

Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats

Guillermo Aguilera, Tomas Roslin, Kirsten Miller, Giovanni Tamburini, Klaus Birkhofer, Berta Caballero-lópez, Sandra Ann-marie Lindström, Erik Öckinger, Maj Rundlöf, Adrien Rusch, et al.

▶ To cite this version:

Guillermo Aguilera, Tomas Roslin, Kirsten Miller, Giovanni Tamburini, Klaus Birkhofer, et al.. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. Journal of Applied Ecology, inPress, pp.1-10. 10.1111/1365-2664.13712. hal-02930267

HAL Id: hal-02930267 https://hal.inrae.fr/hal-02930267

Submitted on 4 Sep 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



RESEARCH ARTICLE





Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats

Guillermo Aguilera¹ | Tomas Roslin¹ | Kirsten Miller^{1,2} | Giovanni Tamburini^{1,3} | Klaus Birkhofer⁴ | Berta Caballero-Lopez⁵ | Sandra Ann-Marie Lindström^{1,6,7} | Erik Öckinger¹ | Maj Rundlöf⁶ | Adrien Rusch⁸ | Henrik G. Smith⁶ | Riccardo Bommarco¹

¹Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; ²School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK; ³Department of Soil, Plant and Food Sciences (DiSSPA-Entomology), University of Bari, Bari, Italy; ⁴Department of Ecology, Brandenburg University of Technology Cottbus-Senftenberg, Cottbus, Germany; ⁵Department of Arthropods, Natural Sciences Museum of Barcelona, Barcelona, Spain; ⁶Department of Biology, Lund University, Lund, Sweden; ⁷Swedish Rural Economy and Agricultural Society, Kristianstad, Sweden and ⁸INRAE, UMR 1065 Santé et Agroécologie du Vignoble, Université de Bordeaux, Villenave d'Ornon, France

Correspondence

Guillermo Aguilera Email: guillermo.aguilera.nunez@slu.se

Funding information

Swedish Research Council FORMAS, Grant/ Award Number: 2016-01168; 2013-2014 BiodivERsA/FACCE-JPI; FORMAS; EU7th framework; Swedish Farmers' Foundation for Agricultural Research, Grant/Award Number: V1133010; Swedish Board of Agriculture, Grant/Award Number: 28-13610-10

Handling Editor: Marney Isaac

Abstract

- 1. In agricultural landscapes, arthropods provide essential ecosystem services such as biological pest control and pollination. Intensified crop management practices and homogenization of landscapes have led to declines among such organisms. Semi-natural habitats, associated with high numbers of these organisms, are increasingly lost from agricultural landscapes but diversification by increasing crop diversity has been proposed as a way to reverse observed arthropod declines and thus restore ecosystem services. However, whether or not an increase in the diversity of crop types within a landscape promotes diversity and abundances of pollinating and predaceous arthropods, and how semi-natural habitats might modify this relationship, are not well understood.
- 2. To test how crop diversity and the proportion of semi-natural habitats within a landscape are related to the diversity and abundance of beneficial arthropod communities, we collected primary data from seven studies focusing on natural enemies (carabids and spiders) and pollinators (bees and hoverflies) from 154 crop fields in Southern Sweden between 2007 and 2017.
- 3. Crop diversity within a 1-km radius around each field was positively related to the Shannon diversity index of carabid and pollinator communities in landscapes rich in semi-natural habitats. Abundances were mainly affected by the proportion of semi-natural habitats in the landscape, with decreasing carabid and increasing pollinator numbers as the proportion of this habitat type increased. Spiders showed no response to either crop diversity or the proportion of semi-natural habitats.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. Journal of Applied Ecology published by John Wiley & Sons Ltd on behalf of British Ecological Society

4. Synthesis and applications. We show that the joint effort of preserving semi-natural habitats and promoting crop diversity in agricultural landscapes is necessary to enhance communities of natural enemies and pollinators. Our results suggest that increasing the diversity of crop types can contribute to the conservation of service-providing arthropod communities, particularly if the diversification of crops targets complex landscapes with a high proportion of semi-natural habitats.

KEYWORDS

agricultural intensification, arable land, crop diversity, diversification, ecosystem services, landscape composition, pollination, predation

1 | INTRODUCTION

Homogenization of agricultural landscapes through the conversion of semi-natural habitat into arable land and the removal of linear perennial habitats has led to declines in farmland biodiversity, threatening the provision of key ecosystem services such as biological pest control and pollination (Connelly, Poveda, & Loeb, 2015; Dainese et al., 2019). Moreover, crop rotations have been substantially shortened following the industrialization of agriculture and due to specialization of crop growing in different landscapes (Bennett, Bending, Chandler, Hilton, & Mills, 2012). As a result, modern landscapes are often characterized by large proportions of arable land covered by a few predominant crop types (Bennett et al., 2012). Nonetheless, how crop diversity in the landscape affects arthropods beneficial to crop production is still not well understood.

