

# Local and landscape effects of agricultural intensification on Carabid community structure and weed seed predation in a perennial cropping system

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## Abstract

**Context** The effects of agricultural intensification on service-providing communities remain poorly studied in perennial cropping systems. However, such systems differ greatly from annual cropping systems in terms of spatio-temporal dynamics and levels of disturbance. Identifying how land use changes at different scales affect communities and ecosystem services in those habitats is of major importance.

**Objectives** Our objectives were to examine the effects of local and landscape agricultural intensification on ground beetle community structure and weed seed predation services.

**Methods** We examined the effects of local vegetation management and landscape context on ground beetle community structure and weed seed predation in 20 vineyards of southwestern France in 2013 and 2014. Vineyards were selected along a landscape

complexity gradient and experienced different management of local vegetation.

**Results** The activity-density of ground beetles decreased with increasing landscape complexity while species richness and evenness remained unchanged. Phytophagous and macropterous species dominated ground beetle communities. Seed predation was positively related to the activity-density of one species, *Harpalus dimidiatus*, and was not affected by local management or landscape context. We found that within-year temporal diversity in ground beetle assemblages increased with landscape complexity.

**Conclusions** Our study shows that increasing the proportion of semi-natural habitats in vineyard landscapes enhances the temporal diversity of ground beetles. However, we also found that measures targeting specific species delivering biological control services are a reasonable strategy if we are to maximize natural pest control services such as weed seed regulation to support crop production and reduce agrochemical use.

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Species turnover

## Introduction

A large body of evidence now indicates that agricultural intensification at different spatio-temporal scales

is a major driver of losses of biodiversity in human-modified landscapes (Stoate et al. 2001; Robinson and Sutherland 2002; Cardinale et al. 2012). The landscape-scale reduction in habitat heterogeneity is known to strongly affect biodiversity and associated ecosystem services (Tschamntke et al. 2005). Among the different service-providing communities, generalist predators contribute to important ecosystem services such as the biological control of insect crop pests (Thies et al. 2011; Rusch et al. 2015b). Several recent meta-analyses provide strong evidence that landscape composition is an important factor affecting these communities (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). Species richness and abundance of natural enemies of pest species are often higher in landscapes with high proportions of semi-natural habitats. However, a large majority of studies examining the effects of landscape complexity on predator communities and natural pest control services are conducted in annual cropping systems; these effects remain poorly studied in perennial cropping systems (Eilers and Klein 2009; Thomson and Hoffmann 2013).

It is usually accepted that high levels of disturbance caused by farming practices have strong negative effects on agricultural biodiversity (Robinson and Sutherland 2002; Benton et al. 2003). Perennial cropping systems, such as orchards or vineyards, differ greatly from annual cropping systems in terms of disturbance for natural enemy communities (Bruggisser et al. 2010; Rusch et al. 2015a). On the one hand, vineyards and orchards usually receive a higher amount of agrochemicals than annual cropping systems (Butault et al. 2010). On the other hand, perennial crops also provide natural enemy communities with much more stable habitats in space and time because they are not subjected to crop rotation and usually have lower levels of soil disturbance (Bruggisser et al. 2010; Trivellone et al. 2012). Perennial agroecosystems may provide important resources and functions for natural enemies such as overwintering sites, alternative hosts or food sources that have positive effects on predator communities, especially if vegetation cover is maintained within the field (Landis et al. 2000; Nicholls et al. 2001; Danne et al. 2010; Rusch et al. 2010). However, inferring how landscape simplification affects the structure of predator communities in such systems is difficult based on current knowledge. One can hypothesize that the effects of landscape simplification may differ in landscapes

dominated by perennial crops when compared with landscapes dominated by annual crops because of variations in population dynamics and limited spillovers that occur between semi-natural habitats and agroecosystems (Rand et al. 2006).

It has recently been hypothesized that landscape context modulates the effects of local management on biodiversity and ecosystem services (Tschamntke et al. 2005, 2012; Kleijn et al. 2011). According to this hypothesis, the benefits of local management on biodiversity and ecosystem services are smaller in complex landscapes (i.e., with a high proportion of semi-natural habitats) that already support high level of biodiversity than in simple landscapes (i.e., dominated by arable land). Batáry et al. (2011) recently tested this hypothesis in a meta-analysis of studies examining the effects of agro-environmental schemes on biodiversity that were implemented along landscape gradients. They demonstrated that this hypothesis holds true in annual cropland but not in perennial grasslands. This suggests that the effects of landscape context on biodiversity might be modulated by crop disturbance regimes. However, to our knowledge, this hypothesis has never been tested.

