# Organic farming expansion drives natural enemy abundance but not diversity in vineyard-dominated landscapes

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# Organic farming expansion drives natural enemy abundance but not diversity in vineyard-dominated landscapes

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## Abstract

Organic farming is seen as a prototype of ecological intensification potentially able to conciliate crop productivity and biodiversity conservation in agricultural landscapes. However, how natural enemies, an important functional group supporting pest control services, respond to organic farming at different scales and in different landscape contexts remain unclear. Using a hierarchical design within a vineyard-dominated region located in southwestern France, we examine the independent effects of organic farming and semi-natural habitats at the local and landscape scales on natural enemies. We show that the proportion of organic farming is a stronger driver of species abundance than the proportion of semi-natural habitats and is an important facet of landscape heterogeneity shaping natural enemy assemblages. Although our study highlights a strong taxonomic group-dependency about the effect of organic farming, organic farming benefits to dominant species while rare species occur at the same frequency in the two farming systems. Independently of farming systems, enhancing field age, reducing crop productivity, soil tillage intensity, and pesticide use are key management options to increase natural enemy biodiversity. Our study indicates that policies promoting the expansion of organic farming will benefit more to ecological intensification strategies seeking to enhance ecosystem services than to biodiversity conservation.

**KEYWORDS**
agricultural landscapes, biodiversity, ecological intensification, natural enemy community, organic farming, semi-natural habitats

## 1 | INTRODUCTION

Biodiversity and agricultural production play a vital role in human society (Cardinale et al., 2012). However, a huge trade-off exists between these two inextricably linked components. Their relationships have been thought in regard to the land sharing—land sparing debate that aims at identifying the best strategies for conciliating them (Phalan, Onial, Balmford, & Green, 2011). To date,

no clear consensus exists on the best landscape planning strategy to optimize synergies between crop production and biodiversity conservation. Two reasons among others are that their relationship is highly taxon-dependent (Martin, Seo, Park, Reineking, & Steffan-Dewenter, 2016) and depends on the spatial scale on which it applies (Ekroos et al., 2016). In addition to conservation goals, biodiversity is generally associated with greater levels of ecosystem functioning and thus offers a path to the development of ecological

intensification of agricultural systems (Bommarco, Kleijn, & Potts, 2013; Cardinale et al., 2012).

Although no ideal model of ecological intensification does exist, organic farming is often seen as a good prototype (Tittonell, 2014). While organic farming is on average 19%–25% less productive than conventional fields (Ponisio et al., 2015), it supports higher levels of biodiversity and ecosystem services than conventional farming (Muneret, Mitchell, et al., 2018; Tuck et al., 2014). Organic farming increases natural enemy abundance and richness as well as pest control services, but its effect is highly context dependent and we lack a good understanding about the mechanisms underlying this context dependency (Lichtenberg et al., 2017; Muneret, Mitchell, et al., 2018; Tscharntke et al., 2012; Tuck et al., 2014).

One hypothesis beyond the context dependency of organic farming performances on biodiversity and ecosystem services is the potential interactions between local farming practices and the surrounding landscape (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Tscharntke et al., 2012). To date, studies examining how landscape context modulates the local effect of farming practices for biodiversity conservation or the provision of ecosystem services have mainly considered the impact of semi-natural habitats but much less attention have been paid to the role of farming practices within the landscape (Rusch et al., 2016; Chaplin-Kramer, O'Rourke, Blitzer, & Kremen, 2011; but see Henckel, Börger, Meiss, Gaba, & Bretagnolle, 2015). Moreover, a recent synthesis at the global scale revealed strong variability in direction and effect size of semi-natural habitats on predators and biological pest control (Karp et al., 2018). Thus, considering farming practices at multiple spatial scales, notably the proportion of organic farming at the landscape scale, should reduce unexplained variation in these relationships (Muneret, Auriol, Thiéry, & Rusch, 2019).

Studies on the effect of organic farming on biodiversity have mostly been conducted at the field scale and the few studies conducted at a landscape scale highlighted that the response of taxon is highly idiosyncratic (Gabriel et al., 2010). Moreover, the effects of semi-natural habitats and organic farming in the landscape could interact because they could potentially support different set of species having either antagonistic, synergistic or even neutral interactions (Letourneau, Jedlicka, Bothwell, & Moreno, 2009; Martin, Reineking, Seo, & Steffan-Dewenter, 2013). Hence, examining the effect of organic farming applied at much larger scales is urgently needed since organic agriculture is expanding exponentially and receives important subsidies, notably in Europe, while very limited knowledge about the performance of such cropping systems in the context of large spatial expansion (Kleijn et al., 2011).