Diversified crop production holds the potential to mitigate or reverse negative impacts on biodiversity and ecosystem services (Kremen & Merenlender, 2018). Locally, communities of serviceproviding insects can be promoted through different farming practices including intercropping, longer rotations with more crop types, extensive management of field edges and the addition of resources through flower strips or flowering crops (Cai, You, & Lin, 2010; Haaland, Naisbit, & Bersier, 2011; Mader et al., 2017; Meena, Sharma, Chander, Sharma, & Sinha, 2019; Pollard & Holland, 2006). These practices are expected to further affect arthropod communities at larger spatial scales because many beneficial arthropods are highly mobile. Landscapes characterized by high crop diversity may support communities of beneficial arthropods by creating a mosaic of habitats that provides continuous and complementary resources throughout the season (Smith et al., 2014). An increase in the availability of resources over time and space potentially reduces bottlenecks that may negatively affect populations of pollinators and pest natural enemies (Bertrand, Burel, & Baudry, 2016; Schellhorn, Gagic, & Bommarco, 2015).

A high crop diversity in the landscape is expected to support pollinator communities by providing a greater variety of floral resources over time. Mass flowering crops in the landscape, in particular, have been shown to influence the abundance and dispersion of pollinators. For example, oilseed rape can have a dilution effect

on pollinator abundances irrespectively of the semi-natural cover in the landscape (Holzschuh et al., 2016), while late-flowering crops like clover can support wild pollinators late in the season (Rundlöf, Persson, Smith, & Bommarco, 2014). However, higher crop diversity may not always guarantee a larger variety of mass flowering crops in the landscape. The diet of social bee pollinators can be very diverse (Leonhardt & Blüthgen, 2012; Requier et al., 2015). This supports the idea that not only resources from the main mass flowering crops but also from leys, pastures and other semi-natural patches can be important for this group (Carrié, Ekroos, & Smith, 2018). To understand the effect of crop diversity on pollinators, we need to disentangle the effect of crop diversity from other types of landscape heterogeneity like the amount of semi-natural habitats. In this context, few previous assessments have focused on how configurational heterogeneity of landscapes (field border density and small field sizes), rather than crop diversity per se, explained higher pollinator richness, abundances and pollination services (Hass et al., 2018; Martin et al., 2019; Sirami et al., 2019). For predaceous arthropods, carabid richness and diversity have been shown to increase with crop diversity in the landscape (Palmu, Ekroos, Hanson, Smith, & Hedlund, 2014). Redlich, Martin, and Steffan-Dewenter (2018) showed that both the biological control of aphid pests and densities of natural enemies were positively affected by crop diversity in the landscape up to a 3-km radius. Similarly, heterogeneous landscapes characterized by small fields and longer rotation regimes have high levels of aphid pest control in Sweden (Rusch, Bommarco, Jonsson, Smith, & Ekbom, 2013). However, for pollinators and natural enemies, we lack an understanding of how crop diversity and semi-natural elements in agricultural landscapes jointly affect their abundance and diversity.

Semi-natural habitats are important to support communities of service-providing arthropods (Holland et al., 2017). In the agricultural landscape, they provide nesting sites and additional forage for both pollinators and natural enemies (Geiger, Wäckers, & Bianchi, 2009; Öckinger & Smith, 2007). However, a recent global synthesis showed that the effect of semi-natural habitats on pests and predators was variable and context-specific (Karp et al., 2018). A possible explanation is that the value of semi-natural habitats for beneficial arthropods is dependent upon other local and landscape features. Local

crop management such as within field rotation, fertilizer and pesticide applications, or the characteristics of field surroundings such as cropland composition, might strongly drive the level of pest control provided by natural enemies (Muneret et al., 2019; Ricci et al., 2019; Tscharntke et al., 2016), limiting the expected benefits of having abundant semi-natural habitats in the landscape (Gagic et al., 2019; Rundlöf, Smith, & Birkhofer, 2016). Moreover, semi-natural habitats may be more important for the temporal stabilization of resource availability in landscapes with simplified crop regimes (Schellhorn et al., 2015). However, the relative importance and synergistic effects of crop diversity and semi-natural habitats in the landscape have been poorly studied.

We explored the importance of crop diversity and the proportion of semi-natural habitats in the landscape for the beneficial arthropod groups of natural enemies (carabids and spiders) and pollinators (wild bees and hoverflies). We collected primary field data from 154 arable fields in the southernmost region of Sweden. We analysed whether the level of crop diversity in the landscape (as Shannon diversity) and the proportion of semi-natural habitats explained variation in the local diversity (as Shannon diversity) and abundance of these arthropod guilds. We expected that crop diversity would enhance the diversity and abundance of beneficial insects by increasing the range of habitats and resources present in the landscape both spatially and temporally. We further expected that an increasing proportion of semi-natural habitats would complement the effect of crop diversity and enhance this positive relationship.

2 | MATERIALS AND METHODS

2.1 | Data collection

We collected community data from seven independent studies carried out in the province of Skåne in southern Sweden (Table 1). The region consists of 39% arable land and 42% forest, grassland, and other semi-natural habitats (Statistics Sweden, 2018). We compiled

original datasets comprising 154 agricultural crop fields in which arthropod predator and pollinator abundances were assessed (Figure 1). The use of similar sampling techniques in the original studies allowed us to merge and analyse the datasets without further modifications. Carabid and spider numbers were estimated with pitfall traps while pollinators were counted along transects (more information about sampling effort in Table 1). Additionally, we only considered data from the centre of the crop fields (not crop edges). For ground-dwelling predators (carabids and spiders), 81 of the sites were winter wheat or barley fields and 21 were winter oilseed rape. Pollinator communities were assessed in 52 fields sown with winter oilseed rape.