Ground beetles are key natural enemies in agroecosystems that provide important ecosystem services by consuming various insect pests and weed seeds (Symondson et al. 2002; Petit et al. 2010; Kulkarni et al. 2015). The effects of landscape context on carabid communities in agroecosystems have thus received a considerable amount of attention (Purtauf et al. 2005; Hendrickx et al. 2009; Woodcock et al. 2010; Rusch et al. 2014). Although it is usually accepted that landscape complexity increases the abundance and species richness of generalist predators, the results for carabids showed much more contrasting patterns, ranging from negative to positive effects (Maisonhaute et al. 2010; Kotze et al. 2011; Winqvist et al. 2011). These mixed results suggest that ground beetles are also affected by other environmental variables, such as habitat quality or disturbance. Moreover, it has been demonstrated that carabids can significantly affect weed populations and that several variables such as farming systems, vegetation cover, soil tillage or the surrounding landscape can also affect seed predation rates (Petit et al. 2010; Sanguaneko and León 2011; Kulkarni et al. 2015). Studying several aspects of communities, such as taxonomic and functional structure, may provide relevant insight into

how communities respond to environmental changes and how these changes within communities affect ecosystem functioning (Laliberté et al. 2010; Cadotte et al. 2011; Rusch et al. 2015b). However, the mechanistic link between ground beetle community structure and levels of weed seed predation remains poorly understood (Trichard et al. 2013).

In this study, we examined the effects of local and landscape intensification on ground beetle community structure and the weed seed predation services they provide in vineyard agroecosystems. We analyzed how local vegetation management and landscape complexity affect the taxonomic and functional structure of ground beetle communities and how, in turn, these affect the level of weed seed predation. We expected a negative effect of landscape simplification on the abundance and species richness of ground beetles and on seed predation rates. We also expected a positive effect of local vegetation maintenance on abundance and species richness of ground beetles in simplified landscapes following the intermediate landscape-complexity hypothesis. Moreover, we hypothesized that landscape complexity will affect species temporal turnover and the functional composition of ground beetles. We particularly expected to find lower temporal beta diversity and communities dominated by small species with good dispersal abilities in simple landscapes.

## Materials and methods

### Study design

We established a study design in the Bordeaux area in southwestern France that allowed testing for the effects of landscape complexity on ground beetle communities and weed seed predation (see Fig. S1). Our study design consisted of 20 independent (minimum distance of 2 km between fields) vineyards selected along a landscape complexity gradient. Landscape complexity was calculated using ArcGIS software (Version 10, ESRI) as the proportion of semi-natural habitats in a 1 km radius around each vineyard. This proportion ranged from 0 to 68 %. In addition, we calculated the proportion of semi-natural habitats at four other spatial extents (i.e., 100, 250, 500, 750 m). We used the proportion of semi-natural habitats in the landscape as it is a common measure of landscape

complexity and is usually highly correlated with other facets of landscape heterogeneity (Roschewitz et al. 2005; Woltz et al. 2012). Semi-natural habitats in these landscapes mainly consisted of woodland, grasslands, hedgerows and shrubs. The cultivar used, Merlot, and vine stock density did not differ between surveyed vineyards (about 5000 vine stocks ha<sup>-1</sup>). Local disturbance differed between studied vineyards in the management of the vegetation between rows due to soil tillage practices as this is a factor affecting ground beetles (Kulkarni et al. 2015). Our design consisted of nine fields with higher local disturbance due to partial grass cover with soil tillage in half of the inter-rows and 11 fields with lower local disturbance due to full grass cover and no soil tillage in the inter-rows.

### Ground beetle sampling

In each vineyard three pitfall traps (diameter 11 cm; depth 11.5 cm) were placed along a transect located in the middle of the field, 30 m from the edge and 15 m from each other (Jeanneret et al. 2003; Sattler et al. 2010; Rusch et al. 2014). Pitfall traps were kept open for seven to nine days during different time periods (Table 1). Ground beetle communities were sampled during six time periods between mid-June and mid-September 2013 and during three time periods in July 2014 (see Table 1). Samples from the three pitfall traps were pooled for a given site and a given time period prior to analysis. Two vineyards were not sampled in 2014 due to technical issues.