Based on a sampling design composed by 42 commercial vineyards, we independently investigated the effects of organic farming and semi-natural habitats at multiple scales on natural enemy communities. The few available studies examining the effect of the proportion organic farming on natural enemies never disentangled the effects of organic farming from the effect of semi-natural habitats at the landscape scale while evidence shows that they are correlated (Norton et al., 2009). Moreover, perennial crops are far less studied than annual ones while

their own cropland biodiversity could be differentially affected by agricultural operations (Bruggisser, Schmidt-Entling, & Bacher, 2010). Such crops provide more refugees and resources for biodiversity but generally received many more pesticide applications over time than annual crops (Muneret, Thiéry, Joubard, & Rusch, 2018). Here, we sampled a wide array of arthropod natural enemies (spiders, harvestmen, ground beetles, rove beetles, lacewings, ants, and earwigs) that are involved in predation of grape moths, leafhoppers and weed seeds (Sentenac, 2011; Unruh et al., 2016). First, we hypothesized that the proportion of organic farming increases natural enemy abundance and diversity but that the effect size is lower than the effect of the proportion of semi-natural habitats. Second, we expected that the positive effect of organic farming at the field scale on natural enemy abundance and diversity is modulated by the landscape context. We assumed a higher positive effect of local organic farming in simple and intensive landscapes than in more extensive ones (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Tuck et al., 2014). In the same way, the positive effect of the proportion organic farming on natural enemies is expected to be greater in simple than in complex landscapes. Third, we hypothesized that several specific farming practices are detrimental to natural enemy community. Specifically, pesticide use intensity, tillage intensity, and crop productivity are expected to reduce natural enemy abundance and diversity.

## 2 | MATERIAL AND METHODS

### 2.1 | Study design

Our study design was located within a vineyard-dominated region, in Southwestern France (near Bordeaux, 44°81'N, −0°14'W). The design consisted of 42 vineyard plots organized in 21 pairs, each pair containing one field managed under organic guidelines and one not (hereafter referred as "conventional"). The average distance between paired fields was about 125 m. Pairs of vineyards have been selected along two uncorrelated landscape gradients: proportion of semi-natural habitats and proportion of organic farming. These gradients were established based on landscape composition calculated at a 1 km radius around each focal vineyard. At this scale, the proportion of semi-natural habitats ranged from one to 75%, and the proportion of organic farming ranged from two 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 semi-natural habitats and organic farming on biodiversity. Among the types of semi-natural habitats, meadows and forests largely dominated and their relative proportions were highly correlated. It was therefore not possible to evaluate their independent effects on natural enemies in our analyses (Figure S1). Landscape variables were also calculated at the 500-m radius around each vineyard using ArcGIS 10.1 (ESRI).

### 2.2 | Arthropod sampling

We sampled natural enemy communities on the soil surface and in the foliage. The community of the soil surface was sampled by

placing on the ground five pitfall traps per vineyard (diameter 11 cm; depth 11.5 cm) under three vine rows that were distant from three vine rows from each other (inter-row distances varied between 1.5 and 3 m). Three pitfall traps were placed at 10-m and two others at 10-m away from the edge. They were opened during seven days at five sampling dates between late May and early October in 2015. The five traps were pooled at each sampling period prior to analyses. In addition, the foliage community was sampled four times between early June and early September by beating 30 vine stocks at least five vine stocks away from each other along two or four vine rows depending on the field size. Harvestmen, spiders, ants, rove beetles, and ground beetles were identified at the species level while lacewings and earwigs were identified at the family level. Ant community collected in pitfall traps were only counted and identified at the first sampling date (i.e., in early June).

## 2.3 | Vineyard management

We collected data on pesticide use (i.e., fungicide, insecticide and herbicide), soil tillage and field age by interviewing the 38 involved vine-growers. The intensity of pesticide application was calculated using the Treatment Frequency Index ("TFI") which is the sum of all the ratios between the applied and the recommended dose for each pesticide application (OECD, 2001). Tillage intensity was evaluated by calculating the "tillage intensity index" which summarizes the number of tilling operations per year weighted by the area involved each time (Muneret et al., 2019). We also measured vine trunk density and crop productivity. To calculate the crop productivity, we multiplied the average number of bunches per vine stock by the average bunch weights and the vine stock density per vineyard (Mg/ha, see Muneret, Thiéry, et al., 2018). Note that crop productivity did not significantly differ between farming systems and that we were not able to estimate crop productivity for two vineyards out of 42 (Muneret, Thiéry, et al., 2018).

## 2.4 | Data analyses

As the above-ground community and the foliage community represent two guilds, we analyzed the response of each community to environmental conditions separately. For each community, we calculated total abundance, species richness, and evenness (Pielou index) over the year. At each sampling date, approximately 10% of the vineyards were not sampled because of pitfall trap destruction ($N = 4$ for the first until the fourth sampling dates and $N = 5$ for the fifth date). Species richness was rarefied to take into account differences in terms of detectability within fields (Gotelli & Colwell, 2001). For the foliage community, we calculated the abundance of ants, spiders, earwigs, and lacewings and the richness of ants and spiders. For the above-ground community, we calculated both the abundance and the richness of ants, spiders, ground beetles, and rove beetles. Finally, we calculated the total abundance of harvestmen (those from both the foliage and the ground). All these metrics represented 21 descriptors of natural enemy communities which were then used

as response variables in our models and data were log-transformed for further analyses when it was necessary.

Linear mixed models were used to investigate the effects of local management intensity, farming systems and landscape composition on each response variable. Because of some trap destructions, we corrected the abundance of the communities for each vineyard having an uncompleted sampling. Therefore, separately for the foliage and the above-ground community, we calculated the relative contribution of each sampling date to the total abundance of the community and we divided the total number of individuals collected by the sum of the relative contribution of the sampling dates that were sampled for the given vineyard. This gave the estimated total abundance of a given community for a given vineyard taking account for which sampling dates were sampled.

We fitted four models of increasing complexity ("M0", "M1," "M2" at 500-m scale and "M2" at the 1,000-m scale) for each response variable and we used a multimodel inference approach to test our hypotheses ($N_{observations} = 40$). We applied this procedure to identify the most relevant spatial scale for natural enemies. M0, the first model, had local covariates as predictors: "field age", "vine stock density", "total TFI", "tillage intensity" and "crop productivity". At this first step, all the possible models were ranked using the Akaike information criteria corrected for small sample size (AICc) and models with a ΔAICc < 2 were retained among the set of top models. Such set of top models was then used to estimate the mean effects and confidence intervals of each explanatory variable using model averaging (Grueber, Nakagawa, Laws, & Jamieson, 2011). Covariates which were significant at this M0 step (i.e., with a confidence interval significantly different from zero and having a relative importance variable equal to 1) were conserved and included in models "M1". M1 included "selected local covariates" and "local farming systems" as predictors. This step allows for evaluating the effect of local farming systems on biodiversity after taking into account potential confounding effects of specific local covariates. We then fitted two different M2 models, one for each spatial scale (i.e., 500-, and 1,000-m) to test our hypotheses related to the effect of the landscape composition and its interaction with local farming systems on biodiversity. In M2, we thus integrated "selected covariates", "local farming systems", "the proportion of semi-natural habitats", "the proportion of organic farming" and three interactions: (a) local farming systems with the proportion of semi-natural habitats, (b) local farming systems with the proportion of organic farming and (c) proportion of semi-natural habitats with proportion of organic farming. All the models at all scales included "field pairs" as random effect.

The same averaging approach was applied for the two M2 models and we calculated the marginal $R^2$ values and conditional $R^2$ values of the model having the lowest AICc at each step to evaluate the amount of variability explained by each model (Nakagawa & Schielzeth, 2013). Before modeling, we standardized all explanatory variables, with mean equal to 0 and standard deviation equal to 0.5 (Schielzeth, 2010).

To identify which level of model complexity, and indirectly which spatial scale, was the most important for explaining natural enemy
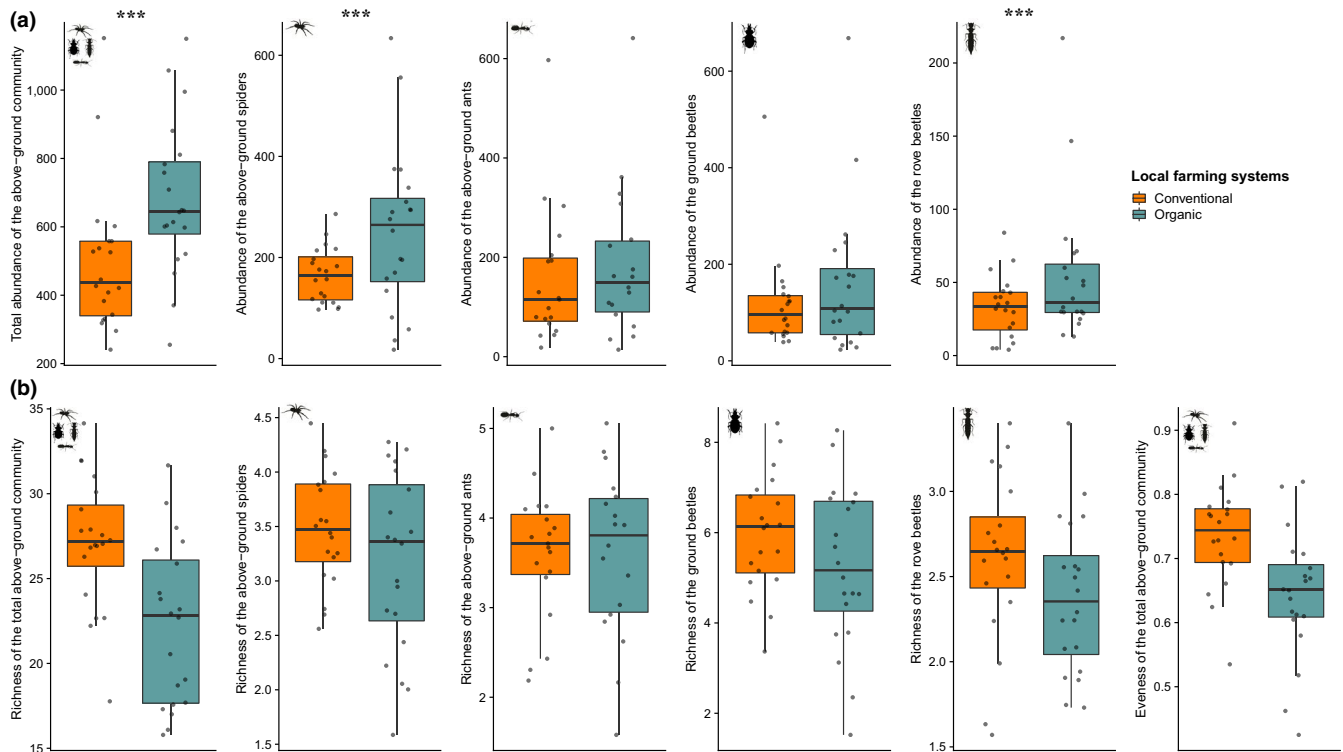
**FIGURE 1** Effect of local farming systems on (a) abundance, (b) rarefied richness and evenness of the above-ground natural enemy community

descriptors, we recalculated the Akaike weights ("Sum Wi") among all of the models from the four different sets (i.e., M0, M1 and M2 at both spatial scales) obtained for each response variable. We therefore estimated the relative importance of each level of complexity for a given response variable. The sum of the Akaike weights of the models obtained at a given level of complexity provided the model's probability of being top model across all scales.

Diagnostic residual plots of all full models were confirmed using the DHARMa package (Hartig, 2017). Using variograms, we detected no spatial autocorrelation in the residuals. Collinearity among explanatory variables was assessed using the Variance Inflation Factor and the highest value was equal to 2.29 for the TFI (correlation matrix between all covariates displayed in the Figure S2).

All analyses were performed using the R software (R Core Team, 2016) and the packages "lme4" (Bates, Mächler, Bolker, & Walker, 2014) and "MuMIn" (Bartoń, 2016).

## 3 | RESULTS

### 3.1 | Description of the natural enemy communities

We identified 41,663 arthropods belonging to 318 taxa. We collected 15,316 spider adults and juveniles (162 taxa), 5,074 ground beetle adults (60 taxa), 1,574 rove beetle adults (47 taxa), 16,911 ant adults (41 taxa), 1,864 harvestman adults and juveniles (6 taxa), 650 earwig adults (one family) and 274 lacewing larvae (one family). 19,549 individuals were collected in the foliage and 22,114

individuals were collected on the soil surface. Across all the 21 descriptors of the natural enemy community, models "M0" with the simplest level of complexity (i.e., including local covariates only) mostly had the highest relative importance of explaining species richness of natural enemy community while their abundances mostly responded to models "M2" with the highest level of complexity (i.e., including local covariates, local farming systems, landscape variables, and interactions; Tables S1 and S2; Figure S3).

### 3.2 | Independent effects of local farming systems and landscape composition on natural enemy communities

At the field scale, organic farming did not impact the foliage community whereas it affected the above-ground community in several ways. Local organic farming increased the abundance of the total above-ground natural enemy community, as well as spider and rove beetle abundances (Table S2; Figure 1a). However, local organic farming negatively affected the total rarefied richness of the above-ground community (Table S2; Figure 1b). The three most abundant species (*Pardosa proxima*, *Lasisus niger*, and *Pseudoophonus rufipes*) are much more abundant in organic than in conventional vineyards (Figure S4) resulting in lower evenness of the above-ground community in organic vineyards (Table S2, Figure 1c). The rarest species (i.e., species that were collected once) appear at the same frequency in organic and conventional vineyards (67 and 66 species in organic and conventional vineyards).

**TABLE 1** Relative effects of explanatory variables selected in the best-fitted models for: total abundance of harvestmen, abundance of the above-ground spiders, abundance of the above-ground ants, abundance of spiders in the foliage, species richness of the total above-ground community, species richness of ground beetles (all the outputs from all the models are reported in Tables S1 and S2). The sum of the Akaike weights ("Sum Wi") of the models obtained at the best scale provided the model's probability of being the top model across all of the scales. Other parameters reported in this table come from models at the best scale of response for each response variable (either M0, M1, or M2). $R^2$ marginal and $R^2$ conditional are reported. $R^2$ values were calculated using the best model at the best scale. The standard deviations of the random terms are reported. Estimates, confident interval (2.5%–97.5%) and relative importance variable were reported for each predictor. "SD Random term" has been obtained based on the best model at a given scale. Values in bold are significant (confident interval did not include zero and relative variable importance equal to 1)

| Response variable | Model with $R^2$ marginal and $R^2$ conditional | Sum Wi | AIC | Explanatory variables selected and random term | Estimates | Confidence intervals | Relative variable importance | SD Random term |
|---|---|---|---|---|---|---|---|---|
| Total abundance of harvestmen | M2 at the 1,000-m scale ($R^2$m = 0.29; $R^2$c = 0.72) | 0.87 | 333.91 | Intercept | 45.86 | (34.77; 57.08) | — | |
| | | | | **Vine stock density** | **15.71** | **(0.78; 30.75)** | **1** | |
| | | | | Local farming system (:Conventional) | 7.06 | (−2.62; 17.64) | 1 | |
| | | | | **% organic farming** | **−23.01** | **(−44.79; −0.97)** | **1** | |
| | | | | % semi-natural habitats | −16.83 | (−49.92; 16.03) | 1 | |
| | | | | Local farming system: % organic farming | 11.80 | (−9.53; 33.79) | 1 | |
| | | | | Local farming system: % semi-natural habitats | 19.79 | (−1.19; 40.69) | 1 | |
| | | | | % organic farming: % semi-natural habitats | 24.41 | (−28.09; 76.24) | 1 | |
| | | | | Pair | | | | 20.16 |
| Abundance of the above-ground spiders | M2 at the 500-m scale ($R^2$m = 0.40; $R^2$c = 0.47) | 0.97 | 435.77 | Intercept | 152.14 | (109.16; 195.18) | — | |
| | | | | **Local farming system (:Conventional)** | **78.18** | **(19.57; 135.93)** | **1** | |
| | | | | % organic farming | −50.95 | (−136.92; 35.53) | 1 | |
| | | | | % semi-natural habitats | −69.19 | (−168.54; 30.19) | 1 | |
| | | | | **Local farming system: % organic farming** | **191.41** | **(69.80; 313.81)** | **1** | |
| | | | | **Local farming system: % semi-natural habitats** | **132.64** | **(11.01; 255.95)** | **1** | |
| | | | | **% organic farming: % semi-natural habitats** | **−214.32** | **(−375.71; −54.08)** | **1** | |
| | | | | Pair | | | | 35.25 |
| Abundance of the above-ground ants | M2 at the 500-m scale ($R^2$m = 0.20; $R^2$c = 0.28) | 0.64 | 417.41 | Intercept | 167.17 | (107.99; 226.34) | — | |
| | | | | Local farming system (:Conventional) | 28.81 | (−52.28; 111.03) | 1 | |
| | | | | % organic farming | −62.43 | (−186.81; 60.25) | 1 | |
| | | | | % semi-natural habitats | −32.19 | (−170.85; 106.51) | 1 | |
| | | | | **Local farming system: % organic farming** | **184.40** | **(13.32; 357.04)** | **1** | |
| | | | | Local farming system: % semi-natural habitats | 57.44 | (−118.35; 227.13) | 1 | |
| | | | | % organic farming: % semi-natural habitats | 217.38 | (−5.65; 440.62) | 1 | |
| | | | | Pair | | | | 43.31 |

(Continues)

**TABLE 1** (Continued)

| Response variable | Model with $R^2$ marginal and $R^2$ conditional | Sum Wi | AIC | Explanatory variables selected and random term | Estimates | Confidence intervals | Relative variable importance | *SD* Random term |
|---|---|---|---|---|---|---|---|---|
| Abundance of spiders in the foliage | M2 at the 1,000-m scale ($R^2$m = 0.41; $R^2$c = 0.75) | 0.78 | 375.36 | Intercept | 153.02 | (124.59; 181.79) | — | |
| | | | | **Total TFI** | **−41.28** | **(−77.20; −5.03)** | 1 | |
| | | | | **Tillage intensity** | **−56.08** | **(−91.18; −21.42)** | 1 | |
| | | | | Local farming system (:Conventional) | 34.13 | (−7.70; 76.75) | 1 | |
| | | | | % organic farming | −19.19 | (−63.69; 26.13) | 1 | |
| | | | | % semi-natural habitats | 27.72 | (−38.46; 95.63) | 1 | |
| | | | | Local farming system: % organic farming | −20.85 | (−64.70; 23.25) | 1 | |
| | | | | Local farming system: % semi-natural habitats | 1.41 | (−41.44; 44.32) | 1 | |
| | | | | % organic farming: % semi-natural habitats | −37.09 | (−144.18; 72.10) | 1 | |
| | | | | Pair | | | | 40.6 |
| Species richness of the total above-ground community | M2 at the 1,000-m scale ($R^2$m = 0.51; $R^2$c = 0.76) | 0.75 | 214.09 | Intercept | 26.10 | (24.24; 27.96) | — | |
| | | | | **Field age** | **4.86** | **(2.34; 7.37)** | 1 | |
| | | | | **Crop productivity** | **−2.87** | **(−5.15; −0.60)** | 1 | |
| | | | | **Local farming system (:Conventional)** | **−3.90** | **(−5.74; −2.06)** | 1 | |
| | | | | % organic farming | 0.39 | (−3.11; 3.89) | 1 | |
| | | | | % semi-natural habitats | −0.42 | (−5.63; 4.79) | 1 | |
| | | | | Local farming system: % organic farming | 0.87 | (−2.12; 5.46) | 0.52 | |
| | | | | Local farming system: % semi-natural habitats | −6.96 | (−15.35; 1.43) | 0.45 | |
| | | | | % organic farming: % semi-natural habitats | −0.43 | (−4.67; 2.75) | 1 | |
| | | | | Pair | | | | 2.7 |
| Species richness of ground beetles | M0 ($R^2$m = 0.25; $R^2$c = 0.43) | 0.55 | 148.62 | Intercept | 5.61 | (5.10; 6.12) | — | |
| | | | | **Field age** | **1.17** | **(0.20; 2.13)** | 1 | |
| | | | | Vine stock density | 0.02 | (−1.08; 1.32) | 0.13 | |
| | | | | Total TFI | 0.08 | (−0.35; 1.30) | 0.17 | |
| | | | | Tillage intensity | −0.13 | (−1.50; 0.32) | 0.23 | |
| | | | | Crop productivity | −0.88 | (−1.95; −0.07) | 0.87 | |
| | | | | Pair | | | | 0.7 |

At the landscape scale, the proportion of organic farming decreased the abundance of harvestmen (Table 1; Figure 2a).
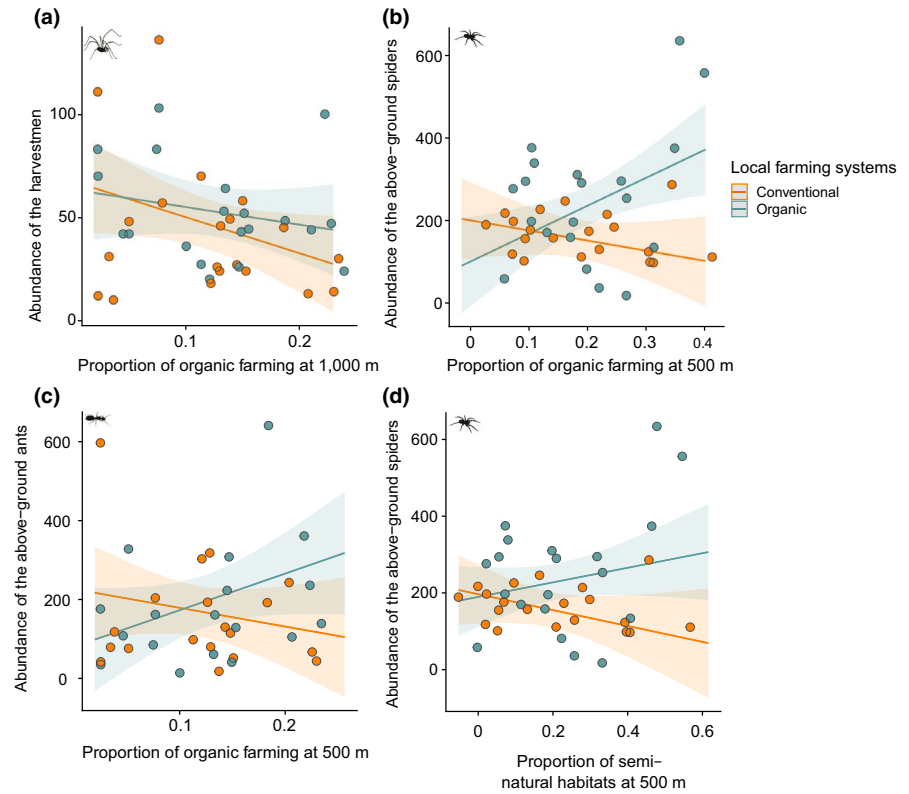
## 3.3 | Interactive effects of local organic farming and landscape composition on natural enemy communities

Two variables responded to the interaction between local farming systems and proportion of organic farming (i.e., abundances of spiders and ants of the above-ground community) and one variable responded to the interaction between local farming systems and proportion of semi-natural habitats (i.e., abundance of spiders of the above-ground community). Contrary to abundance, natural enemy richness and evenness were not affected by interactions between local farming systems and landscape composition.

The proportion of organic farming had a positive effect on both spider and ant abundance of the above-ground community

**FIGURE 2** Interactive effects of landscape composition and local farming systems on natural enemy abundances. (a) effect of the proportion of organic farming at the 1,000-m scale and local farming systems on harvestman abundance; (b) effect of the proportion of organic farming at the 500-m scale and local farming systems on above-ground spider abundance; (c) effect of the proportion of organic farming at the 500-m scale and local farming systems on the abundance of the above-ground ants; (d) effect of the proportion of semi-natural habitats at the 500-m scale and local farming systems on abundance of the above-ground spiders. $R^2$ marginal are respectively equal to (a) 0.29, (b) 0.40, (c) 0.20, and (d) 0.40. See also Table 1



in organic vineyards, but a negative effect in conventional ones (Table 1; Figure 2b,c). Similarly, the proportion of semi-natural habitats had a positive effect on spider abundance of the above-ground community in organically managed vineyards, but a negative effect in conventionally managed ones (Table 1; Figure 2d).

In addition, interaction between proportions of semi-natural habitats and organic farming had a significant effect on the abundance of above-ground spiders (Table 1). Both proportions increased their abundance but the proportion of organic farming benefited even more to spider abundance in landscapes having a low proportion of semi-natural habitats than in landscapes with high proportion of semi-natural habitats.

## 3.4 | Effect of the local management intensity on natural enemy communities

Independently of local farming systems, specific farming practices were important predictors of natural enemy community structure. We found positive effects of field age and vine trunk density on natural enemy communities. Field age had a positive effect on the richness of the total above-ground community and on the ground beetle richness (Table 1; Figure 3a,b). Vine trunk density had a positive effect on harvestman abundance (Table 1; Figure 3c). On the opposite, crop productivity, tillage intensity and pesticide use intensity had negative effects on natural enemy communities. Crop productivity reduced the richness of the total above-ground community (Table 1; Figure 3d) while tillage intensity and pesticide use intensity

had a negative effect on abundance of spiders in the foliage (Table 1; Figure 3e,f).

## 4 | DISCUSSION

This study provides novel results about the independent effects of organic farming and semi-natural habitats at different spatial scales on natural enemy communities. Globally, we found that farming practices at multiple spatial scales were stronger drivers of community abundance than the proportion of semi-natural habitats. However, we found that there were no unique responses of natural enemy communities to land use changes in viticultural landscapes. Moreover, independently of farming systems, specific practices such as enhancing field age, reducing crop productivity, soil tillage intensity and pesticide use were key management options to increase natural enemy biodiversity.

Farming systems at multiple spatial scales are key drivers of natural enemy community structure in vineyard landscapes. Considering the hidden heterogeneity related to farming practices in the landscape is a major aspect to understand natural enemy community structure in agricultural landscapes (Vasseur et al., 2013). Recent syntheses have highlighted the strong variability in the responses of natural enemies and pests to the proportion of semi-natural habitats with approximately the same amount of studies with positive and negative effects (Karp et al., 2018; Tscharntke et al., 2016). We provide one key explanation for these
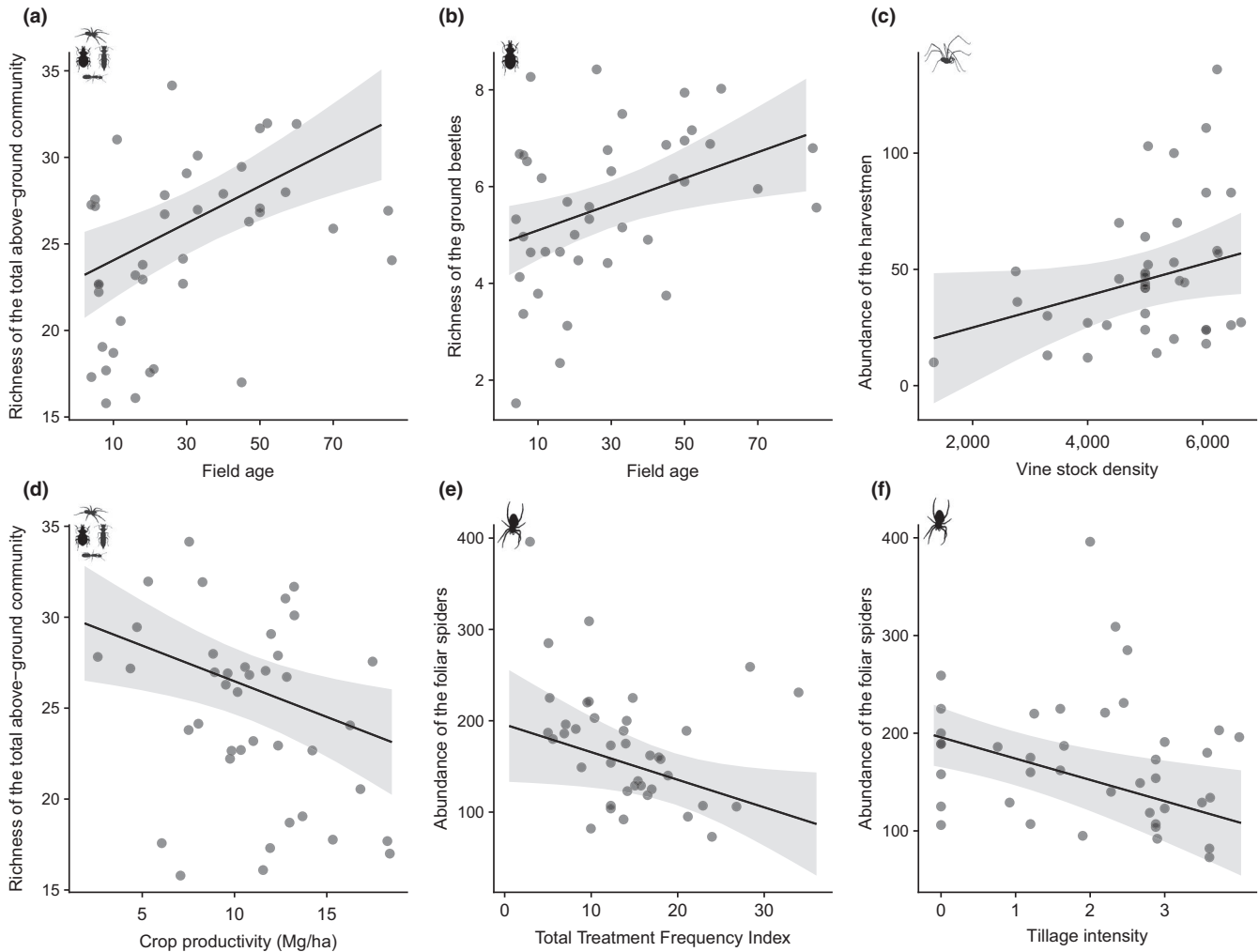
**FIGURE 3** Effect of local covariates on abundance and richness of natural enemies. Effect of field age on (a) the rarefied richness of the total above-ground community and (b) the rarefied richness of the ground beetles; (c) effect of vine trunk density (number of vine stocks by hectare) on harvestman abundance; (d) effect of crop productivity on the rarefied richness of the total above-ground community. Effect of (e) treatment frequency index and (f) tillage intensity on the abundance of the spiders in the foliage. $R^2$ marginal are equal to (a) 0.51, (b) 0.25, (c) 0.29, (d) 0.51, (e) 0.41 and (f) 0.41

variable effects of landscape composition by showing that farming practices within the landscape matrix are strong determinants of meta-communities and can therefore modulate the effects of semi-natural habitats on natural enemies. Meta-community dynamics governed by spillover of predators between farming system types in the landscape are likely to explain these patterns (Leibold et al., 2004; Vasseur et al., 2013).

Our results clearly illustrate the strong taxonomic group-dependency in the observed effects of organic farming at multiple spatial scales, which is in line with previous studies on other groups (Gabriel et al., 2010). Other recent studies have explored the effect of organic farming proportion on diversity of other trophic levels and revealed contrasted results (Diekötter, Wamser, Wolters, & Birkhofer, 2010; Djoudi et al., 2018; Henckel et al., 2015; Inclan et al., 2015; Petit et al., 2016; Puech, Poggi, Baudry, & Aviron, 2015; Rundlöf, Bengtsson, & Smith, 2008). In these studies, the beneficial effect of the proportion of organic farming on plant diversity appears as a robust pattern

while it seems to fade away with increasing trophic levels suggesting that bottom-up effects of plant diversity might be blurred by pest management or strongly depend on key functional traits of species (Wood et al., 2015). Our results about the taxonomic group-dependency in the effect of organic farming at multiple spatial scales highlight that there is no a unique strategy at a dedicated scale for conservation management but that strategies should be adapted to regional context (Gabriel et al., 2010).

Although organic farming at the local scale enhances abundance of natural enemies, increasing the area under organic farming at the landscape scale (here until 25% of land cover) might not be sufficient to contribute to biodiversity conservation. Indeed, among all the response variables tested in this study, the proportion of organic farming alone was never positively correlated with natural enemy abundance or diversity while local organic farming clearly increases natural enemy abundances. Moreover, we found that organic farming reduces natural enemy richness and benefits to the most dominant species in vineyards

(Figure S4). As we previously demonstrated that organic farming fosters pest control services in vineyard landscapes (Muneret et al., 2019), our studies suggest that pest control might be provided by a limited number of dominant species. This is in line with a recent synthesis on another key ecosystem services, showing that pollination is provided by a restrictive number of abundant pollinator species in croplands (Kleijn et al., 2015). Furthermore, the fact that organic farming at the field scale reduces natural enemy richness could be due to negative interactions between natural enemy species (e.g., competition, interference). The high abundance of dominant species under organic farming could reduce the probability of occurrence of the rare and sub-dominant species and therefore reduce natural enemy richness.

Contrary to our expectation, the proportion of semi-natural habitats had only one significant effect in interaction with local famring systems on spider abundance suggesting two nonexclusive mechanisms about arthropod movements in such landscapes. First, movements of arthropods between vineyards and semi-natural habitats might be lower in these landscapes compared to annual landscapes. Agrobiont species can find food resources and refuges throughout the year in such perennial crops and may accomplish their whole life cycle within fields especially when spontaneous vegetation is present within the field (Rusch, Delbac, & Thiéry, 2017). Spillover effects that are generally observed between semi-natural habitats and crops may therefore contribute to natural enemy assemblages within-field much more in annual than in perennial crops (Batáry et al., 2011). Second, it is possible that semi-natural habitats increase intraguild predation by recruiting top predators and reducing arthropod natural enemy abundance within fields (Barbaro et al., 2017; Martin et al., 2013). Such effects may therefore blur the potential spillover of natural enemy communities between semi-natural habitats and crops.

Beyond the type of farming systems, specific farming practices such as pesticide use intensity, tillage intensity, and crop productivity are key factors impacting natural enemy abundance and species richness. Our results clearly highlight that reducing management intensity at the field scale is beneficial for natural enemy abundance and diversity (Winter et al., 2018). Field age was also a strong factor explaining natural enemy richness. Indeed, a long-term history assembly could be involved in the current assembly of a given community (Chase, 2003). Old vineyards could shelter species that have good ability for dispersal and species implemented for a long time, that are well adapted to the specific conditions of the field contrary to more recent fields (Le Provost et al., 2017). We advocate that further studies conducted in perennial crops should better integrate field age as a covariate to explain biodiversity patterns at the landscape scale. These results therefore suggest that increasing field age and decreasing management intensity at the field scale are efficient management options to develop ecological intensification of vineyard independently of the type of farming systems.

The diversity of farming practices at multiple spatial scales is an important aspect of landscape heterogeneity that affects natural enemy assemblages in agricultural landscapes. Considering farming practices within the landscape helps in making sense of the context dependency of the effects of the proportion of semi-natural habitats on natural enemies and biological control services. We demonstrated that organic farming at the local scale has a strong effect on abundances of dominant species but not on species richness and that there is no unique response of biodiversity to organic farming expansion. All these results indicate that policies promoting the expansion of organic farming could benefit to ecological intensification strategies (e.g., enhancing pest control services) if dominant predator species are the most efficient species to control pests. However, the expansion of organic farming is not a sufficient agro-environmental measure to support biodiversity conservation. Finally, we show that reducing pesticide use intensity, soil tillage intensity and crop productivity are efficient management options that benefit to natural enemy abundance and richness independently of the type of farming systems in vineyards.

## CONFLICT OF INTEREST

None declared.

## AUTHOR CONTRIBUTIONS

L.M., D.T. and A.R. conceived and designed the study. L.M., A.A., O.B., S.R.C., and A.R. collected the data. L.M. and A.R. analyzed the data. L.M. wrote the first draft of the manuscript and all authors contributed substantially to the writing of the final manuscript and gave final approval for publication.

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## OPEN RESEARCH BADGES

This article has earned an Open Data Badge for making publicly available the components of the research methodology needed to reproduce the reported procedure and analysis. All materials are available

at [https://data.inra.fr/dataset.xhtml?persistentId=doi:10.15454/UCRZO7; https://doi.org/10.15454/UCRZO7].

## DATA AVAILABILITY STATEMENT

Data available from Portail Data Inra: https://doi.org/10.15454/UCRZO7.

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## SUPPORTING INFORMATION

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