2.2 | Arthropod diversity and abundances

We calculated abundances for carabids and spiders as the sum of pitfall trap catches per site. Diversity was measured using the Shannon index for the sum of pitfall trap catches per site using the VEGAN package in R (Oksanen et al., 2019). We chose to use the Shannon index because it accounts for species numbers and their evenness, which we expected to vary with different levels of crop diversity because we intend to capture changes in the arthropod communities driven by additional species or changes in the evenness of the communities. We therefore focus our discussion on the Shannon diversity index. To glean additional insight from a metric less sensitive to rare species and more reflective of the evenness of the communities, we provided a simultaneous analysis using the Simpson diversity index. We decided to consider carabids and spiders separately for calculating Shannon diversity indices as they are two different guilds providing different ecosystem services since the former are omnivorous predators (control of insects and plant pests) and the latter are carnivorous (control of insect pests).

For pollinators, we calculated abundance as the sum of observations per field. Because we lacked exhaustive information about all pollinator species present in the dataset, we grouped together

TABLE 1 Characteristics of the studies from which data were extracted for this study

Original study/project	Number of landscapes	Crop	Organisms studied	Year of data collection	Sampling effort per site
Rusch, Birkhofer, Bommarco, Smith, and Ekbom (2014)	42	Barley	Carabids + spiders	2011	42 (6 pitfall traps × 7 days open)
Gagic et al. (2017; Swedish dataset)	16	Wheat	Carabids + spiders	2014	40 (4 pitfall traps × 10 days open)
Caballero-López et al. (2012)	24	Barley/wheat	Carabids	2007	21 (3 pitfall traps \times 7 days open)
Tamburini (2017)	10	Oilseed rape	Carabids + spiders	2017	315 (15 pitfall traps \times 21 days open)
Aguilera (2017)	11	Oilseed rape	Carabids + spiders	2017	168 (42 pitfall traps \times 4 days open)
Lindström, Herbertsson, Rundlöf, Smith, and Bommarco (2016)	20	Oilseed rape	Pollinators	2011-2012	Three 100 m transect (four visits × 5 min)
Holzschuh et al. (2016; Swedish dataset)	32	Oilseed rape	Pollinators	2011-2012	Two 150 m transects (2 \times 15 min visits)

Region of Skåne (Southern Sweden)

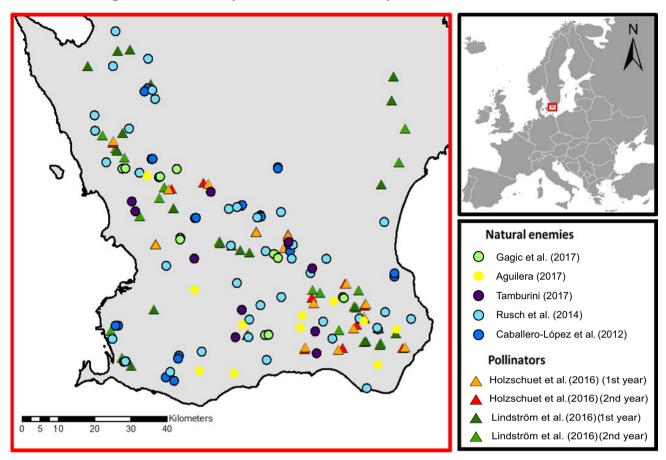


FIGURE 1 Location of the landscapes used in this study. The colour indicates the original study where the dataset was collected and the symbol type indicates the guilds sampled (circles for carabids and spiders; triangles for pollinators)

bees (including bumblebees and solitary bees) and hoverflies for calculating Shannon diversity. Thus, we calculated the Shannon diversity for pollinators considering the three main groups (bumblebees, hoverflies and solitary bees) and their abundances. Since honeybees are managed by humans, we excluded them from the main analysis (see Appendix S1 for the results of the model with honeybees). For information about how abundances of each individual pollinator group responded to crop diversity and semi-natural habitats, see Appendix S2.

2.3 | Landscape variables

Landscape composition was calculated based on digitalized maps of land use measured at a 1-km radius around each sampling site. This scale is considered meaningful for arthropods in European agricultural landscapes (Martin et al., 2019). For each landscape buffer, we calculated crop diversity using a GIS layer provided by the Swedish Board of Agriculture that contains information regarding every crop cultivated at each farmland for every year (Jordbruksverket, 2018). We classified the crops into 11 crop

categories used by the EU for describing crop patterns (Eurostat, 2012; see also Appendix S3 and Redlich et al., 2018). We used these categories rather than crop species as a way to group crops with similar functional traits and that can provide very similar resources (e.g. barley and wheat grouped as cereals). Based on crop category and area cover per category, we calculated the Shannon diversity index using the VEGAN package in R (Oksanen et al., 2019) and used this metric to represent crop diversity. We calculated the proportion of semi-natural habitats in each landscape radius using a land-use digitalized map layer (Terrängkartan, Lantmäteriet, 2018) in ArcMap software, version 10.3.1 (ESRI, USA). The most common semi-natural habitats were pastures and a small proportion of small forest patches. Other land cover types were water and urban land, but these were, on average, lower than 3% and 1% respectively.