**Table 1** Summary of ground beetle sampling periods in 2013 and 2014

Year	Sampling date
2013	10 June–17 June
	17 June–24 June
	24 June–30 June
	30 June–06 July
	27 August–03 September
	03 September–11 September
2014	01 July–08 July
	08 July–15 July
	15 July–22 July

## Weed seed predation experiment

Weed seed predation by phytophagous invertebrates was measured in July 2014 using seed cards (Menalled et al. 2000). The experimental design consisted of three replicates each of two exclusion treatments: (i) three seed cards with vertebrate exclusion cages (diameter: 15 cm; height: 10 cm; mesh size:  $1.7 \text{ cm}^2$ ) excluding vertebrates but allowing invertebrates to enter the cage and (ii) three seed cards with total exclusion (vertebrates + invertebrates) (diameter: 15 cm; height: 10 cm; mesh size:  $0.9 \text{ mm}^2$ ; Menalled et al. 2000; Trichard et al. 2013). On each card, 30 seeds (10 seeds  $\times$  3 species) were glued onto a 10 cm  $\times$  10 cm brown sand paper (grain size 120); species used were *Capsella bursa-pastoris* (L.) Medik., *Chenopodium album* L. and *Plantago lanceolata* L. The seeds of these species were used because they differ in their size and weight (Menalled et al. 2007; Trichard et al. 2013). For each pair, the two exclusion treatments were randomly placed along a single transect in the inter-row, 30 m apart from the edge of the vineyard and separated from each other by 10 m. This transect was parallel to the pitfall trap transect (i.e., 20 m) to minimize interference between ground beetle sampling and the quantification of weed seed predation. The cards were located at the soil surface and exposed to predation during seven days at the beginning of July. This experiment allowed us to measure weed seed predation by phytophagous invertebrates, of which ground beetles are assumed to be one of the key groups. However, other groups such as ants might also be involved in seed predation (Westerman et al. 2003).

## Ground beetle community structure

We calculated activity-density, species richness (rarefied) and community evenness (Pielou index) for each site and sampling year. In addition, we collected information from the literature on several important functional traits of ground beetles (Lindroth 1985; Luff 1998). We particularly selected traits related to wing morphology, diet and body size (Rusch et al. 2014) because these traits provide relevant information related to predation function (Rusch et al. 2015b). Our species were classified into three categories related to wing morphology: brachypterous, macropterous, dimorphic. Three diet categories were also considered: carnivorous, omnivorous or phytophagous. Instead of

using body size data from the literature, we measured the body length on our samples to take intraspecific variability into account (range 2.6–28.8 mm). For each trait, we calculated the community-weighted mean trait (CWM), which is the abundance-weighted mean trait value in the community (Garnier et al. 2004). Categorical traits were treated as independent binary variables, allowing us to calculate CWM values for each category (Leps et al. 2006). In this case, CWM values can be interpreted as the proportion of individuals carrying a given trait modality within the community. In addition, we calculated species richness, evenness and activity-density of carabids within each diet category because these variables are assumed to affect weed seed predation by carabids (Trichard et al. 2013). CWM values were calculated using the *FD* package (Laliberté et al. 2014).

In addition, we calculated species richness in both early (June–early July) and late (August–early September) assemblages in 2013 using species estimator Chao 1 that makes species richness comparable between sites with different sampling effort; this was the case between our sampling periods. Moreover, we calculated within-year temporal beta diversity to examine the temporal dynamics in ground beetle communities. The variation in species composition across time was measured as the dissimilarity between early (June–early July) and late (August–early September) assemblages. We used the overall Sørensen (presence/absence) dissimilarity index and the command *beta.temp* from the package *betapart* (Baselga and Orme 2012). This procedure computes the overall dissimilarity ( $\beta_{\text{SOR}}$ ) between time periods and partitions it into two additive components: turnover ( $\beta_{\text{sim}}$ ) and nestedness ( $\beta_{\text{nes}}$ ). These two components,  $\beta_{\text{sim}}$  and  $\beta_{\text{nes}}$ , reflect (i) the substitution of some species by others between time periods and (ii) the loss or gain of species in which an assemblage is a strict subset of another, respectively (Baselga 2010). Two fields were not included in the temporal beta diversity analyses because no sampling was available in the late time period due to technical issues.

