Temporal variation of the effects of landscape composition on lacewings (Chrysopidae: Neuroptera) in vineyards

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Abstract

1. Increasing landscape heterogeneity, both in terms of composition and configuration, can promote natural enemies and biological control in agricultural landscapes. However, relatively poor information exists about the effects of landscape heterogeneity on lacewings, which are a major group of predators. Furthermore, temporal changes of landscape effects on natural enemy dynamics remain largely unexplored.

2. Here, we investigated how landscape composition and configuration affect lacewings and their biological control potential on leafhoppers. Lacewings and leafhoppers were sampled from April to July in 10 vineyards located in southwestern France. The vineyards were selected along a gradient of a proportion of semi-natural habitats in the landscape.

3. The proportion of semi-natural habitats positively affected the abundance of adults and eggs, as well as species richness, of lacewings, alone or in interaction with the sampling month. Landscape configuration was never found to enhance abundance or species richness of lacewings. Finally, the predator–prey ratio increased through time but did not respond to landscape composition or configuration.

4. Our study highlights that the proportion of semi-natural habitats increases both abundance and diversity of lacewings in vineyard landscapes but that this effect varies over time. This result indicates the need to assess the variability of landscape effects over time to maximize biological pest control services in agricultural landscapes.

Keywords Conservation biological control, lacewings, landscape, seasonality, semi-natural habitat, vineyard.

Introduction

Modern agriculture is characterized by landscape homogenization and by the intensive use of agrochemicals that have strong negative impacts on the environment (Fahrig, 2003; Tscharntke *et al.*, 2005; Tilman *et al.*, 2011). There is increasing evidence that the intensification of agriculture strongly contributes to global biodiversity decline (Fischer *et al.*, 2018). For instance, pesticide use has substantial negative impacts on the natural enemies of crop pests or on pollinators that support major regulation services for crop production (Geiger *et al.*, 2010; Rundlöf *et al.*, 2015). These impacts strongly affect the sustainability of farming systems and highlight the need to develop alternative farming methods. Among potential alternatives, the ecological intensification of farming systems based on enhancing ecological

processes to replace the use of agrochemicals offers a promising way to combine crop productivity with a low environmental footprint (Bommarco *et al.*, 2013; Kleijn *et al.*, 2018).

Biological pest control is a major ecosystem activity that could contribute to the reduction of pesticide use in agricultural landscapes (Naranjo *et al.*, 2015; Rusch *et al.*, 2017). Conservation biological control consists of modifying farming practices and managing surrounding habitats with the aim to enhance the activity and density of communities of natural predators or parasitoids (Barbosa, 1998; Landis *et al.*, 2000). Semi-natural habitats such as forests, grasslands or hedgerows are important for beneficial species as they provide overwintering sites, shelters, favourable microclimates or alternative foods and hosts (Landis *et al.*, 2000; Rusch *et al.*, 2010). Landscape composition and configuration are known to influence natural enemy abundance and, therefore, the potential biological control they deliver (Fahrig *et al.*, 2011; Martin *et al.*, 2016). Landscape composition provides information about the relative amount of each habitat type in the

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landscape, whereas landscape configuration gives information about their spatial arrangement (*e.g.*, patch size and connectivity). Recent studies have demonstrated that the proportion of semi-natural habitats in the landscape enhances natural enemy (vertebrates and invertebrates) abundance and diversity, as well as pest control services (Chaplin-Kramer *et al.*, 2011; Rusch *et al.*, 2016). Other studies showed that increasing landscape connectivity between habitats also had a positive effect on the diversity and abundance of natural enemies (Martin *et al.*, 2016; Dominik *et al.*, 2018) because it can improve the dispersion of species (Fagan *et al.*, 1999). However, there is a gap in the knowledge that connects how the configuration and composition of semi-natural habitats influence natural enemy populations. Several studies tested how landscape composition and configuration simultaneously explain abundances of target species (Perović *et al.*, 2015; Collins & Fahrig, 2017; Hass *et al.*, 2018; Reynolds *et al.*, 2018) or the level of pest control they provide (Baillod *et al.*, 2017; Ardanuy *et al.*, 2018), but their effects still remain unclear and strongly depend on the taxa under study. A recent meta-analysis from Martin *et al.* (2019) shows that the abundance of arthropods in agricultural landscapes depends on the interaction between landscape configuration and composition, with the highest abundance in landscapes that combine high edge density with high proportions of semi-natural habitats. However, this study also highlights that considering specific response traits such as dispersal ability or habitat used for overwintering revealed a contrasted effect of landscape context. Therefore, the relative effects of landscape composition and configuration on natural enemies and pest infestations need more investigation to provide clear and efficient management options at the landscape scale to optimize pest control services.

Furthermore, although several studies have explored the effect of landscape context on natural enemies and pest control services in a spatial context, much less is known about the temporal dynamics of landscape context and its effects on predators and pest control services (Bertrand, *et al.*, 2016; Bianchi *et al.*, 2015; Raymond *et al.*, 2015). Spillover of beneficial insects between semi-natural habitats and crops has been highlighted as one of the mechanisms driving the effects of landscape context on community assemblages and predator–prey dynamics (Rand *et al.*, 2006; Blitzer *et al.*, 2012; Tscharntke *et al.*, 2012). Spatio-temporal variability in resource availability in interaction with key functional traits (*e.g.*, dispersal ability) are assumed to drive the magnitude and the direction of spillover through complementation or supplementation (Rand *et al.*, 2006). Therefore, complex landscapes with a high proportion of semi-natural habitats in the landscape are likely to allow early colonization of crops by natural enemies and to support earlier pest control services compared with simple landscapes (Costamagna *et al.*, 2015). For instance, linyphiid spiders are more abundant in landscapes supporting higher boundary length but only early in the growing season (Öberg *et al.*, 2008). In such a case, biological pest control services are expected to be more important in complex landscapes compared with simple landscapes. Although this is a key question for pest management in agricultural landscapes, very few studies have examined the temporal variation of landscape context effects on natural enemies and pest control services (Chaplin-Kramer *et al.*, 2011; Schellhorn *et al.*, 2014).

In France, viticulture accounts for 3.3% of the French agricultural area and demonstrates a high level of pesticide use. For instance, the average number of pesticide treatments in 2016 in France was around 20, of which 83% was dedicated to fungicides, followed then by insecticides–acaricides (13%) and herbicides (4%) (Agreste, 2019). The main insect pests in vineyard are grape moths, mainly *Lobesia botrana* and *Eupoecillia ambiguella* (Lepidotera: Tortricidae) (Reineke & Thiéry, 2016; Thiéry *et al.*, 2018); mealybugs (*Parthenolecanium* spp. and *Neopulvinaria innumerabilis*) (Hemiptera: Coccidae); leafhoppers [*Scaphoideus titanus* vector of 'Flavescence dorée' (Chuche & Thiéry, 2014), *Hyalesthes obsoletus* the 'bois noir' vector and *Empoasca vitis*, not known as a vector but causing barnacles] (Hemiptera: Cicadellidae); mites; drosophila; and, to a lesser extent, aphids (Phylloxera). These pests are potential food sources for lacewings (Neuroptera: Chrysopidae) [*e.g.*, *Chrysoperla carnea* gr. species feeding on *Tuta absoluta* (Lepidotera: Gelechiidae), Zappala *et al.*, 2013]. Lacewings are known to be voracious aphidophagous predators and are often used to control pests of vegetables or orchards (Daane & Hagen, 2001; Maisonneuve, 2001; Tommasini & Mosti, 2001). However, they still remain poorly studied, especially in perennial crops such as grapevines.

Lacewing diets greatly differ according to species and development stage. At the adult stage, only species of the genus *Chrysopa* are still predatory, whereas other species, such as those of the *Chrysoperla* genus, feed on nectar, pollen and honeydew, which increase longevity, fecundity and – subsequently – biological control (Robinson *et al.*, 2008). They commonly overwinter in semi-natural elements, in dead leaves, litter or bark, and can be found in unheated areas of country houses, such as attics, or in barns (*i.e.*, *Chrysoperla affinis*) (Canard *et al.*, 1984). Lacewings from the *Chrysoperla* genus emerge from diapause when temperatures reach an average of 10 °C and migrate from overwintering sites to other habitats, such as trees or agroecosystems, to feed on pollen and nectar and to breed (Villenave & Rat-Morris, 2007). In early summer, they disperse to feed and reproduce on the lowest layer of vegetation (herbaceous and cultivated plants). In late summer, when the photoperiod declines, adults enter into reproductive diapause and migrate to semi-natural habitats for overwintering (Villenave & Rat-Morris, 2007). Lacewing species such as *Chrysoperla* spp. therefore need a significant diversity of habitats and resources, both spatially and temporally, during their life cycle. This implies that the distribution of food resources, as well as the occurrence of overwintering sites in the landscape, can potentially affect population dynamics. For all these reasons, lacewings are an interesting study model to analyse the seasonal effects of landscape composition and configuration on population dynamics and its potential biological pest control services in vineyard landscapes.

The objectives of our study are to (i) describe lacewing assemblages and their temporal dynamics in vineyard landscapes, (ii) assess the relative effects of landscape composition and configuration on lacewing communities and population dynamics and (iii) explore their potential as a predator of leafhoppers in vineyard landscapes. We decided to study lacewing as a potential predator of leafhoppers as they are key pest species in the studied region and because previous studies suggest

that lacewings can be efficient predators of leafhoppers (Daane *et al.*, 1996; McEwen *et al.*, 2007). We hypothesized that greater areas of semi-natural habitat should increase lacewing abundances and species richness by providing key food resources and overwintering sites. We also hypothesized that the magnitude of landscape context effect on lacewing communities is changing with sampling date, thereby revealing colonization patterns from semi-natural habitats to crops. Finally, we hypothesized that more edges between semi-natural habitats and vineyards should enhance the biological pest control potential by enhancing spillover of lacewings from semi-natural habitats to crops.

Methods

Study sites and landscape description

The study was conducted in 2018 in the Bordeaux region of southwestern France (44° 31′ 54″ N; 00° 20′ 34″ W). We selected 10 vineyards (white varieties) along a landscape gradient based on the proportion of semi-natural habitats (composed of forests, wooded areas and hedges – see below) in a landscape of 1-km radius. This region is largely dominated by wine production. A temperate oceanic climate prevails. Spring is humid and warm, with an average temperature of 12 °C. During summer, the average temperature in July (warmest month) is 20 °C. During winter, the average temperature in January (the coldest month) is around 5 °C (climate-data.org).

The average plot size was 1.13 ha (min = 0.58 ha, max = 3.12 ha). The land use around each plot was digitized according to the classifications from 'BD-Ortho' and 'BD-Forest 2015' of the National Institute of Geographical and Forestry Information, coupled with intensive field surveys. The different land use types considered were forest, wooded area (including small wooded areas not included in the 'BD-Forest 2015' of the IGN), meadow, garden/park, vineyard, crop, water (permanent bodies of water and waterways), hedge, highway and urban area. For all landscapes, we calculated four metrics, two metrics each of both compositional and configurational heterogeneity. These metrics were respectively: the proportion of semi-natural habitats (considering forest, wooded areas and hedges), the Shannon diversity index considering all land cover types (SHDI), the average Euclidean distance between the plot monitored and the different patches of semi-natural habitats and the length of the interface between grapevines and semi-natural elements. We only considered forest, wooded areas and hedges as semi-natural habitats because most meadows are grazed in this area and because this type of habitat is not known to be potential overwintering habitats for lacewings. These indices were calculated within a 1-km radius around each plot as this scale is usually relevant to explain predator assemblages in agricultural landscapes (Chaplin-Kramer *et al.*, 2011; Martin *et al.*, 2013). We only retained the proportion of semi-natural habitats and length edge because of collinearity among variables (Table S1). The amount of semi-natural habitats varied from 8.7% to 87.3% with a mean of 43.1%, and the edge length varied from 3403 m to 19 862 m with a mean of 12 827 m (see Table S2 for detailed values). Landscape analyses were carried out using QGIS 3.0 and Chloe 4.0 software (Boussard & Baudry, 2017).

Lacewing and leafhopper sampling

Three attractive food traps (17 cm in diameter) were placed in each plot to capture adult lacewings. Each trap contained 500 mL of apple must diluted with 20% of water and a few drops of surfactant (dishwashing liquid). The first trap was located in the centre of the plot, and the other two were spaced 10 rows away along the diagonal of the plot. Insects were collected from these traps once a week from March 26th to the end of July. Visual counting of lacewing eggs and leafhopper larvae was conducted on 50 randomly selected leaves (2 leaves per plant) along five transects of 25 m every 15 days from May 14th to the end of July. Finally, active sampling of lacewing larvae was performed by beating on 50 trunks per plot selected randomly along five transects of 45 m, and at intervals of least 5 m to limit disturbance, every 15 days from May 29th (at the beginning of the first hatching period) to the end of July. Adults were sexed and identified at the species level with the identification key developed by Mazel *et al.* (2006), whereas larvae were determined at the genus level (Díaz-Aranda & Monserrat, 1995). Abundances per species (for adults) and per life stage (*i.e.*, eggs, larvae or adults) were separately pooled by month, leading to 16 replicates for adults (weekly sampling during 4 months), 5 for eggs (fortnightly sampling during 2.5 months) and 4 replicates for larvae (fortnightly sampling during 2 months).

Statistical analyses

We used generalized linear mixed models (GLMM) with a Gaussian distribution of errors to investigate the relative effects of landscape composition and configuration on lacewing abundance (for each life stage), species richness and predator–prey ratio (calculated as the ratio between lacewing larvae abundance and leafhopper larvae abundance). In each model, field was considered as a random effect because of repeated measures on the same field at different times. All quantitative response variables were normalized by a log-transformation ($\log x + 1$) prior to analysis, and no interactions between landscape composition and configuration were included in our models. Predictors were scaled before the analyses by subtracting the mean and dividing by the standard deviation. In all models, we added an interaction term between each landscape variable and date (*i.e.*, month) to explore variability of landscape effects over time. All models were then simplified using a multi-model inference approach (Grueber *et al.*, 2011; Harrison *et al.*, 2018) based on the Akaike information criterion (AIC) corrected for a small sample size (AICc) [model averaging with ΔAICc <2 (Grueber *et al.*, 2011)]. Only results from the best-fitted model are presented here. April was not considered for the analysis of lacewings eggs, lacewing larvae and predator–prey ratios because no individuals were collected. In preliminary analyses, we explored the correlation between local variables such as type of management (*e.g.*, organic, conventional), the Treatment Frequency Index (indicator of pesticide use considering here insecticides, fungicides and biocontrol products or field area) and landscape variables (correlation matrix in Table S2). Because of limited statistical power and because these local variables were not correlated with the explanatory variables of interest, we decided to only include the month, the proportion of semi-natural habitats and

the edge length as explanatory variables. No significative correlation between the percentage of semi-natural habitats and edge length was found (Table S1). Correlations among covariates in models were assessed using Variance Inflation Factors (all VIF < 2) (James *et al.*, 2013). For each model, we checked for over-/under-dispersion. Diagnostic residual plots of all full models confirmed a good fit for all. Spatial correlation in the residuals was checked using the 'bubble' function from the 'sp' package, and no spatial correlation was detected (Fig. S1). All analyses were performed with R version 3.5.2 (2018-12-20) and the packages 'lme4', 'MuMIn', 'multcomp', 'sp' and 'ggplot2'.

Results

Lacewing and leafhopper assemblages and their temporal dynamics in vineyard landscapes

A total of 382 adult lacewings were captured from March 26th to July 31st, and they belonged to nine species and three genera (*Chysoperla*, *Chrysopa* and *Pseudomallada*): *C. lucasina* (representing 40.58% of the total number of adults), *P. flavifrons* (21.73%), *C. affinis* (10.47%), *P. inornatus* (8.12%), *P. prasinus* (6.81%), *C. carnea* (2.36%), *P. abdominalis* (1.57%), *C. phyllochroma* (0.26%) and *C. pallens* (0.26%). Thirty individuals (7.85% of the total adult abundance) of the Chrysoperla genus could not be identified at the species level. The first species to colonize the vineyard plots is *C. affinis* at the beginning of April, followed by *C. carnea* and *C. lucasina* at the end of April (Fig. S2). A total of 149 eggs and 149 larvae of lacewings were sampled from May 14th and May 29th, respectively, to July 24th. Larvae were all of the genus *Chrysoperla*, except one individual belonging to the *Pseudomallada* genus. The number of species collected per plot varied slightly (mean = 4.80 species/plot, SD ± 1.40). Very few lacewings were trapped from May to June (<20 individuals/month), whereas the abundance of lacewings of all stages strongly increased at the beginning of July. A total of 937 leafhopper larvae were collected from May 14th to July 24th. We identified four different species: *E. vitis* (representing 73.43% of the total number of larvae), *S. titanus* (24.76%), *Zygina rhamni* (1.07%) and a few *Metcalfa pruinosa* (0.75%). The first peak of leafhopper abundance occurred at the end of May (mean = 27.60 larvae/plot, SD ± 28.07) followed by a second peak in early July (mean = 22.50 larvae/plot, SD ± 26.87) (Fig. S3).

Lacewings (all species confounded), eggs and larvae were significantly most abundant in June and July compared with April and May (Table 1; Fig. 1). The highest abundances were recorded in July (Table 1; Fig. 1). Overall species richness and *Chrysoperla* spp. abundance decreased significantly in May but increased in June and July, respectively (Table 1; Fig. 1). *Pseudomallada* spp. abundance and predator–prey ratio increased significantly in July compared with other months (Table 1; Figs 1 and 2).

Effect of landscape composition and configuration on lacewing abundance, species richness and biological control potential on leafhoppers

The abundance of adults, the abundance of *Pseudomallada* spp. and the species richness of lacewings were found to be significantly affected by the interaction between the proportion of semi-natural habitats and the sampling month (Table 1; Fig. 3). Our analyses revealed that the effects of the proportion of semi-natural habitats in the landscape on adult abundance were positive for all months except for May (Fig. 3). A positive effect of the proportion of semi-natural habitats in the landscape on the abundance of *Pseudomallada spp.* was only detected for the month of July. The number of eggs per field increased significantly with the proportion of semi-natural habitats in the landscape but without interaction with the sampling month, indicating a similar effect of the proportion of semi-natural habitats despite an effect of the sampling month on the average number of eggs (Table 1; Fig. 3). The abundance of lacewing larvae, the abundance of *Chrysoperla* spp., the abundance of leafhopper larvae and the predator–prey ratio were never affected by any landscape variables (Table 1). The length of interface between vineyards and semi-natural habitats never had a significant effect on any of the response variables.

Discussion

Our study reveals that sampling month and landscape composition affect lacewing communities in vineyard landscapes. Larvae and *Chrysoperla* spp. abundance, as well as the predator–prey ratio, was affected only by the sampling month, whereas the abundance of adults and *Pseudomallada* spp. and species richness were affected by landscape composition in interaction with the sampling month. Abundance of lacewing eggs was affected by the landscape composition and the sampling month but without interaction between these two factors. Leafhopper abundance and the predator–prey ratio were never affected by any landscape variables. Contrary to our initial hypothesis, landscape configuration did not affect lacewings or the potential biological control service they provide.

Temporal dynamics in vineyards

The month was always selected as a key explanatory variable in all models, indicating a strong temporal dynamic in lacewing population dynamics. The effect of the sampling period on lacewings is the result of species phenology and potential differences among genera. Individuals of the *Chrysoperla* genus are the first to appear in the season because they overwinter at the adult stage and emerge earlier from diapause (*i.e.*, starting in March) than the other genera. Individuals from the *Chrysopa* and *Pseudomallada* genus overwinter at prepupae and larval stages, respectively (Canard, 2005). This could explain why most *Pseudomallada* species individuals were collected later than those of *Chrysoperla* spp., from late June onwards. These differences in colonization patterns explain why species richness, as well as overall adult abundance, increases over time and was higher later in the season (*i.e.*, July).

No particular temporal dynamic of *Chrysopa* spp. was highlighted in our data because very few individuals were collected. This very low number of individuals trapped may be due to the collection method, which consisted of a food trap based on apple must at a time when most *Chrysopa* spp. are still carnivorous at the adult stage.

Table 1 Parameter estimates of fixed effects of generalized linear mixed models to evaluate effects of landscape context (proportion of semi-natural habitat for composition and edge length between semi-natural habitat and vineyard for configuration) on the abundance of adults of all species, lacewings eggs and larvae, genus *Chrysoperla* or *Pseudomallada*, species richness, leafhoppers larvae and predator−prey ratio

Response variable	Predictors	Estimate	SE	z or t value	P
Adults total abundance	% semi-natural habitats	0.11	0.19	0.57	0.57
	May	−0.39	0.20	1.94	0.05
	June	1.05	0.20	5.27	**<0.01**
	July	2.25	0.20	11.28	**<0.01**
	% semi-natural habitats * May	−0.42	0.20	2.08	**0.04**
	% semi-natural habitats * June	0.11	0.20	0.57	0.57
	% semi-natural habitats * July	0.48	0.20	2.35	**0.02**
	Edge length	0.03	0.09	0.36	0.72
Egg abundance	June	0.88	0.23	3.74	**<0.01**
	July	2.42	0.23	10.31	**<0.01**
	% semi-natural habitats	0.26	0.11	2.41	**0.02**
	Edge length	0.02	0.06	0.26	0.80
Larvae abundance	June	0.76	0.16	4.70	**<0.01**
	July	2.55	0.16	15.88	**<0.01**
Chrysoperla spp. abundance	May	−0.64	0.24	−2.69	**0.01**
	June	−0.04	0.24	−0.18	0.86
	July	1.95	0.24	8.26	**<0.01**
Pseudomallada spp. abundance	May	0.25	0.16	1.55	0.13
	June	0.21	0.16	1.30	0.21
	July	2.15	0.16	13.43	**<0.01**
	% semi-natural habitats	0.00	0.12	0.00	1.00
	% semi-natural habitats * May	−0.18	0.16	−1.09	0.29
	% semi-natural habitats * June	0.02	0.16	0.10	0.92
	% semi-natural habitats * July	0.83	0.16	5.08	**<0.01**
Species richness	May	−0.36	0.13	2.84	**<0.01**
	June	0.50	0.13	3.96	**<0.01**
	July	1.07	0.13	8.48	**<0.01**
	% semi-natural habitats	0.12	0.12	1.03	0.30
	% semi-natural habitats * May	−0.40	0.13	3.09	**<0.01**
	% semi-natural habitats * June	0.08	0.13	0.64	0.52
	% semi-natural habitats * July	0.01	0.13	0.09	0.93
	Edge length	0.01	0.03	0.17	0.87
Abundance of leafhoppers larvae	June	−0.61	0.36	−1.67	0.11
	July	0.51	0.36	1.39	0.18
Predator−prey ratio	June	0.24	0.15	1.61	0.13
	July	0.54	0.15	3.60	**<0.01**

Only the best model retained after multi-model inference is presented. *P*-value <0.05 are in bold characters.

In France, the first emergence peak of lacewings is commonly recorded from May to June, and the mass flight period of adults ranges from June to August under the temperate climate of Europe (Szentkiralyi, 2001; Trouvé *et al.*, 2002; Villenave, 2006). In our study, abundances within vineyards remain very low until early July for all stages. This may be explained by the very rainy spring that might have delayed the second lacewing generation or by the absence of potential preys in vineyards, such as moths or leafhoppers, until mid-May. Our study would therefore benefit from expanded temporal scale and multiple-year observations to investigate how several species or life stages respond to landscape composition all along the year and how variation in meteorological parameters modulate lacewings' responses.

Landscape effects on lacewing abundances and species richness

Our results show that the proportion of semi-natural habitats affects the abundance of adults, eggs and *Pseudomallada* spp.

individuals. This indicates that conserving semi-natural habitats in the landscape increases the abundance of lacewings in vineyards. The magnitude of the positive effect of a semi-natural habitat on lacewings was larger when abundances of lacewings were the highest, suggesting that the statistical detection of landscape effects was only possible after a certain level of colonization. This positive effect can be explained by the life cycle and the ecological requirements of the lacewing genera found in our study. Indeed, semi-natural habitats such as forests or hedgerows provide key overwintering sites for lacewings that enhance winter survival and lead to higher emergence in spring (Pfiffner & Luka, 2000; Griffiths *et al.*, 2008; Woltz *et al.*, 2012). Moreover, such habitats provide key food resources, such as pollen, nectar and alternative prey, that can enhance longevity and fecundity of lacewings, which could explain the increase in egg numbers (Landis *et al.*, 2000; Robinson *et al.*, 2008; Gonzales *et al.*, 2016). Complementation (*i.e.*, seasonal movements between two complementary resources) and supplementation (*i.e.*, substitutive resources distributed in different patches) processes might be involved in the
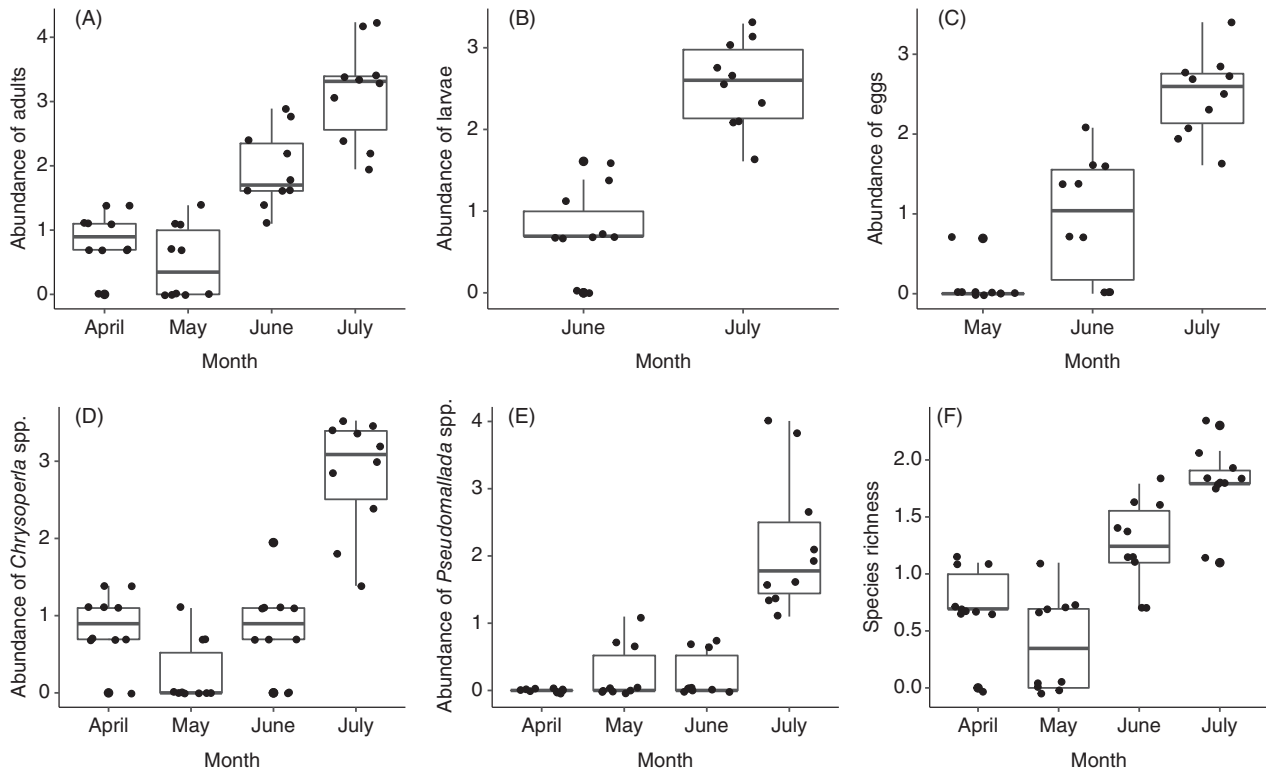
Figure 1 Abundance of (A) adult lacewings, (B) larvae, (C) eggs, (D) *Chrysoperla* spp., (E) *Pseudomallada* spp. and (F) species richness collected per field from April to July. Response variables are log $(x + 1)$ transformed. For the abundance of larvae, only June and July are represented as no larvae were sampled before that; similarly, for the abundance of eggs, only May, June and July are represented as no eggs were sampled before that.
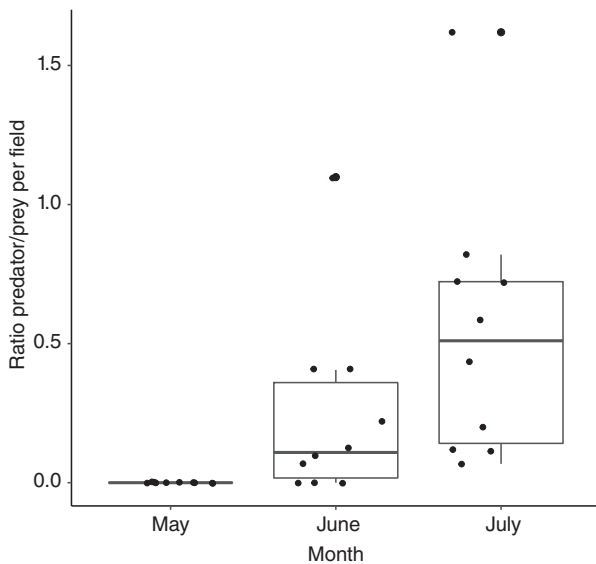

Figure 2 Predator–prey ratio per field across months from May to July. Response variable is log $(x + 1)$ transformed.

observed positive effect of semi-natural habitats on lacewings (Dunning *et al.*, 1992).

Our results confirmed previous studies on other natural enemies, such as ladybugs (Woltz & Landis, 2014), spiders

(Gardiner *et al.*, 2010), parasitoids or predatory thrips (Thomson & Hoffman, 2010). These results therefore suggest possible synergies between biological pest control services delivered by several taxonomic groups. We did not measure any effect of landscape composition and configuration on larvae abundance because the larvae population is mostly driven by the selection of egg-laying sites. Moreover, larvae cannot disperse and might be more affected by local conditions involving prey abundance and farming practices (see Porcel *et al.*, 2013) at other life stages.

Contrary to our initial hypothesis and to results for other species, landscape configuration had no effect on the abundance of adults or any other life stages. For instance, Holzschuh *et al.* (2010) found a positive effect of field edge density rather than total area of uncultivated habitats on predatory wasps, suggesting that higher edge density resulted in increased connectivity and facilitated movements. Increasing edge length is expected to enhance the flow of organisms exploiting multiple resources in different ecosystems at the landscape scale, leading to increased spillover effects from semi-natural habitats to crop fields and *vice versa* (Dunning *et al.*, 1992; Rand *et al.*, 2006). Our study demonstrates that lacewings are much more affected by mass effects determined by the number of semi-natural habitats in the landscape than by increasing the configurational heterogeneity between semi-natural and crop habitats. Martin *et al.* (2019) showed in a recent meta-analysis that enemies overwintering in outside crops benefited from high edge density, especially in landscapes with less than 10% of semi-natural
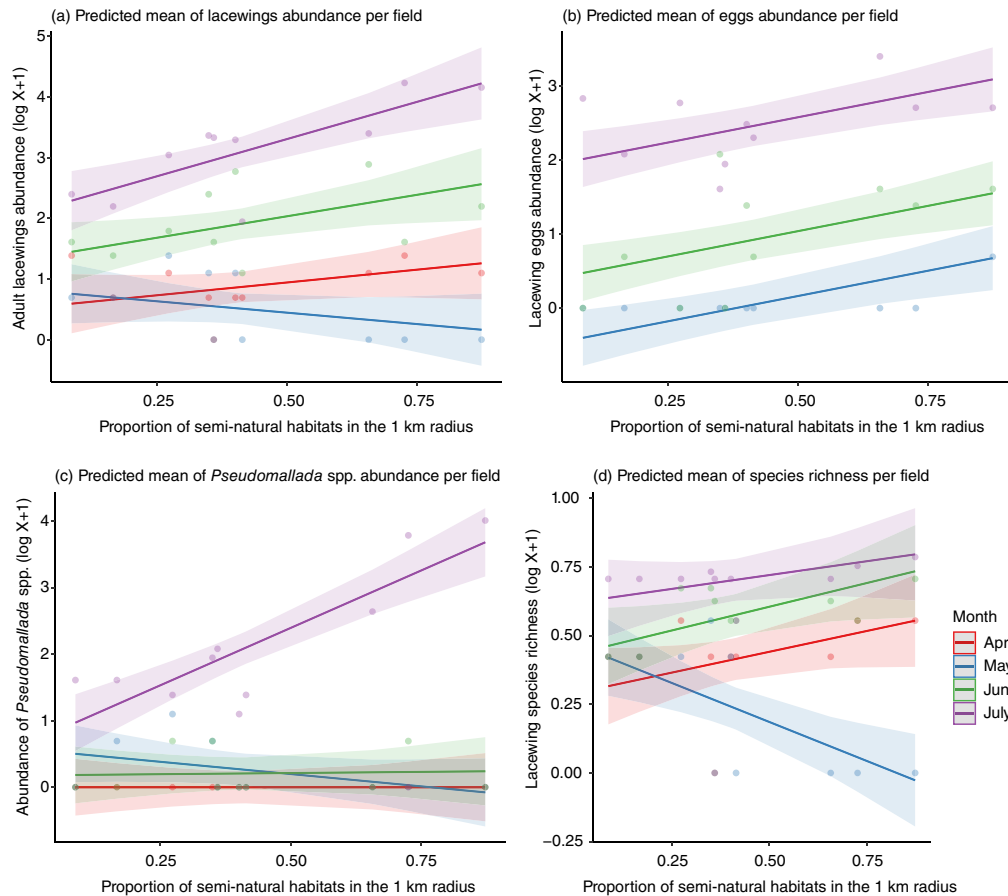
Figure 3 Effect of the proportion of semi-natural habitats in the 1-km radius by month, from April to July, on: (a) abundance of adults, (b) abundance of eggs, (c) abundance of *Pseudomallada* spp. and (d) species richness. Figures represent model predictions and confidence intervals of the proportion of semi-natural habitat for each month. No eggs were sampled in April. [Colour figure can be viewed at wileyonlinelibrary.com].

habitats for flyers. In our study, the large majority of landscapes had more than 10% of semi-natural habitats providing a potential explanation for the lack of configurational effects.

How effective are lacewings as predators of leafhoppers?

In the present study, leafhoppers were mostly represented by *E. vitis* and were collected as early as mid-May, whereas lacewing larvae did not appear until late June in the monitored plots, as did most adults. This observation suggests that lacewings cannot control the first generation of leafhoppers in the spring but may act as natural enemies of the summer populations. Daane *et al.* (1996) showed that releases of *C. carnea* on vines significantly reduced the density of leafhoppers of the first and the second generations by 33.6% and 31.4%, respectively, when *C. carnea* was released at 19 768 larvae/ha. These densities are very much larger than those observed in plots studied under natural conditions and those measured in our study, therefore indicating that lacewings alone might not be able to strongly limit leafhopper populations.

Moreover, despite significant effects of landscape composition on lacewings and contrary to the results of other studies, our study revealed that the predator–prey ratio was not affected by any landscape variables (Martin *et al.*, 2019). This result therefore suggests that the positive effect of the proportion of semi-natural habitats measured on lacewings abundance and richness does not cascade to lower trophic levels. This could be because the biological control potential may occur later in the season, at the end of summer, when lacewing populations reach their peak abundance and diversity. Moreover, this could be due to local farming practices that may limit the effects of lacewings on leafhopper populations. Indeed, farming practices such as pesticide use, vegetation management and soil tillage can strongly affect natural enemy and pest population dynamics in vineyards (Winter *et al.*, 2018; Muneret *et al.*, 2019).

Landscape effects, seasonality and biological control

We found positive interactions between landscape context and sampling period on lacewing population dynamics, indicating changes in landscape context effects on lacewings throughout the season. This confirms the conclusions of Bertrand *et al.* (2016), who found that the sampling time and seasonality modulate landscape composition and configuration effects on activity density and species richness of carabids and spiders. This strong temporal dynamic in the context of landscape effects is one

potential explanation for the variable effect of landscape complexity on natural enemies and pest control services observed at the global scale as a large majority of previous research used snapshot studies with a very low number of temporal repetitions (Chaplin-Kramer *et al.*, 2011; Karp *et al.*, 2018). Results about landscape effects on natural enemies or biological control in the literature may be biased by a low number of temporal repetitions, as well as data pooled over the whole year (Chaplin-Kramer *et al.*, 2011). We therefore advocate for further investigations of temporal dynamics in landscape structure effects on predator and prey communities as this could have major consequences for pest control in agricultural landscapes.

Conclusions

Enhancing natural enemy abundance and activity in agroecosystems is a major challenge for agroecologists. Our study highlights that conserving semi-natural habitats increases the abundance and species richness of lacewings in vineyard landscapes. We particularly show that compositional heterogeneity is affecting lacewing communities and that the effect of compositional heterogeneity depends on the sampling date. Our study suggests that temporal variations of landscape complexity effects on lacewings reveal patterns of crop colonization from semi-natural habitats to crops. Further research linking potential effects of landscape composition on lacewings using capture–mark–recapture approaches would clearly help in understanding the variability of landscape composition effects on lacewings. Our study has important implications for practitioners and policy makers concerned with biodiversity conservation and commodity production in agricultural landscapes as it shows that maintaining semi-natural habitats benefits lacewings. However, further research is needed to examine the consequences of higher abundance and diversity of lacewings on actual pest control. We also advocate for additional studies investigating landscape effects on longer temporal scales on population dynamics of natural enemies and associated pest control as it is a major knowledge gap in the literature.

Acknowledgements

Data Availability Statement

The data that support the findings of this study are available from the corresponding author.

Supporting information

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

File S1 Supporting information files.

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