The study sites varied by the amount of semi-natural habitat and the crop diversity in their surrounding landscape. The landscapes surrounding the sampling locations had an average land cover of 19.2% semi-natural habitats (min = 0; max = 89.4). Crop diversity had an average Shannon index of 1.3 across sites (min = 0.1; max = 1.9; see Appendix S4 for ranges per study). We checked for spatial

autocorrelation of the response variables using the Moran's I index and the residuals of the model with a variogram.

2.4 | Statistical analyses

To explore the effects of crop diversity and semi-natural habitats on the diversity of all arthropods, carabids, spiders and pollinators we used linear mixed-effects models (Bates, Maechler, Bolker, & Walker, 2015) and generalized linear mixed-effects models assuming a Poisson distribution for analysing their abundances.

The models included crop diversity and the proportion of semi-natural habitats in the landscape plus their interaction, as well as crop type (oilseed rape or cereal for natural enemies) and arthropod guild (pollinators, carabids, spiders) all as fixed factors (for a summary of the models see Appendix S5). Study was included as a random factor to account for differences in sampling intensity and data dependencies within studies. Additionally, abundance models included sampling effort as an offset and an observational-level random effect to account for overdispersion. We did not include random slopes for crop diversity and seminatural habitat proportion since it did not improve the delta AIC. We simplified all models by removing the interaction between crop diversity and the amount of semi-natural habitats for presenting crop diversity and semi-natural habitat individual effects. To standardize the units of the continuous explanatory variables, we scaled them to a mean of zero and unit variance across studies, but doing so for each study gave qualitatively equal results. Additionally, effects on diversity and abundances of each guild were tested separately with the same model structure for a better grip on guild-specific effects. All models were fitted in R (R Core team, 2019), with the LME4 package and tested with a type III ANOVA. To account for a possible confounding effect

between the proportion of semi-natural habitat and crop diversity, we examined the variance inflation factors in each model. For all models, we found the variance inflation values to be lesser than 2 for all variables and thus inferred that collinearity was not a problem (Dormann et al., 2013; also see correlation values between both variables across and within-study in Appendix S6).

3 | RESULTS

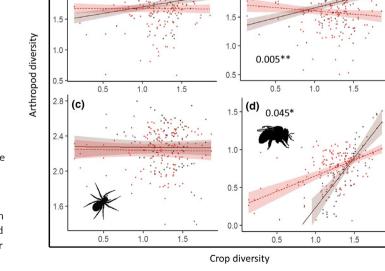
3.1 | Arthropod diversity

The overall arthropod Shannon diversity was enhanced by crop diversity only in landscapes with a higher proportion of semi-natural habitats ($F_{1,224} = 4.09$, p = 0.043; Figure 2a; Table 2). When the interaction was removed, the overall arthropod diversity was significantly enhanced by an increasing proportion of semi-natural habitats in the landscape ($F_{1,223} = 4.23$; p = 0.041).

The guilds differed in their responses to landscape composition (Table 2). The carabid diversity was positively related to crop diversity in landscapes with a high proportion of semi-natural habitats but negatively related to crop diversity in landscapes with a low proportion of semi-natural habitats (interaction crop diversity × proportion of semi-natural habitats: $F_{1.96} = 7.80$, p = 0.005, Table 2; Figure 2b). Similarly, wild pollinator diversity was enhanced by crop diversity and this effect increased with the proportion of semi-natural habitats in the landscape ($F_{1.47} = 4.64$, p = 0.031; Figure 2d). Spider diversity was not significantly affected by the landscape variables or their interaction (Table 2; Figure 2c). For effect sizes and significance of the other fixed effects (crop type and guild) see Appendix S7. Simpson's index of arthropod diversity was not affected by crop diversity or the amount of semi-natural habitats. However, Simpson diversity of carabids showed a positive interaction between both

% Semi-natural

habitats



2.0

0.044*

2.0

FIGURE 2 Effect of crop diversity on the (a) total arthropod diversity (Shannon) and the diversity of each guild (b = carabids, c = spiders, d = pollinators) in landscapes with high (black = landscape with 30% SNH) and low (red = landscape with 10% SNH) proportions semi-natural habitats. Crop diversity and arthropod diversity are both calculated as a Shannon diversity index. Shown are fitted lines and 95% confidence intervals and p-values for the interaction

TABLE 2 Summary of the outputs for the models on arthropod community. Rows correspond to the response variables whereas columns show effect sizes and p-values for the two explanatory variables (in a reduced model with no interaction) and their interaction (bold values denote statistical significance at *p < 0.01; **p < 0.005; ***p < 0.001). Results for the other fixed variables see Appendix S7