## Data analysis

### *Response of ground beetle communities to landscape complexity and grass cover management*

Generalized linear models with negative binomial error distributions were used to examine the effects of

the proportion of semi-natural habitats at a given scale, the type of grass cover management at the local scale, as well as their interaction, on the activity-density of ground beetles. The family and link functions used were selected based on residual deviance and overdispersion (Zuur et al. 2009). General linear models were used to examine the effects of the proportion of semi-natural habitats at a given scale, the type of grass cover management at the local scale, as well as their interaction on species richness (rarefied and Chao 1), community evenness (for the entire community or by diet category), temporal variation in community composition and community-weighted mean traits (CWM) for each functional trait. When needed, the response variables were arcsin square root-transformed to meet the assumptions of the model. For each response variable, different models including the proportion of semi-natural habitat calculated at one of the five spatial scales (i.e., 100, 250, 500, 750, 1000 m) were fitted and compared using their Akaike Information Criterion. For each model, variable selection was carried out using a stepwise backward selection procedure based on the Akaike Information Criterion, removing the interaction term first. Autocorrelation in the residuals of the different models was examined and no spatial autocorrelation was found. Separate analyses were performed for 2013 and 2014 because sampling efforts varied between year and this may affect the ground beetle communities due to differences in phenology.

#### *Effects of landscape complexity, grass cover management and carabid community structure on weed seed predation*

In the 2014 experiment, we examined the effects of exclusion treatment, weed species, and ground beetle community structure on weed seed removal using generalized linear mixed models with binomial error distributions, the response variable being defined as the number of predated seeds versus the number of non-predated seeds per weed species. We selected the relevant aspects of community structure as explanatory variables of predation rates: activity-density (overall and for dominant species: *Harpalus affinis*, *H. honestus*, *H. dimidiatus*, *H. smaragdinus*, *H. pygmaeus*, *Pseudoophonus rufipes*), species richness, CWM body length and CWM values for phytophagous species. Sites and pairs within the sites were used as

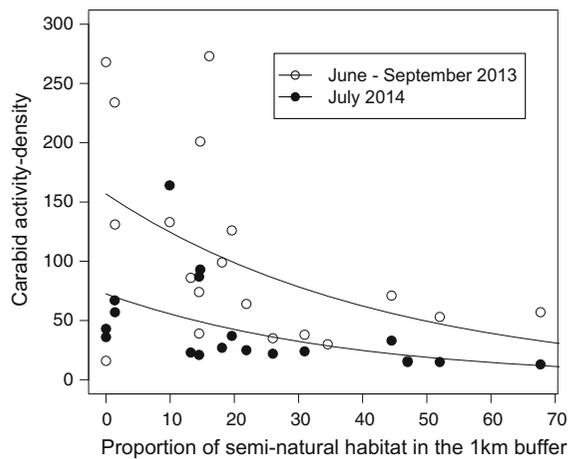
random factors to account for spatial dependence in the data. The structure of fixed effects was simplified by backward elimination of non-significant interactions and the main effects ( $p > 0.05$ ). All first-order interactions were initially considered into the models. Only carabid community variables that had a significant effect on seed predation rates were kept in the following analyses (Trichard et al. 2013). During a second step, we added grass cover management and the proportion of semi-natural habitat at a given spatial extent as explanatory variables to explore potential effects of environmental variables that were not explained by ground beetle community structure. The family and link functions used were selected based on residual deviance and overdispersion (Zuur et al. 2009). Pairwise differences between treatments were based on z values from a generalized linear mixed model summary. All the analyses were performed using R, version 2.15 (R Development Core Team 2015) and the packages *MASS* and *lme4*.

## Results

A total of 39 species of ground beetles (2,044 individuals) were sampled in 2013; 30 species (803 individuals) of ground beetles were sampled in 2014. Communities were dominated by the four genera: *Amara*, *Calathus*, *Harpalus* and *Pseudoophonus* (Table S1). In both years the species *H. affinis*, *H. honestus*, *H. dimidiatus*, *H. smaragdinus*, *H. pygmaeus*, *P. rufipes*, *Amara aenea* and *Calathus fuscipes* were the dominant species in the assemblages, representing more than 5 % of the sampled community.

#### Activity-density, species richness and community evenness

Activity-density of ground beetles in vineyards decreased with the proportion of semi-natural habitats in the landscape (Fig. 1; Table 2) but was not affected by grass cover management. This negative effect was found for both years and was also observed when studying the independent effect of grasslands and woodlands (see Table S2). The best-fitting models were always found at the largest spatial extent (i.e., 750-m or 1-km radius) (Table 2). Species richness and community evenness did not change along the



**Fig. 1** Relationship between ground beetle activity-density in vineyards and the proportion of semi-natural habitats in the 1 km buffer for 2013 and 2014 sampling dates

landscape complexity gradient or with grass cover management in both 2013 and 2014.

#### Temporal variation in ground beetle assemblages

We found no effect of grass cover management and landscape complexity on estimated species richness (Chao 1) for each time period. Overall within-year temporal variation of site assemblages ( $\beta_{\text{SOR}}$ ) between early and late sampling periods were  $0.59 \pm 0.15$ . The nestedness component of within-year temporal beta

**Table 2** Summary of the final generalized linear models (with negative binomial error distribution) testing for the effects of the proportion of semi-natural habitats at a given spatial extent,

Year	Explanatory variable	Spatial extent (m)	Value $\pm$ SE	z value	p	AIC
2013	% of semi-natural habitat	1000	$-0.023 \pm 0.008$	-2.853	0.004	221.13
		750	$-0.017 \pm 0.008$	-2.158	0.030	224.15
		500	-	-	-	-
		250	-	-	-	-
		100	-	-	-	-
2014	% of semi-natural habitat	1000	$-0.026 \pm 0.007$	-3.776	<0.001	164.54
		750	$-0.024 \pm 0.006$	-3.528	<0.001	165.33
		500	$-0.017 \pm 0.006$	-2.776	0.005	168.48
		250	$-0.016 \pm 0.006$	-2.361	0.018	169.52
		100	-	-	-	-

The type of grass cover management at the local scale, as well as its interaction with landscape complexity, were never retained in the final model at any spatial extent. “-” indicates that no variables were retained during the variable selection procedure

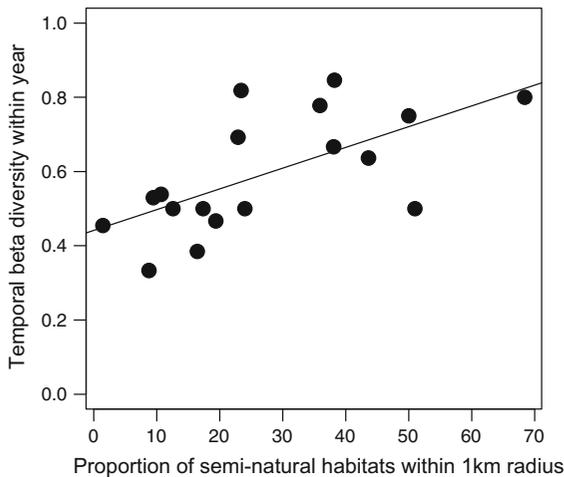
AIC Akaike Information Criterion

diversity ( $\beta_{\text{nes}}$ , mean = 0.38, SD = 0.21) was usually higher than the turnover component ( $\beta_{\text{sim}}$ , mean = 0.20, SD = 0.19). We found that  $\beta_{\text{SOR}}$  increased linearly with the proportion of semi-natural habitat in the 1 km radius; this indicated that higher temporal variation in species composition existed between early and late assemblages in complex landscapes when compared with simple landscapes (Fig. 2; Table S3). Neither turnover nor the nestedness components of temporal beta diversity were significantly related to grass cover management or landscape complexity. This suggests that both processes are involved in the overall change in species composition along the landscape gradient.

#### Functional diversity

Ground beetle communities were largely dominated by phytophagous species, and this was consistent among the 2 years studied here. In 2013, 75.1 % of the sampled individuals were phytophagous, 8.3 % were carnivorous, fewer than 1 % were omnivorous and 16.2 % were not assigned to any particular diet regime based on a lack of basic knowledge of those species. In 2014, 82.1 % of the individuals were phytophagous, 2.4 % were carnivorous, fewer than 1 % were omnivorous and 15.1 % had unknown diet regimes. Models fitted by diet regimes revealed similar effects of the proportion of semi-natural habitats on activity-density, species richness and evenness of phytophagous

the type of grass cover management at the local scale, as well as their interaction, on the activity-density of ground beetles



**Fig. 2** Relationship between within-year variation in species assemblage (temporal beta diversity) and the proportion of semi-natural habitats in the 1 km buffer. The variation in species assemblage across time was measured as the dissimilarity between early (June–early July) and late (August–early September) assemblages. We used the overall Sørensen (presence/absence) dissimilarity index

species (Table S4). We particularly found a negative effect of semi-natural habitats on the activity-density of phytophagous species (Table S4). No effects on species richness and evenness were found. As previously noted, the best-fitting models were always found at the larger spatial scales (i.e., 750-m or 1-km radius) for phytophagous species. No effects of landscape variables were detected for activity-density, species richness or evenness of carnivorous and omnivorous species.

Community-weighted mean traits for phytophagous, carnivorous and omnivorous species were never affected by landscape complexity or by grass cover management. This indicates no change in diet composition within communities along the landscape complexity gradient or under different grass cover management. Ground beetle communities were mainly dominated by macropterous individuals (Fig. 3). For both years, grass cover management was found to be associated with wing morphology composition of ground beetles (Table S5). The proportion of macropterous individuals within communities was always significantly lower in vineyards with partial grass cover and therefore the proportion of dimorphic individuals was always higher in vineyards with partial grass cover (Figs. 3, S2, Table S5). CWM

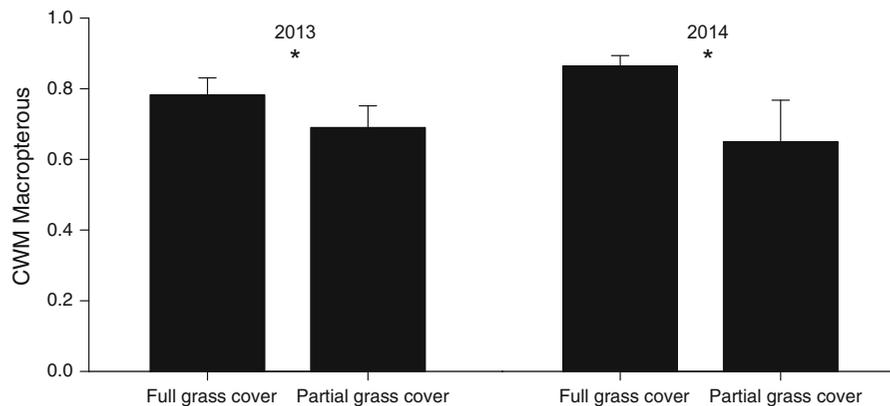
values for body length of ground beetles were never affected by landscape complexity, grass cover management and their interaction.

### Weed seed removal

The mean seed predation rate by invertebrates during our experiment was  $13.7 \pm 23.1$  %. Three explanatory variables retained by model selection significantly explained seed removal in our experiment including exclusion treatments ( $\chi^2 = 17.8$ ,  $p < 0.001$ ), weed species ( $\chi^2 = 57.8$ ,  $p < 0.001$ ) and the activity-density of *Harpalus dimidiatus* ( $\chi^2 = 8.96$ ,  $p < 0.001$ ). This species was one of the most abundant (ranked fourth) species in 2014, representing more than 8 % of the assemblage. Significantly more seeds were removed in the vertebrate exclusion treatment than in the total exclusion treatment (Table 3; Fig. S3). More seeds of *Capsella bursa-pastoris* were removed followed by seeds of *Plantago lanceolata* and *Chenopodium album* (Table 3; Fig. 4). Among variables related to community structure, only the activity-density of *H. dimidiatus* was retained in model selection. This variable was positively related to the number of seeds removed (Table 3). None of the variables related to landscape context or grass cover management were retained during the second step of model selection, indicating no effect of these variables on the number of seed removed.

### Discussion

In this study, we analyzed how agricultural intensification at both local and landscape scales affects ground beetle communities and seed predation rates in a perennial agroecosystem. Our results revealed that the activity-density of ground beetles increased with landscape simplification while no changes in species richness or evenness were detected. Moreover, we found that within-year temporal variation in species assemblages (temporal  $\beta$  diversity) increased with landscape complexity; this indicated more dissimilar communities occurred over time in those landscapes compared to more stable communities in very simple landscapes. Our analysis also revealed that ground beetle communities were dominated by phytophagous and macropterous species and that the overall



**Fig. 3** Effects of local vegetation management on the proportion of macropterous species in ground beetle assemblages in 2013 and 2014. Values are mean  $\pm$  SD. Asterisks indicates significant differences in wing-morphology composition

between vineyards that had full grass cover (grass cover in all inter-rows) and vineyards that had partial grass cover (grass cover in half of the inter-rows). CWM community-weighted mean trait

**Table 3** Summary of the final generalized linear mixed model (with binomial error distribution) testing for the effects of exclusion treatment, weed species and activity-density of *H.*

*dimidiatus* on the proportion of seed removed at the end of our experiment; sites and pairs within the sites were used as random factor to account for spatial dependence in the data

Variables	Value $\pm$ SE	z value	p
Exclusion treatment (total exclusion)	0.803 $\pm$ 0.190	-4.227	<0.001
Species			
<i>Chenopodium album</i>	-2.734 $\pm$ 0.519	-5.261	<0.001
<i>Plantago lanceolata</i>	-1.295 $\pm$ 0.208	-6.199	<0.001
Activity-density of <i>H. dimidiatus</i>	0.158 $\pm$ 0.053	2.934	<0.001

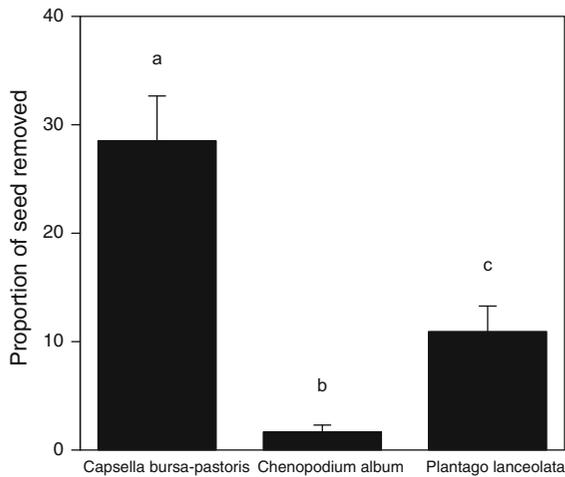
The structure of fixed effects was simplified by backward elimination of non-significant interactions and main effects ( $p > 0.05$ )

proportion of seeds removed was positively related to the activity-density of one species, *H. dimidiatus*.

Our findings did not support our initial hypothesis stating that activity-density and species richness of ground beetles would increase with landscape complexity. We particularly found a negative effect of landscape complexity on activity-density of ground beetles. This effect was found for both years and was also observed when studying the independent effect of grasslands and woodlands (see Table S2). First, our results are not in line with the growing body of evidence related to the positive effects of landscape complexity on the abundance and diversity of predators (including ground beetles) (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). The fact that a large majority of studies used in the meta-analyses were not focused on ground beetles and were performed in annual crops might explain this difference. Indeed,

perennial cropping systems, such as orchards or vineyards, greatly differ from annual cropping systems in terms of disturbance and temporal resource availability (Bruggisser et al. 2010; Rusch et al. 2015a). This could strongly modulate the effects of landscape complexity on natural enemy communities. Secondly, studies examining the effects of landscape complexity on ground beetles have found contrasting results ranging from positive to negative effects (Schweiger et al. 2005; Maisonhaute et al. 2010; Winqvist et al. 2011; Jonason et al. 2013). For instance, Winqvist et al. (2011) found a very similar response of ground beetles to landscape complexity as reported here, with a decrease of activity-density along a landscape complexity gradient.

Two non-exclusive mechanisms could explain the negative effects of landscape complexity reported here. First, some ground beetle species may be



**Fig. 4** Proportion of seed removed by invertebrates for each weed species. Results are based on a GLMER model (binomial error distribution). Error bars indicate standard error of the mean. The effect of species on seed removal was highly significant ( $\chi^2 = 17.8$ ,  $p < 0.001$ ). Different letters above bars indicate significant differences between treatments ( $p < 0.01$ )

relatively well-adapted to open habitats and intensive agricultural landscapes dominated by perennial cropping systems such as vineyards. Such habitats can provide overwintering sites and food during the season that allows populations to increase over time (Holland and Luff 2000; Landis et al. 2000; Rusch et al. 2010). This is particularly true for the four genera dominating communities in our study (*Amara*, *Calathus*, *Harpalus* and *Pseudoophonus*). These species are all known to be typical in open habitats and are able to overwinter within a field or nearby (Holland and Luff 2000; Roume et al. 2011). Some authors have reported that maintaining grass cover within fields enhances the abundance and diversity of beneficial insects in vineyards, which is the case in our region (Nicholls et al. 2001; Danne et al. 2010). Second, semi-natural habitats in the landscape may act as a sink for a subset of species that spillover between agroecosystems and semi-natural habitats, especially late in the season (Rand et al. 2006; Winqvist et al. 2011; Blitzer et al. 2012). The two mechanisms probably coexist and may contribute to the observed pattern. Further research including the use of thorough measures of population dynamics within time and measures of species dispersal in relation to resources across space and time is therefore needed (Schellhorn et al. 2015).

Our results supported our initial hypothesis related to the positive effects of landscape complexity on the temporal variation in species assemblages within a year. This indicates that very similar communities were found over time in simple landscapes whereas more dissimilar communities were found as the proportion of semi-natural habitats in the landscape increased. This result strongly suggests that exchanges of species between crop and non-crop habitats may occur, which could explain the higher observed variability in species assemblages in more complex landscapes. This agrees with a study performed in Ecuador on hymenopterans, where lower temporal beta diversity was found in more disturbed habitats when compared with less disturbed habitats, including semi-natural habitats (Tylianakis et al. 2005).

Surprisingly, no relationship between ground beetle community structure and the level of seed predation were found. In particular, seed predation rates were not linked to activity-density or species richness of phytophagous species, which agrees with the results of Trichard et al. (2013) in winter-cereal fields. However, we found a significant positive effect of the activity-density of a common species (*H. dimidiatus*) in vineyards on the level of seed predation, suggesting that this species might be involved in seed regulation in vineyards. This species is known to be a phytophagous species that consumes seeds (Lundgren 2009; Trichard et al. 2014). Moreover, our results also agree with recent studies investigating the real-world relationships between biodiversity and ecosystem functioning (Kleijn et al. 2015; Winfree et al. 2015). These studies demonstrated that it is the abundance of a small number of common species that drives the delivery of ecosystem services rather than species richness. In our study we only measured seed predation during one time period. Therefore, it would be interesting to link temporal variation in species assemblages to the level and the stability of seed predation over time. Finally, the overall weed seed predation was relatively low compared to levels of seed predation found in other studies (Menalled et al. 2007; Trichard et al. 2013). This low level of weed seed predation may be due to relatively low carabid populations found in vineyards. Moreover, the high resource availability in vineyards compared to annual crop, due to grass cover between rows, which may dilute the weed seed predation potential.

Contrary to what was expected, we did not find any effects of local vegetation management on ground beetle activity-density, species richness or seed predation rates. However, we found an effect of local vegetation management on wing-morphology composition, with a lower proportion of macropterous individuals found in partially tilled vineyards. This difference in terms of wing-morphology composition can be explained by the local disturbance regime created by vegetation management. Macropterous species are supposed to have higher dispersal abilities than dimorphic or brachypterous ones (Hendrickx et al. 2009), and a higher level of local perturbation may have caused higher dispersal rates for these species resulting in a lower proportion of macropterous species within these communities. However, this could also be the result of a change in composition of other correlated traits that were not considered in our analysis.

## Conclusions and implications

Our study shows that increasing landscape complexity decreased the activity-density of ground beetles whereas no changes in species richness or evenness were detected. However, increasing the proportion of semi-natural habitats enhanced temporal species turnover within assemblages, supporting more dissimilar communities in time in those landscapes when compared with similar communities in very simple landscapes. Furthermore, our results show that the proportion of seed predation was positively related to the activity-density of one species, *H. dimidiatus*, and was not affected by local management or landscape context.

Our study provides insight that can be used to guide agroecological measures in vineyard-dominated landscapes depending on the goals of land managers. Our results suggest that if the aim is to enhance species diversity, increasing the proportion of semi-natural habitats in those landscapes will diversify the associated ground beetle communities over time and thus appears to be a promising option. However, if the aim is to maximize natural pest control services, such as weed seed predation, with the goal of supporting crop production, then measures that target specific species that deliver these services appear to be a relevant strategy.

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## Compliance with ethical standards

**Conflicts of interest** The authors have no conflicts of interest to declare.

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