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Organic farming and host density affect parasitism rates of tortricid moths in vineyards

A. Rusch[a,b,*], L. Delbac[a,b], L. Muneret[a,b], D. Thiéry[a,b]

[a] INRA, ISVV, UMR 1065 Santé et Agroécologie du Vignoble, F-33883 Villenave d'Ornon, France
[b] Université de Bordeaux, UMR 1065 Santé et Agroécologie du Vignoble, Bordeaux Sciences Agro, CS 20032, 33882 Villenave d'Ornon Cedex, France

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ABSTRACT

Natural pest control by predators and parasitoids is an important ecosystem service supporting crop production. It is now well known that the proportion of semi-natural habitats as well as organic farming enhance abundance and species richness of natural enemies in agroecosystems. However, few studies have examined how these environmental variables affect natural pest control services. Moreover, most studies have been performed in annual cropping systems and almost nothing is known about the effect of landscape complexity and organic farming in perennial crops, which differ greatly from annual ones in terms of disturbance regimes. In this study, we analyzed how landscape composition and farming systems affect abundance of insect pests of grape and their parasitism rates in 79 vineyards in southwestern France. Our results show that farming systems and host density affect biological control of tortricid moths by their parasitoids. Surprisingly, organic fields had lower parasitism rates compared to conventional ones and this rate was negatively correlated to host density at the field scale. We also found that moth community composition depended on the proportion of grapevine crop in the landscape in a 1 km radius but that pest abundance and parasitism rates did not change with landscape complexity. Our results suggest that some farming practices that are frequent in organic farming, such as organic-certified insecticides, copper or sulfur, can reduce parasitoid populations and thus limit biological control in vineyards. Negative density dependence relationship between parasitism rates and host abundance suggest a dilution effect of the biological control potential at the landscape scale and potential mechanisms such as variable parasitoid population sizes, relatively limited female longevity or fecundity, as well as increase in handling time. Further research on the effect of organic and conventional farming practices are now needed to provide a more mechanistic understanding of how these agricultural practices shape ecological processes such as biological control of pests.

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1. Introduction

Agricultural production systems are facing a challenge. Rising demand for agricultural products in yields and quality will increase pressure to further intensify farming systems while there is a need to minimize negative impacts on the environment (Bommarco et al., 2013; Tilman et al., 2002). Ecological intensification of cropping systems thus appears to be a promising alternative to meet such a challenge, by enhancing the services provided by biodiversity and reducing the negative impacts of agriculture on the environment (Bommarco et al., 2013; Godfray and Garnett, 2014). Achieving food security and environmental well-being therefore require improved understanding of the factors affecting service-providing communities and about how to integrate the management of ecosystem services into our farming systems (Bommarco et al., 2013; Power 2010; Rusch et al., 2010).

Natural pest control by predators and parasitoids is an important ecosystem service supporting crop production (Losey and Vaughan 2006). It is now well known that this process is affected by several variables acting at different spatio-temporal scales, such as crop management at the field scale or landscape context (Rusch et al., 2010; Tscharntke et al., 2007). A growing body of evidence suggests that the proportion of semi-natural habitats in the landscape strongly influences natural enemy communities and trophic interactions in agroecosystems (Bianchi et al., 2006; Tscharntke et al., 2007), and it is now demonstrated that landscape complexity enhances abundance and diversity of natural enemies (Chaplin-Kramer et al., 2011) that can lead to higher parasitism or

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* Corresponding author at: INRA – UMR SAVE – Santé et Agroécologie du Vignoble, 71 Avenue Edouard Bourlaux, 33883 Villenave d'Ornon, France. Fax: +33 557122621.
E-mail address: adrien.rusch@bordeaux.inra.fr (A. Rusch).

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predation rates of phytophagous pests (Letourneau et al., 2009; Rusch et al., 2013; Thies et al., 2003). This positive effect of landscape complexity is due to the fact that semi-natural habitats provide several key resources for natural enemies such as alternative host and prey, nectar, overwintering sites or favorable microclimatic conditions (Landis et al., 2000; Rusch et al., 2010; Sarthou et al., 2014). Thus, it is usually assumed that higher proportion of arable land in the landscape will increase pest pressure due to reduced biological control by natural enemies and higher food resources for pest populations (Meehan et al., 2011). However, very few studies have considered the effect of landscape context on pest populations and pest damage (Chaplin-Kramer et al., 2011; Rusch et al., 2013).

Several studies show that organic farming practices at the field scale enhances the abundance and the diversity of natural enemies compared to conventional farming practices (Bengtsson et al., 2005; Hole et al., 2005; Tuck et al., 2014). This effect is usually attributed to the use of synthetic pesticides and higher levels of disturbance in conventional farming (Bengtsson et al., 2005). However, each type of farming system encompasses a wide range of practices and their relative and combined effects on natural enemy communities and pest control remain largely unexplored (but see Puech et al., 2014). It can be hypothesized that organic fields have higher rates of biological control and higher spatio-temporal stability in the biological control due to higher species richness and functional complementarity between species (Crowder et al., 2010). However, a very limited number of studies have examined the effect of farming systems on the level of natural pest control and these studies have produced contrasting results (Crowder et al., 2010; Lohaus et al., 2013; Macfadyen et al., 2009; Roschewitz et al., 2005; Sandhu et al., 2010). Moreover, it has been recently hypothesized that the effect of organic farming at the local scale on biodiversity is modulated by landscape context ("the intermediate landscape complexity hypothesis"—Tscharntke et al., 2012). According to this hypothesis, the benefits of organic farming at the local scale on biodiversity are smaller in very complex landscapes (that already support high level of biodiversity) or in very simple landscapes (with a poor species pool) compared to landscapes of intermediate complexity. However, this hypothesis remains poorly tested on natural enemy communities and biological control (but see Rusch et al., 2014). There is therefore a need for additional studies in contrasted farming systems to understand the relationships between management and functioning in annual and perennial agroecosystems.

In addition to a direct effect of landscape structure on parasitoid populations, parasitism is also likely to be influenced by host abundance (Doak, 2000). The distribution of parasitism rates in relation to host density varies between species (Hassell and Waage, 1984). Some cases reported positive density dependence, in which parasitism rates increased with host density whereas other reported negative density dependence or density independence (Costamagna et al., 2004; Latto and Hassell, 1988; Ray and Hastings, 1996). It has been demonstrated that the relationships between parasitism rates and host density may vary with parasitoid life-history traits and behavior as well as with the spatial or temporal scales (Doak, 2000; Klemola et al., 2014; Roland and Taylor 1997; Teder et al., 2000). Several traits of the parasitoid, such as searching behavior or dispersal abilities, could lead to density dependent parasitism rates. Parasitoids use two main categories of information to localize and parasitize their host: those related to the resource of their host (plant kairomones or plant habitats characteristics such as plant abundance or shape), and those related to the host itself, such as host kairomones (Esch et al., 2005; Finch and Collier, 2000). Host density is probably the most documented driving factor of parasitoid attraction (Walde and Murdoch, 1988). However, most studies document density dependence mechanisms at the plant scale and almost nothing is known about density dependence at larger scales (field or landscape scales for instance). Studying host density at these scales could lead to different patterns. Examining it at the field scale could lead to negative density dependence due to dilution of parasitism capacity because of increase in total handling time or egg depletion, while studying host density effects at smaller scales (e.g., plant) could lead to positive density dependence due to reduced search rate between hosts or natural-enemy aggregation (Rothman and Darling, 1991; Walde and Murdoch, 1988). Moreover, because landscape structure is known to directly affect pest populations as well as their natural enemies, it is of major importance to disentangle the relative effect of host density and landscape context on the level of natural pest control. However, this remains largely unknown as very few studies have examined their relative and interactive effects (but see Costamagna et al., 2004).

Four tortricid moths species are usually found in European vineyards and are distributed mainly according to their climatic requirements: the European grapevine moth *Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae), the grape berry moth *Eupoecilia ambiguella* (Hübner) and the grape tortix *Argyrotaenia ljungiana* (Thunberg) are polyvoltine, while the leaf-rolling tortrix *Sparganothis pilleriana* (Denis & Schiffermüller) is univoltine. These species are the major grapevine pests in Europe, and larvae naturally develop on most grapevine cultivars (Thiéry and Moreau, 2005; Thiéry et al., 2014). Larvae are polyphagous and can feed on berries (*L. botrana* and *E. ambiguella*) or on leaves and berries (*A. ljungiana* and *S. pilleriana*). Several alternative host plants such as *Clematis*,*Lonicera, Ampelopsis* or *Cormus* species are known to occur in semi-natural habitats such as woodlot or hedgerows located in the surroundings but their occurrence is unknown (Thiéry, 2008). Even if the larvae are polyphagous, *Vitis vinifera* L. is their main host in vineyard-dominated areas (Maher and Thiéry, 2006). A wide range of species are known to be natural enemies of tortricid moths on grape (Sentenac, 2011; Thiéry et al., 2001). Insect parasitoids classically found in Europe are egg parasitoids (mainly Trichogrammatidae) and larval/pupal parasitoids (Ichneumonidae, Braconidae, Chalcididae, Pteromalidae, Eulophidae, Elasmidae, Tachinidae). The most frequent and efficient species in European vineyards is the solitary larval endoparasitoid *Campoplex capitator* (Aubert) (Xuéreb and Thiéry, 2006). This species is known to diapause in its host, is specialized on tortricids and has a rather large dispersal range (Thiéry, 2008). Therefore, parasitoid populations may disperse from other vineyards as well as from semi-natural habitats in the surrounding environment. However, the different factors affecting the distribution of tortricid moths and their natural enemies have mainly been studied at the field scale and nothing is known about the effect of farming systems and landscape context on these communities (Thiéry and Moreau, 2005; Thiéry et al., 2014).

We studied tortricid moths and their parasitoids as a model system to examine the effect of organic and conventional farming systems on pest community composition and parasitism rates along a landscape complexity gradient in a vineyard region. We first hypothesized that moth community composition depends on landscape context and particularly that pest abundance would increase with the proportion of grapevine crop in the landscape due to higher resources availability. Based on the literature, we also hypothesized that parasitism rates of tortricid moths would be higher in organic fields and that this positive effect of organic farming is modulated by the landscape context. We expected a larger effect of organic farming on natural pest control in landscapes of intermediate complexity compared to complex landscapes, in which biodiversity and ecosystem services are already maximized, or to very simple landscapes, in which biodiversity and ecosystem services are very low (Tscharntke et al., 2012). Finally, we hypothesized a negative density dependence relationship between parasitism and host density at the field scale due to dilution effect on parasitism capacity.

2. Materials and methods

2.1. Study site and design

The study was carried out in Bordeaux area in southwestern France during three years between 2009 and 2011 in 79 different vineyards (Table 1). Some vineyards were surveyed during one year whereas others were surveyed during more than one year. In the Bordeaux area (Aquitaine region), organic vineyards represented about 5% of the vineyards between 2009 and 2011 but that proportion is increasing rapidly. Vine stock density did not differ greatly between the surveyed vineyards (mean: 5495 ± 764 plant/ha). Landscapes in this area vary from extremely simplified, where only grapevines are cultivated, to complex ones characterized by a high proportion of semi-natural habitats such as woodland and grassland. Organic and conventional vineyards were selected along a landscape complexity gradient to examine the relative effects of farming system and landscape on tortricid abundance on grapes and the extent of pest population reduction by their parasitoids (Table 1). The landscape around each vineyard was characterized by calculating the proportion of semi-natural habitats and agricultural areas within a 1000 m radius using ArcView 10 (ESRI) and data from the Corine Land Cover database (Büttner et al., 2002). For each sampled vineyard, two within-field variables were recorded: the use of insecticide (organic-certified or synthetic) during the last two years (qualitative assessment: yes or no) and the type of grass cover management (qualitative assessment: no vegetation left, half-covered or totally covered). These variables can potentially affect pest and parasitoid populations, and allow a better description of differences between fields in terms of crop management (Danne et al., 2010; Nash et al., 2010; Thomson and Hoffmann, 2007).

2.2. Sampling method

The larvae of the four tortricid species studied build individual nests in their spring generation. The proportion of plant attacked by tortricid moths was thus assessed by scoring the number of larval nests at bloom on 100 grape clusters (for *L. botrana, E. ambiguella* and *A. ljungiana*) and on 100 leaves (for *S. pilleriana*). One grape cluster and one leaf per plant were selected on 100 randomly chosen plants. All the collected samples (larval nests) were brought to the laboratory and were maintained in small boxes with freshly collected bunches and larvae were fed ad libitum until the end of their development (Moreau et al., 2009). Larval populations were checked until pupation, upon which, pupae were removed from the flower buds and isolated in glass tubes and stored at 22 °C, 60% RH and 16/8 L/D. Adult moths and parasitoids were identified after emerging using the taxonomic key of Sentenac (2011).

2.3. Statistical analysis

2.3.1. Tortricid moths and parasitoid community composition

To analyze how farming systems and the proportion of vineyard affect tortricid moths and parasitoid community composition (relative species abundance), we used PERMANOVA on a Hellinger distance matrix between sites using the 'vegan' package in R (function 'adonis') (Oksanen et al., 2013). Hellinger distance was used to reduce the effect of high abundance values in the matrix. A year effect was also added to examine change in species composition between years. PERMANOVA results were calculated based on 999 permutations. To test for multivariate dispersion, we used the 'betadisper' function from the 'vegan' package. To visualize patterns in species composition, we used non-metric multidimensional (NMDS).

2.3.2. Pest abundance and moth parasitism rates

Generalized linear mixed effect model (GLMM) with quasi-binomial error distribution was fitted to analyze the effects of farming systems and the proportion of vineyards in the 1 km radius on the proportion of grape with tortricid larvae (function glmmPQL from R package MASS). A quasi-binomial distribution was used to account for overdispersion. Following this analysis, the use of insecticide during the two preceding years (yes or no) was added in the full model in order to explicitly test for the effect of the use of insecticides (either synthetic or organic-certified) on pest pressure, independently of the farming system.

GLMM with binomial error distribution was fitted to examine the effect of host density, farming systems and the proportion of semi-natural habitats on overall mean parasitism rates of grape berry moths. Following this analysis, two within-field variables were added in the full model (the use of insecticide during the previous two preceding years (yes or no) and the type of grass cover between rows (no vegetation, half-covered and totally covered)) in order to explicitly test for the effect of these variables on biological control, independently of the farming system. In addition to overall mean parasitism rates of grape berry moths we also built models for parasitism rates from *C. capitator* (the largely dominant parasitoid species in our communities). Because non-linear interaction between landscape complexity and local farming system could be expected, we compared models (GLMMs) including a quadratic or an exponential term of landscape complexity. Non-linear terms and their interactions with local management were never significant and model fits (assessed using AIC) were always worst for GLMM including non-linearity terms. Only GLMM without non-linear terms are therefore presented.

In all GLMM, year and site were included as nested random effect to account for repeated measures in the same year and in the same site during several years, and the structure of fixed effects was simplified by backward elimination of non-significant

Table 1
Characteristics of the sampled vineyards between 2009 and 2011. Proportions of semi-natural habitats were calculated with the Corine land cover database.

Year	Farming system	Number of vineyards	Proportion of semi-natural habitats (range in%)
2009	Organic	5	0–28
	Conventional	18	0–100
2010	Organic	12	0–100
	Conventional	20	0–100
2011	Organic	13	0–91
	Conventional	30	0–95

interactions and main effects ($p > 0.05$). In the results the minimum adequate models for each response variable are presented. We used the R packages 'lme4' (function 'glmer') and 'MASS' (function 'glmmPQL') to build GLMMs. Fields where very low larval populations (<10 individuals) were collected were not considered when analyzing moth and parasitoid community composition as well as parasitism rates. Grape cultivar was not included as an explanatory variable because vineyards were largely dominated by one cultivar (more than 65% of the vineyards sampled used 'Merlot' cultivar) and because it has been previously demonstrated that grape cultivar does not affect tortricid moths abundance and parasitism rates (Thiéry et al., 2014; Xuéreb and Thiéry, 2006).

3. Results

The mean proportion of grape stock attacked by tortricid moths per field (±SD) was 16.2 ± 13.2 % (min: 3%; max: 46 %) in 2009, 15.7 ± 18.27% (min: 1%; max: 70%) in 2010 and 30.1 ± 29.3 % (min: 1%; max: 100%) in 2011. A total of 2745 moth larvae were collected during the study among which 365 were parasitized. The mean parasitism rate per field was 23.1 ± 22% (min: 0%; max: 100%). From the unparasitized larvae, we identified the four main tortricid species mentioned above. These were dominated by *L. botrana* (~76%) and *E. ambiguella* (~23%) whereas *A. ljungiana* and *S. pilleriana* were rarely found (<1 % of the unparasitized larvae). Most of the parasitized larvae were parasitized by *C. capitator* (~ 91 %). Other parasitoid species were: *Phytomyptera nigrina* (<1%), *Tranosomella praerogator* (<2%), *Diadegma fenestrale* (<1%), *Agrypon anxium* (<1%), *Charmon* sp. (<1%), *Elasmus* sp. (<1%). Approximately 5% of parasitoids were not identified due to mortality at the nymphal instar. They all had the characteristics of the Hymenoptera, especially those of the Ichneumonidea nymphs, but no other morphological traits allowed a more precise identification.

3.1. Tortricid moths and the parasitoid community composition

Community composition of tortricid moths was not affected by farming systems but changed along the proportion of vineyard in the 1 km radius (Table 2). The fit of significant environmental variables to moth community NMDS scores indicated that change in community composition mainly came from an increased abundance of *E. ambiguella* with the proportion of vineyard in the landscape whereas the abundance of *L. botrana* was not affected by landscape context (Fig. 1). Our results did not reveal any differences in terms of community composition between the three successive years but indicated changes in composition between years depending on the farming system (significant farming system × year interaction, Table 2). Our results revealed that community composition of parasitoids did not change among farming systems, landscape context or between years (Table 2). In fact, parasitoid communities were largely dominated by *C. capitator*. The occurrence of *P. nigrina* should be noticed as a new species in the Bordeaux Area, this species expanding its geographical distribution from the South.

3.2. Tortricid moths pressure

No differences in the proportion of grapes attacked by moths were found between organic and conventional vineyards (Table S1, Fig. 2) or between vineyards that received at least one insecticide (organic-certified or synthetic) during the last two years or not (Fig. S1 in the appendices). Similarly, the proportions of grapes attacked by tortricid moths were not related to the proportion of vineyard in the 1 km radius (Table S1, Fig. 2). Indeed, none of the candidate explanatory variables was retained in the minimal generalized linear mixed-effect model after model simplification.

3.3. Parasitism rates

The minimal generalized linear mixed-effect model explaining the proportion of parasitized larvae indicated that the overall parasitism rate of tortricid larvae was negatively related to host abundance and was lower in organic than in conventional fields (Table 3, Fig. 3). No effect of the proportion of semi-natural habitats, the use of insecticides or grass cover management on parasitism rates was found (Fig. 4). We found the same results on parasitism rates from the dominant species *C. capitator*. Parasitism rate from *C. capitator* was negatively related to host abundance and was lower in organic than in conventional fields (Table 3, Fig. 4).

4. Discussion

In this study, we found that farming systems and host density at the field scale affected parasitism rates of tortricid moths in vineyards. Surprisingly, we found that organic vineyards had lower parasitism rates compared to conventional ones and that the parasitism rate (mainly by *C. capitator*) was negatively correlated to host density at the field scale. Moth community composition was affected by the proportion of vineyard in the landscape but landscape context did not affect pest pressure nor parasitism rates.

Contrary to what was expected, parasitism rates of tortricid moths were higher in conventional vineyards compared to organic ones and landscape context did not affect rates of parasitism. Taking into account insecticide use (organic-certified or synthetic) and grass cover management, irrespectively of farming systems, did not help to explain differences in parasitism rates, suggesting that this difference is derived from other co-variables related to farming systems. It has been well demonstrated that organic farming increases species richness and abundance of different taxa

Table 2
Effects of farming system, proportion of vineyard in a 1 km radius, and sampling year on tortricid moth community composition and parasitoid community composition based on permutational analysis of covariance. Significant effects are shown in bold ($P < 0.01$).

Variables	Totricid moth			Parasitoid		
	df	F	P-value	df	F	P-value
Farming syst.	1	0.08	0.741	1	0.13	0.95
Proportion of vineyard	1	12.51	**0.007**	1	0.01	0.50
Year	2	8.98	0.153	2	3.31	0.13
Farming syst. × proportion of vineyard	1	1.06	0.305	1	3.19	0.14
Farming syst. × year	2	7.05	**0.005**	2	0.68	0.80
Proportion of vineyard × year	2	2.27	0.165	2	5.39	0.10
Farming syst. × proportion of vineyard × year	2	0.13	0.831	2	1.59	0.10
Residuals	34			28		
Total	45			39		

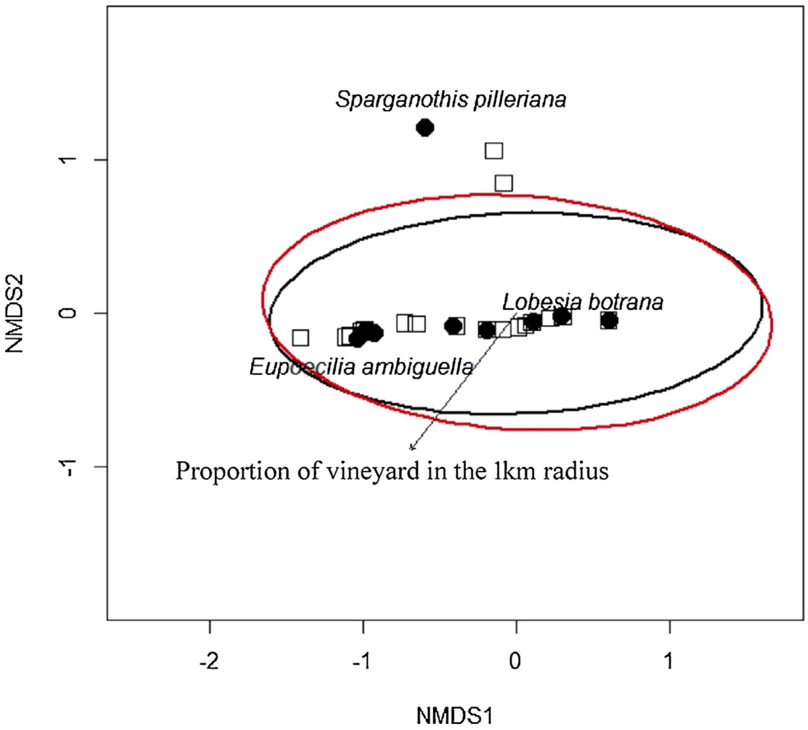

Fig. 1. Non-metric multidimensional scaling ordination of study sites based on similarity in species composition (2-dimensional stress = 0.005) with 95% confidence ellipses. The clustering of sites in NMDS ordination space indicates that parasitoid composition is similar between farming systems (white squares, black ellipse = conventional fields; black dots, red ellipse = organic fields). Symbols represent site values and confidence ellipses are drawn around the group centroid. The angle and length of vector loadings indicate the direction and strength of associations, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

including natural enemies of crop pests (Bengtsson et al., 2005; Tuck et al., 2014). However, the mechanisms behind the effect of farming systems on the level of natural pest control remains poorly understood. Several studies have examined the effect of organic farming on the rate of biological control by parasitoids in different agroecosystems (Lohaus et al., 2013; Maalouly et al., 2013;

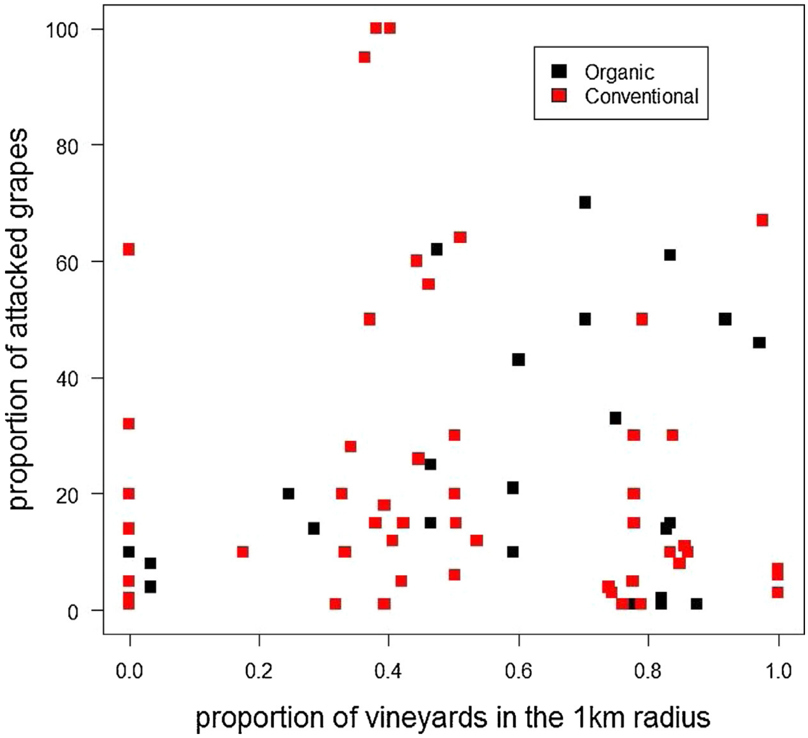

Fig. 2. Proportion of grapes attacked by tortricid moths in relation to the proportion of vineyards in the 1 km radius and farming systems (organic or conventional). No significant effect of the proportion of vineyard as well as the type of farming system were found. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Summary of the generalized linear mixed-effects model relating host density, farming system and landscape complexity to overall parasitism rates and parasitism rates from *Campoplex capitator*. Results are showing the minimum adequate model resulting from manual backward elimination of non-significant interactions and main effects ($P > 0.05$).

Parasitism rates	Variable	Estim.	SE	*z*	*P*
Overall parasitism rates	Host density	−0.03	0.007	−4.97	<0.001
	Farming system (=organic)	−1.03	0.43	−2.35	0.018
Campoplex capitator	Host density	−0.03	0.007	−5.00	<0.001
	Farming system (=organic)	−1.08	0.43	−2.48	0.013

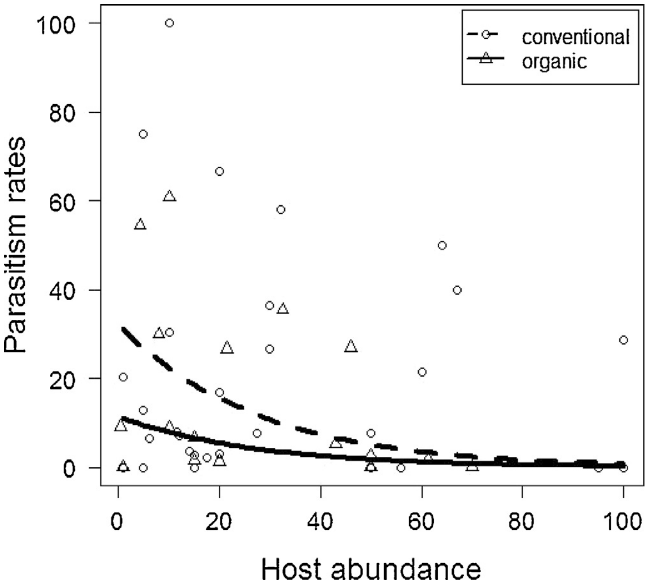

Fig. 3. Relationship between overall parasitism rates of tortricid moths and host abundance for organic (triangle and solid line) and conventional (circle and dashed line) vineyards. The effect of host abundance as well as the difference between organic and conventional farming systems were significant (see Table 3 for statistics).

Macfadyen et al., 2009, 2011; Meyling et al., 2013; Roschewitz et al., 2005). Most of these studies did not detect any differences in parasitism rates between organic and conventional farming, even if the structure of food webs was affected by the type of farming system in some cases. Only one study found higher parasitism rates in organic than in conventional orchards (Maalouly et al., 2013). Our study is therefore the first one highlighting a negative effect of organic farming on the rate of biological control by parasitoids. This pattern may be due to several characteristics of the system studied. First, both organic and conventional vineyards used insecticides (organic-certified and synthetic respectively) that can have strong impacts on natural enemies (Fig. S1). In their study, Bahlai et al. (2010) found that some organic-approved insecticide have similar or even greater negative impact on natural enemies, and that they were more detrimental to biological control than were some synthetic insecticides. Secondly, even if organic systems do not use synthetic pesticides, it is known that organic vineyards tend to have higher number of farming interventions (e.g., mechanical weeding, tillage, insecticides, fungicides) that might result in a higher disturbance regime compared to conventional fields depending on the species considered (Delbac et al., 2012). Such regimes may have limited natural pest control by parasitoids (Jonsson et al., 2012). Moreover, the main difference between organic and conventional vineyards is the higher use of copper and sulfur in organic fields as fungicide against various grapevine diseases (*unpublished data*). These products are known to affect arthropods in general and natural enemies in particular so that could explain lower parasitism rates in organic vineyards (Nash et al., 2010). For instance, several studies have shown the negative effect of sulphur on a wide range of natural enemies including parasitoids, predatory mites and spiders (Gent et al., 2009; Martinson et al., 2001; Nash et al., 2010). Our findings suggest the need for a more detailed description of farming systems to provide a more mechanistic understanding of the way farming systems shape ecological processes such as biological control of pests (Puech et al., 2014; Rusch et al., 2011).

Our results confirmed the initial hypothesis about negative density dependence between parasitism rate and host density at the field scale. A range of relationships between host density and parasitism rate have been reported before (Costamagna et al., 2004; Doak, 2000). In a literature survey including 75 studies, Walde and Murdoch (1988) found positive density dependence in 23% of the studies, negative density dependence in 28% and density independence in 49 %. The spatial scales at which the studies were performed and differences in life-history traits of parasitoid species are potential explanations for these variable effects. The negative density dependence observed at the field scale combined with the fact that landscape complexity did not affect pest abundance and parasitism rates suggests different mechanisms including variable population sizes of the parasitoids colonizing a given patch, relatively limited female longevity and/or fecundity (temporally egg-limited) or increase in handling time. Indeed, such mechanisms have been found to be responsible for the negative density dependence pattern in host–parasitoid interactions

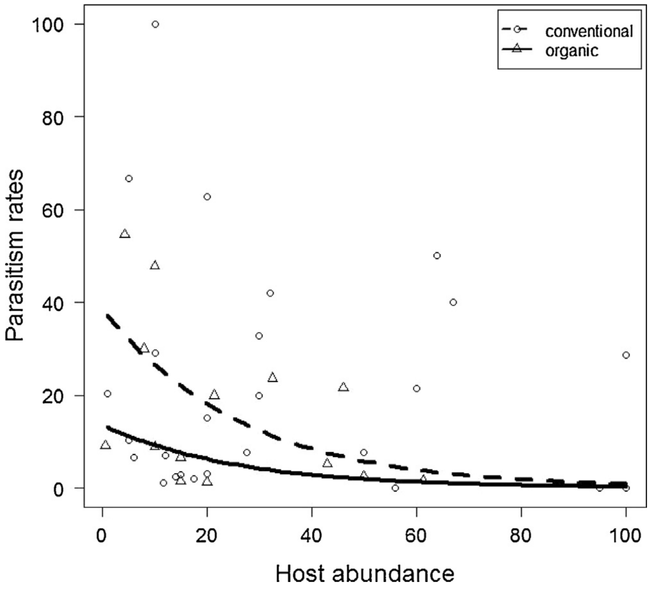

Fig. 4. Relationship between parasitism rates of moths from *Campoplex capitator* and host abundance for organic (triangle and solid line) and conventional (circle and dashed line) vineyards. The effect of host abundance as well as the difference between organic and conventional farming system were significant (see Table 3 for statistics).

(Heimpel and Rosenheim, 1998; Walde and Murdoch, 1988). Our results may also suggest relatively low mobility between patches at the landscape scale or at least low spillover between low-density (where host population is largely exploited) and high-density patches (where host population is underexploited). If spillover between patches were important then they would have compensated for low parasitism rates in high-density patches and no density-dependence would have been observed. However, more detailed studies about life-history traits of the main parasitoid species *C. capitator*, and particularly about the patterns of host patch use, and factors influencing the behavior and the fitness of the parasitoid in the field, are necessary to reveal the exact mechanisms involved in the negative density dependence pattern found here.

Our results did not support our hypothesis about higher pest pressure in simple landscape due to lower biological control by their parasitoids and/or higher food availability, as pest abundance and parasitism rates did not vary along the landscape complexity gradient. Moreover, our findings did not support the intermediate landscape-complexity hypothesis, which suggests a larger effect of organic farming on ecosystem services in landscapes of intermediate complexity compared to extremely simple or complex landscapes, as no interacting effect of landscape complexity and farming system was detected. Even if overall pest abundance did not change with the landscape context, we found that community composition of tortricid larvae was affected by the proportion of vineyard in the 1 km radius, with increased abundance of *E. ambiguella* in landscapes supporting a higher density of vineyards. However, *L. botrana* remained the dominant species in any landscape context. This result suggests that *E. ambiguella* responded to an increase in resources availability in the landscape.

It has been demonstrated that biological control by parasitoids is often stronger in more complex landscapes because they rely on semi-natural habitats to find key resources such as alternative hosts, nectar resources and refuge from disturbance (Landis et al., 2000; Rusch et al., 2010). Our results indicate that the solitary parasitoid *C. capitator*, the main parasitoid species found in our study, may not strongly depend on semi-natural habitats for maintaining populations at the landscape scale. Vineyard landscapes in this study may support enough nectar resources for the parasitoid. In the light of knowledge about the biology of the species, our findings suggest that *C. capitator* may be well adapted to intensified vineyard landscapes, as it is a polyvoltine species relatively well specialized on its host, able to parasitized all generations of tortricid moth (up to three in our area) and not strongly dependent on semi-natural habitats.

5. Conclusions

Our study demonstrates that the level of biological control of tortricid moths in vineyards is negatively related to host abundance and by some organic farming practices. Organic farming is often considered to be of low impact, favoring biodiversity and associated ecosystem services (Tuck et al., 2014). While this has largely been demonstrated in annual cropping systems, our results show that the positive effect of organic farming on ecosystem services is highly context-dependent and might not hold in perennial cropping systems such as grapevines where differences between organic and conventional farming may be less pronounced than in annual cropping systems. Further research on the effects of organic and conventional farming systems on other groups of natural enemies and their trophic interactions in this cropping system are thus needed. To provide a more mechanistic understanding of the way farming systems shape ecological processes such as biological control of pests, we advocate for a more detailed description of farming practices within those broad farming categories (see Puech et al., 2014).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.08.019.

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