	Crop diversity		% Semi-natural habitats		Interaction	
Explanatory variable	Effect size	p-value	Effect size	p-value	Effect size	p-value
Diversity (Shannon index)						
Total	0.031 ± 0.024	0.187	0.049 ± 0.024	0.041*	0.053 ± 0.026	0.044*
Carabids	$0.059 \pm 0.0.039$	0.130	0.087 ± 0.038	0.022*	0.124 ± 0.044	0.005**
Spiders	-0.003 ± 0.033	0.930	0.026 ± 0.033	0.423	0.001 ± 0.043	0.981
Pollinators	0.051 ± 0.034	0.134	-0.034 ± 0.033	0.298	0.110 ± 0.051	0.031*
Diversity (Simpson index)						
Total	0.010 ± 0.010	0.310	0.015 ± 0.010	0.132	0.008 ± 0.011	0.455
Carabids	0.017 ± 0.014	0.221	0.037 ± 0.013	0.006**	0.040 ± 0.015	0.012*
Spiders	0.002 ± 0.004	0.720	0.001 ± 0.005	0.805	-0.003 ± 0.006	0.567
Pollinators	0.028 ± 0.034	0.430	-0.035 ± 0.032	0.260	-0.003 ± 0.052	0.959
Abundance						
Total	0.037 ± 0.051	0.476	-0.009 ± 0.052	0.852	0.044 ± 0.059	0.454
Carabids	-0.012 ± 0.072	0.983	-0.198 ± 0.069	0.004**	-0.064 ± 0.087	0.458
Spiders	0.091 ± 0.057	0.114	0.089 ± 0.055	0.109	-0.017 ± 0.074	0.815
Pollinators	-0.180 ± 0.110	0.092	0.473 ± 0.101	<0.001***	-0.229 ± 0.159	0.148

landscape variables, displaying the same trends when compared to Shannon diversity (Table 1).

3.2 | Arthropod abundance

The overall arthropod abundance was not affected by crop diversity or the proportion of semi-natural habitats in the landscape (Table 2). However, guilds differed in their responses (Table 2).

The abundance of carabids decreased with the proportion of semi-natural habitat in the landscape ($F_{1,95}=8.19$, p=0.004) while pollinator abundances increased along the same gradient ($F_{1,48}=22.10$, p<0.01) and spiders remained unaffected. None of the arthropod groups abundances were affected by crop diversity (carabids p=0.98, pollinators p=0.09, spiders p=0.109). There were no significant interaction effects of crop diversity and semi-natural habitat in the landscapes for any of the guilds (Table 2). For effect sizes and significance of the other fixed effects (crop type and guild) see Appendix S7.

4 | DISCUSSION

Our study reveals a positive synergistic effect of crop diversity and landscape semi-natural cover, being the diversity of arthropod communities mostly benefited by a higher diversity of crops in landscapes that are rich in semi-natural habitats. In landscapes with low proportions of semi-natural habitats, the effect of crop diversity on arthropod community was not significant. Moreover, the responses of arthropods to crop diversity differed between guilds. Carabid and

pollinator diversities were enhanced by crop diversity, especially in landscapes with a high proportion of semi-natural habitats. The only group not affected by this interaction was ground-dwelling spiders. It is important to note that these effects, which will be discussed below, were mainly visible when looking at the Shannon diversity index. Only carabids showed the same response when considering Simpson's diversity index. This discrepancy indicates that evenness of carabid communities was proportional to the increase of new species in the community, while the diversity in pollinator communities was probably more influenced by higher abundances of certain groups.

The diversity of carabids from landscapes with high proportions of semi-natural habitats and high crop diversity being consistent with previous findings (Sirami et al., 2019). Spiders can benefit from noncrop habitat in the landscape (Garratt, Senapathi, Coston, Mortimer, & Potts, 2017; Opatovsky, Weintraub, Musli, & Lubin, 2017; Pompozzi, Marrero, Haedo, Fritz, & Torretta, 2019) and even more than carabids in some cases (Li, Liu, Duan, Yu, & Axmacher, 2018). However, our data do not show any trend that would indicate an effect of crop diversity or semi-natural habitats on spider diversity. A possible explanation is that we only sampled ground-dwelling spiders that are well adapted to arable fields, and by not accounting for other spider guilds such as web-building or crab spiders we may have excluded an important part of these groups that would be more prone to be affected by semi-natural habitats. Landscapes with a diverse composition of crops and semi-natural habitats are more likely to provide a wide range of resources (food and shelter) over time, which can be essential for carabids in agricultural landscapes (Diehl, Wolters, & Birkhofer, 2012). Mobile carabid species often colonize crop fields from nearby source habitats (e.g. overwintering

sites, Wamser, Dauber, Birkhofer, & Wolters, 2011) and in agricultural landscapes, semi-natural patches like forests, fallows or grasslands can provide such habitats (Birkhofer, Fevrier, Heinrich, Rink, & Smith, 2018). Thus, a high proportion of semi-natural habitats in the landscape can complement a high crop diversity and reinforce its effects, reporting higher species numbers of beneficial arthropods. Contrarily, crop fields in landscapes with a low proportion of semi-natural habits would produce relatively low species numbers of mobile and omnivorous carabids (Hanson, Birkhofer, Smith, Palmu, & Hedlund, 2017), irrespective of the surrounding crop diversity. It has recently been proposed that one reason why semi-natural habitats sometimes fail to provide crop fields with sufficient biological pest control is that the amount of semi-natural habitats in agricultural landscapes is often too low to increase the abundance of natural enemies in the crop fields (Tscharntke et al., 2016). Our results show how diversifying the number of crop types at the landscape scale can be particularly beneficial in landscapes that also contain a high semi-natural habitat cover. Interestingly, carabid and spiders were affected by crop type. Oilseed rape fields had a higher diversity of carabids and higher abundances of carabids and spiders (see Appendix S7).

Pollinator diversity increased with crop diversity in landscapes with high cover of semi-natural habitat. Agricultural intensification can have detrimental effects for wild pollinators (Le Féon et al., 2010). Mass flowering crops can enhance abundances at the landscape scale by providing greater resources (Westphal, Steffan-Dewenter, & Tscharntke, 2003). However, the overall effect of mass flowering crops on pollinators is debated since they also have been shown to reduce pollinator abundances at the local scale (Holzschuh et al., 2016). The most abundant mass flowering crop in the study area is oilseed rape, becoming a massive resource that can completely change the availability of flowering resources of a landscape. However, the flowers of oilseed rape, field bean, or clover fields are open for a relatively short period of time. Pollinators, therefore, need secondary food sources throughout the season. Increased crop diversity in the landscape could mean greater resource continuity for pollinators, explaining the enhanced pollinator richness in diverse landscapes. In the case of bumblebees, crop rotation and local management affect their community composition in the field edges (Marja et al., 2018). Crop diversity can also enhance the presence of nesting sites for wild pollinators. Ley crops, for example, are perennial mixes of grasses and legumes, common in this region, that remain un-tilled for 2-4 years. Ley crops provide flower resources for pollinators (Carrié et al., 2018), but also their low-intensity management regime makes them structurally similar to grazed pastures or other natural habitats that provide nesting sites for wild bees (Kim, Williams, & Kremen, 2006). We observed that crop diversity was more correlated with mass flowering crop cover than with ley cover which would highlight the importance of mass flowering crops. Our additional analysis showed that only hoverflies drove this result being positively affected by the amount of ley in the landscape (correlation values and models for each pollinator group in Appendix S8). However, these suggestions are only based on correlations so it is

not possible to make strong statements about them. Therefore, it is hard to argue in favour of either mass flowering crops or ley crops as the main driver of the positive effect of crop diversity on pollinators. However, it seems correct to think that both could explain part of the crop diversity effect in this group of insects based on existing literature

As opposed to diversity, the overall abundance of beneficial arthropods was neither affected by crop diversity nor the proportion of semi-natural habitat. These contrasting results together with the non-significant effect on Simpson diversity index pinpoints that the diversity differences may be due to additional and rare species in the case of ground-dwelling arthropods. Each guild showed a different response in their abundances. This variability of responses between guilds is most probably due to the composition of crops and the resources they provide. For example, increasing the landscape crop diversity by adding flowering crops may be important for pollinators but not as important for ground-dwelling carabids or spiders. In other words, each crop type will have specific values and impacts for each guild. Hence, a functional description of the landscape for each specific guild may have higher predictive power than using crop diversity (Vasseur et al., 2013). This way of classifying the landscape by crop categories should provide a more mechanistic understanding of the effect of crop diversity and the actual temporal and spatial resource continuity.

Carabid abundance showed a negative response with the increasing amount of semi-natural habitats. Crop habitats and local management are important for carabids (Bertrand et al., 2016; Labruyere, Ricci, Lubac, & Petit, 2016; Schneider, Krauss, Boetzl, Fritze, & Steffan-Dewenter, 2016) and an increase in semi-natural habitats in detriment of arable land could affect carabid abundances; however, our dataset does not contain landscapes with an extremely low amount of arable land. More importantly, abundances were not affected by crop diversity. A plausible explanation is that carabids, being crop field 'specialists' mostly affected by management rather than crop types (Lys & Nentwig, 1992; Menalled, Smith, Dauer, & Fox, 2007). We found spider abundances not to be affected by the proportion of semi-natural habitats and we detected a non-significant positive trend with increasing crop diversity. Such effects contradict some recent results (Garratt et al., 2017; Opatovsky et al., 2017; Pompozzi et al., 2019), but these seem to indicate that the abundances of ground-dwelling spiders are affected not only by the noncrop habitats in the landscape (Muneret et al., 2019).

Pollinator abundances increased with the amount of semi-natural habitats but not crop diversity, even though the latter effect was negative for this group when considering honeybees (Appendix S1). This result could indicate that honeybees, which can be highly abundant in the landscape, may benefit from a lower diversity of crop types that offer a large number of resources rather than a more diverse diet. However, honeybee abundances can be also affected by the placement of hives, so the result may be related to the number of hives in relation to the amount of resources. The positive effect of semi-natural areas on pollinators seemed to be driven by hoverflies and bumblebees. This result was unexpected since others have

shown how pollinators are influenced by flowering crops (Holzschuh et al., 2016; Westphal et al., 2003). Thus, in terms of pollinators and their services, it can be more relevant to ask which crops pollinators use and when do they use them, rather than investigating overall crop diversity or pool all flowering crops together. Finally, it is important to consider that we used landscapes of 1-km radius to generalize our findings to various arthropod groups. However, these groups differ in their mobility so the scale of effect could be smaller (for carabids and spiders) or larger (for more mobile pollinators such as honey bees).

4.1 | Synthesis and management implications

Crop diversity can contribute to the mitigation of the decline of arthropod diversity in agricultural landscapes, and this positive effect is often strengthened by the presence of semi-natural habitats. An increase in the number of cultivated crop species may foster biodiversity and enhance related ecosystem services in productive agricultural landscapes. This approach is particularly interesting for farmers as increasing crop diversity does not necessarily reduce levels of crop production (Bommarco, Kleijn, & Potts, 2013; Sirami et al., 2019) and interestingly the EU includes crop diversity as a measure of greening in the common agricultural policy (CAP, European Commission). However, the crop diversity 'units' described by the CAP may be revised since crops with similar structures and resources for beneficial insects are considered different when, in fact, they are functionally alike. We, therefore, think that these criteria are low and that crop functional groups should be used rather than individual crop species.

Finally, considering the landscape as a continuous surface rather than creating distinctions between agricultural and semi-natural habitats and incorporating traits/resources available for arthropods of different habitats in the following evaluations may be the key to better understand these complex interactions in future.

ACKNOWLEDGEMENTS

We thank the people who participated in the original projects. We thank Chloë Raderschall for her valuable inputs in the data analysis and in earlier versions of this manuscript. We thank two anonymous reviewers for providing helpful comments on earlier drafts of the manuscript. We acknowledge the Faculty of Natural Resources and Agricultural Sciences at the Swedish University of Agricultural Sciences for funding a faculty professor starting grant to R.B. This research was funded by the Swedish Research Council FORMAS (grant-number 2016-01168) to R.B. and T.R. G.T. and E.Ö. were supported by the STACCATO project funded by the 2013-2014 BiodivERsA/FACCE-JPI joint call for research proposals, with the national funders FORMAS. H.G.S. and R.B. received funding from FORMAS for SAPES and from the EU7th framework for STEP and LIBERATION. S.A.-M.L. and R.B. were funded by the Swedish Farmers' Foundation for Agricultural Research (V1133010) and the Swedish Board of Agriculture (28-13610-10).

AUTHORS' CONTRIBUTIONS

G.A., R.B., K.M. and T.R. conceived the idea and designed methodology; All authors contributed in the data compilation. G.A. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.3bk3j9kgr (Aguilera et al., 2020).

ORCID

Guillermo Aguilera https://orcid.org/0000-0001-9166-1100

Kirsten Miller https://orcid.org/0000-0001-8352-7649

Giovanni Tamburini https://orcid.org/0000-0001-7546-8183

Sandra Ann-Marie Lindström https://orcid.

org/0000-0002-8403-3509

Maj Rundlöf https://orcid.org/0000-0003-3014-1544

Riccardo Bommarco https://orcid.org/0000-0001-8888-0476

REFERENCES

Aguilera, G. (2017). [Arthropod survey]. Unpublished raw data.

Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., & Caballero-Lopez, B., ... Bommarco, R. (2020). Data from: Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.3bk3j9kgr

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using Ime4. *Journal of Statistical Software*, 67, 10–48. https://doi.org/10.18637/jss.v067.i01

- Bennett, A. J., Bending, G. D., Chandler, D., Hilton, S., & Mills, P. (2012). Meeting the demand for crop production: The challenge of yield decline in crops grown in short rotations. *Biological Reviews*, 87, 52–71. https://doi.org/10.1111/j.1469-185X.2011.00184.x
- Bertrand, C., Burel, F., & Baudry, J. (2016). Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, 31, 451–466. https://doi.org/10.1007/s10980-015-0259-4
- Birkhofer, K., Fevrier, V., Heinrich, A. E., Rink, K., & Smith, H. G. (2018). The contribution of CAP greening measures to conservation biological control at two spatial scales. *Agriculture, Ecosystems & Environment*, 255, 84–94. https://doi.org/10.1016/j.agee.2017.12.026
- Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, 28, 230–238. https://doi.org/10.1016/j.tree.2012.10.012
- Caballero-López, B., Bommarco, R., Blanco-Moreno, J. M., Sans, F. X., Pujade-Villar, J., Rundlöf, M., & Smith, H. G. (2012). Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biological Control*, *63*, 222–229. https://doi.org/10.1016/j.biocontrol.2012.03.012
- Cai, H., You, M., & Lin, C. (2010). Effects of intercropping systems on community composition and diversity of predatory arthropods in vegetable fields. *Acta Ecologica Sinica*, 30, 190–195. https://doi. org/10.1016/j.chnaes.2010.06.001
- Carrié, R., Ekroos, J., & Smith, H. G. (2018). Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *Biological Conservation*, 227, 48–55. https://doi.org/10.1016/j.biocon.2018.08.022
- Connelly, H., Poveda, K., & Loeb, G. (2015). Landscape simplification decreases wild bee pollination services to strawberry. *Agriculture, Ecosystems & Environment, 211, 51–56.* https://doi.org/10.1016/j.agee.2015.05.004

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., ... Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, 5, eaax0121. https://doi.org/10.1126/sciadv.aax0121

- Diehl, E., Wolters, V., & Birkhofer, K. (2012). Arable weeds in organically managed wheat fields foster carabid beetles by resource- and structure-mediated effects. *Arthropod-Plant Interactions*, 6, 75–82. https://doi.org/10.1007/s11829-011-9153-4
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x
- Eurostat. (2012). Agri-environmental indicator Cropping patterns -Statistics explained. Retrieved from https://ec.europa.eu/eurostat/ statistics-explained/index.php/Agri-environmental_indicator_-_ cropping_patterns
- Gagic, V., Hulthen, A. D., Marcora, A., Wang, X., Jones, L., & Schellhorn, N. A. (2019). Biocontrol in insecticide sprayed crops does not benefit from semi-natural habitats and recovers slowly after spraying. *Journal of Applied Ecology*, 56, 2176–2185. https://doi.org/10.1111/ 1365-2664.13452
- Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H. B., Elek, Z., ... Bommarco, R. (2017). Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecology Letters*, 20, 1427–1436. https://doi.org/10.1111/ele.12850
- Garratt, M. P., Senapathi, D., Coston, D. J., Mortimer, S. R., & Potts, S. G. (2017). The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. Agriculture, Ecosystems & Environment, 247, 363–370. https://doi.org/10.1016/j.agee.2017.06.048
- Geiger, F., Wäckers, F. L., & Bianchi, F. J. J. A. (2009). Hibernation of predatory arthropods in semi-natural habitats. *BioControl*, *54*, 529–535. https://doi.org/10.1007/s10526-008-9206-5
- Haaland, C., Naisbit, R. E., & Bersier, L. F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, 4, 60–80. https://doi.org/10.1111/j.1752-4598.2010.00098.x
- Hanson, H. I., Birkhofer, K., Smith, H. G., Palmu, E., & Hedlund, K. (2017). Agricultural land use affects abundance and dispersal tendency of predatory arthropods. *Basic and Applied Ecology*, 18, 40–49. https://doi.org/10.1016/j.baae.2016.10.004
- Hass, A. L., Kormann, U. G., Tscharntke, T., Clough, Y., Baillod, A. B., Sirami, C., ... Batáry, P. (2018). Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172242. https://doi. org/10.1098/rspb.2017.2242
- Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R. W., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. Agronomy for Sustainable Development, 37, 31. https://doi.org/10.1007/s13593-017-0434-x
- Holzschuh, A., Dainese, M., González-Varo, J. P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., ... Steffan-Dewenter, I. (2016). Massflowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters*, 19, 1228–1236. https://doi. org/10.1111/ele.12657
- Jordbruksverket. (2018). Retrieved from https://www.Jordbruksverket.se/ Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., ... Zou, Y. I. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proceedings of the National Academy of Sciences of the United States of America, 115, E7863-E7870. https://doi.org/10.1073/ pnas.1800042115
- Kim, J., Williams, N., & Kremen, C. (2006). Effects of cultivation and proximity to natural habitat on ground-nesting native bees in california

- sunflower fields. *Journal of the Kansas Entomological Society*, 79, 309–320. https://doi.org/10.2317/0507.11.1
- Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. Science, 362, https://doi.org/10.1126/science. aau6020
- Labruyere, S., Ricci, B., Lubac, A., & Petit, S. (2016). Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. *Agriculture, Ecosystems & Environment*, 231, 183–192. https://doi.org/10.1016/j.agee.2016.06.037
- Lantmäteriet. (2018). Retrieved from https://www.lantmateriet.se//sv/ Kartor-och-geografisk-information/geodataprodukter/terrangkar
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., ... Burel, F. (2010). Intensification of agriculture, land-scape composition and wild bee communities: A large scale study in four European countries. Agriculture, Ecosystems & Environment, 137, 143–150. https://doi.org/10.1016/j.agee.2010.01.015
- Leonhardt, S. D., & Blüthgen, N. (2012). The same, but different: Pollen foraging in honeybee and bumblebee colonies. *Apidologie*, 43, 449–464. https://doi.org/10.1007/s13592-011-0112-y
- Li, X., Liu, Y., Duan, M., Yu, Z., & Axmacher, J. C. (2018). Different response patterns of epigaeic spiders and carabid beetles to varying environmental conditions in fields and semi-natural habitats of an intensively cultivated agricultural landscape. Agriculture, Ecosystems & Environment., 264, 54-62. https://doi.org/10.1016/j.agee.2018.05.005
- Lindström, S. A. M., Herbertsson, L., Rundlöf, M., Smith, H. G., & Bommarco, R. (2016). Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia*, 180, 759-769. https://doi.org/10.1007/s00442-015-3517-x
- Lys, J., & Nentwig, W. (1992). Augmentation of beneficial arthropods by strip-management. *Oecologia*, 92, 373–382. https://doi.org/10.1007/BF00317463
- Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V., & Birkhofer, K. (2017). Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. *Insect Conservation and Diversity*, 10, 236–247. https://doi.org/10.1111/icad.12220
- Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M., & Batáry, P. (2018). Crop rotation and agri-environment schemes determine bumblebee communities via flower resources. *Journal of Applied Ecology*, 55, 1714–1724. https://doi.org/10.1111/1365-2664.13119
- Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., ... Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22, 1083–1094. https://doi.org/10.1111/ele.13265
- Meena, A., Sharma, R. K., Chander, S., Sharma, D. K., & Sinha, S. R. (2019). