study revealed that the proportion of organic farming in the landscape had a positive effect on weed seed removal, while it did not significantly affect larval or egg removal. Our study suggests that the granivorous species involved in the weed seed predation service, which potentially includes carabids, rodents, and birds, respond positively to organic farming in the landscape, at the 1-km or smaller spatial

TABLE 4. Selection table for models explaining the temporal variability of each type of predation in vineyards.

Sentinel prey, model, and explanatory variables selected	Sum W_i	AIC	df	Estimates	CI	Relative variable importance
Larva						
M0 ($R^2_{\mathrm{m}} = 0.17$; $R^2_{\mathrm{c}} = 0.40$)	0.04	279	7			
Intercept				13.74	9.58, 17.90	
Field age				0.11	−8.96, 9.24	0.76
Vine stock density				3.58	−5.95, 13.11	1
Total TFI				9.71	2.45, 16.98	1
Tillage intensity				1.75	−5.77, 10.29	0.77
Crop productivity				−5.8	−14.72, 3.11	1
M1† ($R^2_{\mathrm{m}} = 0.12$; $R^2_{\mathrm{c}} = 0.19$)	<0.01	285	5			
Intercept				13.62	7.77, 19.47	
Local farming system (Conventional)				0.56	−8.91, 10.03	1
Total TFI				7.47	−2.15, 17.08	1
M2 at the 250-m scale† ($R^2_{\mathrm{m}} = 0.29$; $R^2_{\mathrm{c}} = 0.45$)	0.74	271	8			
Intercept				10.52	5.60, 15.43	
Local farming system (Conventional)				9.54	3.10, 15.98	1
Proportion of organic farming				−0.09	−9.44, 9.26	1
Proportion of seminatural habitats				4.45	−3.31, 12.22	1
Local farming system × Proportion of organic farming				9.67	−3.48, 22.83	1
Local farming system × Proportion of seminatural habitats				20.88	5.00, 36.77	1
Egg						
M0† ($R2_{\mathrm{m}} = 0.13$; $R2_{\mathrm{c}} = 0.49$)	0.14	334	7			
Intercept				48.37	40.85, 55.89	
Field age				9.93	−4.63, 24.48	1
Vine stock density				−2.16	−18.96, 14.64	1
Total TFI				−2.29	−13.97, 9.38	1
Tillage intensity				−7.69	−20.86, 5.48	1
Crop productivity				−6.66	−22.28, 8.96	1
M1† ($R^2_{\mathrm{m}} = <0,01$; $R^2_{\mathrm{c}} = 0.34$)	< 0.01	351	5			
Intercept				46.58	37.48, 55.68	
Local farming system (Conventional)				3.71	−6.89, 14.32	1
M2 at the 250-m scale† ($R^2_{\mathrm{m}} = 0.16$; $R^2_{\mathrm{c}} = 0.37$)	0.3	331	9			
Intercept				45.73	36.59, 54.86	
Local farming system (Conventional)				9.59	−2.44, 21.61	1
Proportion of organic farming				−1.24	−18.94, 16.47	1
Proportion of seminatural habitats				8.51	−6.32, 23.34	1
Local farming system × Proportion of organic farming				16.47	−7.66, 40.60	1
Local farming system × Proportion of seminatural habitats				24.5	−4.47, 53.46	1
Seed						
M0† ($R^2_{\mathrm{m}} = 0.66$; $R^2_{\mathrm{c}} = 0.27$)	0.09	1,150	7			
Intercept				72.08	63.55, 80.61	
Field age				3.27	−12.83, 19.38	1
Vine stock density				−10.79	−29.51, 7.93	1
Total TFI				7.24	−5.56, 20.03	1
Tillage intensity				−8.64	−23.16, 5.88	1
Crop productivity				10.34	−6.97, 27.65	1
M1† ($R^2_{\mathrm{m}} = 0.03$; $R^2_{\mathrm{c}} = 0.23$)	<0.01	1,169	4			
Intercept				66.25	56.35, 76.16	
Local farming systems (Conventional)				11.61	0.89, 22.34	1
M2 at the 750-m scale† ($R^2_{\mathrm{m}} = 0.08$; $R^2_{\mathrm{c}} = 0.27$)	0.33	1,146	8			
Intercept				66.43	56.45, 76.41	
Local farming system (Conventional)				11.95	1.30, 22.60	1
Proportion of organic farming				8.09	−12.98, 29.17	1
Proportion of seminatural habitats				−2.48	−24.03, 19.08	1

Table 4. (Continued)

Sentinel prey, model, and explanatory variables selected	Sum W_i	AIC	df	Estimates	CI	Relative variable importance
Local farming system × Proportion of organic farming				8.06	−15.26, 31.38	1
Local farming system × Proportion of seminatural habitats				20.78	−2.05, 43.61	1

Notes: The table reports the explanatory variables selected, estimates, confidence intervals (2.5–97.5%), and the relative importance of the best model. The sum of the Akaike weights normalized across each spatial scale (Sum W_i) provides the probability of a given level of complexity to appear among the top models. Relative variable importance gives the probability of the explanatory variable being in the set of top models at the given scale (a value of 1 means that the variables are in all the best model at this scale). R^2 marginal and R^2 conditional are reported. R^2, AIC, and degrees of freedom (df) values were calculated using the best models at this scale. Random terms were calculated using the full model at each scale and reported in the Table S4. TFI, treatment frequency index.

†Only one model was retained at top model at this scale.

scales (Holmes and Froud-Williams 2005, Diekötter et al. 2016). This spatial scale falls within the spatial-scale range of the effects of landscape context on these groups (Guerrero et al. 2010, Trichard et al. 2013). We initially hypothesized a positive effect of organic farming on all biological control functions considered here. The variable responses of each prey type to organic farming in the landscape strongly suggest that different sets of natural enemy species are involved in the measured biological pest control functions, and that they respond differently to organic farming in the landscape. These results are in line with studies in which the effects of organic farming at multiple spatial scales on several components of biodiversity were revealed (Gabriel et al. 2010, Inclan et al. 2015). Gabriel et al. (2010) explored the multiple scale effects of organic farming on several taxa, including plants, earthworms, epigeal arthropods, and birds, and revealed clear variations in the effect of organic farming among groups, with some responding positively and some negatively, at different spatial scales. Our study shows that such effects are also true when examining multiple ecological functions supported by different species or communities.

Negative effects of seminatural habitats on biological control

Surprisingly, we found no evidence for any positive effects of the proportion of seminatural habitats in the landscape on the level of biological pest control potential, which was contrary to what was initially hypothesized and had been reported in other studies (Chaplin-Kramer et al. 2011, Rusch et al. 2016*a*). Our results revealed a negative effect of landscape complexity on the level of egg removal. Our study, therefore, strongly suggests that the subset of natural enemy species involved in the biological control of moth eggs, moth larvae, and weed seed contains agrobiont species that do not depend on seminatural habitats during their life cycle. These results corroborate those of several recent studies that also reported contrasted effects of landscape complexity on biological control or natural enemy activity density (Jonason et al. 2013, Costamagna et al. 2015, Rusch et al. 2016*b*, Karp et al. 2018). Such effects are expected when crops provide more important resources for natural enemies than seminatural habitats over the course of a year, which might be the case in perennial systems (Tscharntke et al. 2016). Other explanations for this negative effect of seminatural habitats on egg predation could be that intraguild predation or alternative prey may be more important in more complex landscapes, leading to lower levels of biological control (Martin et al. 2013). Globally, our results refute our initial hypothesis that seminatural habitats were more important for providing natural enemies involved in biological control than organic fields.

Effects of specific farming practices on biological control

Our study indicates the importance of considering local farming practices, such as pesticide use and crop productivity, beyond the type of farming systems (the classic organic and conventional dichotomy) when examining biological pest control in agroecosystems (Mehrabi et al. 2017). Our analyses particularly revealed that increasing pesticide use decreased the removal rates of moth eggs and increasing crop productivity decreased the removal rates of moth eggs while increased weed seed removal. This confirmed that several biological control functions can have opposite responses to management intensity (Rusch et al. 2017*b*). Direct negative effects of pesticides on natural enemies may limit the biological control potential of grape moths, which explains the negative relationships between crop productivity or pesticide use and biological control services (Geiger et al. 2010, Bommarco et al. 2011). The higher pesticide use intensity applied in conventional farming compared to organic farming can partly explain this positive effect of organic farming on biological control. Actually, TFI is two-fold lower in organic than in conventional vineyards (i.e., 9.38 and 18.96 in organic and conventional vineyards respectively; Appendix S1: Table S1, see Muneret et al. 2018). Moreover, we cannot rule out that the negative relationship between crop productivity and egg removal may result from a dilution effect, because more grapes per unit area results in larger area to cover for oophagous consumers in a given field.

The positive effect of crop productivity on weed seed removal is in line with several recent studies on seed biological control by carabids in agricultural landscapes. Jonason et al. (2013) found that landscape intensification, measured through landscape simplification, enhances weed seed predation by carabids, suggesting that the granivorous species responsible for this may be well adapted to intensive crop habitats. Moreover, the more productive vineyards could have lower weed cover that could favor bird predation (Barbaro et al. 2017). These results suggest that the granivorous species involved in the predation of weed seeds in vineyards are well adapted to open habitats and relatively intensive agricultural landscapes.

Little support for interactions between local management and landscape composition

Our results showed no support for interactions between local management and landscape composition on the mean level of biological control as previously hypothesized in the literature (Tscharntke et al. 2005). However, we found that the proportion of seminatural habitats in the 250-m scale strongly increased the temporal variability in larval removal in conventional fields, while the temporal variability of larval removal was much less affected by the proportion of seminatural habitats in organic fields. This result confirmed our initial hypothesis on the positive effect of organic farming on the temporal stability in biological pest control and corroborates results from other studies (Macfadyen et al. 2011, Gagic et al. 2012). The potential perturbations resulting from crop management are expected to be buffered by the higher abundance and diversity of natural enemies found in organic systems (Macfadyen et al. 2011). Our results did not validate the hypothesis stating that conventional fields benefited more from landscape complexity or organic farming in the landscape than organic fields. In addition, we found that landscape complexity increased the variability of larval removal rates. These results therefore suggest that the core group of species providing biological control services in these landscapes are mainly agrobiont species and do not heavily rely on seminatural habitats (Tscharntke et al. 2016).

Sentinel approach.—In this study, we used a sentinel approach to estimate removal rates of key pest in vineyards. It has been noted that immobilized larvae are also removed by scavengers in other agrosystems resulting in a possible overestimation of biological control potential (Zou et al. 2017). In our study, we could not disentangle the effect of scavengers from the effect of predators on larval removal rates and we therefore did not interpret these results as pure predation rates but as proxies for biological control potential (Meehan et al. 2012). While such approach can provide relevant information about the relative effects of contrasted environmental contexts on biological control potential, we acknowledge that future research should combine sentinel approaches with either video monitoring or gut content analyses of dominant predator species to identify consumers of sentinel preys (Birkhofer et al. 2017). Such combination will provide relevant information about the identity of key predators.

CONCLUSIONS

Organic farming, at the local and landscape scales, as well as the proportion of seminatural habitats influenced biological pest control potential in vineyards. Overall, data supported our initial hypothesis about the positive effect of organic farming at the local and landscape scale on the mean and temporal stability of biological control potential. However, our results clearly highlight that the relative importance of each scale was strongly dependent of the type of pest. Contrary to our initial hypotheses, and what is found in the literature, our analyses revealed weak or negative effects of seminatural habitats in the landscape on biological control potential suggesting that the core group of species delivering biological control services tend to be agrobiont species. Our results therefore highlight that biological control potential can be significantly increased in vineyard-dominated landscapes if low intensity management systems, such as organic farming, are largely developed. Although we need to consolidate our results on a larger set of functions involved in pest control (e.g., other insect pest or diseases), our study demonstrates the need to consider potential trade-off between pest control strategies based on ecological functions supported by biodiversity and pest control based on biodiversity-disruptive practices (i.e., pesticide use) when designing functional landscapes optimizing biological control services.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1818/full

DATA AVAILABILITY

Data available from Data Inra Portail: https://doi.org/10.15454/nqmzwz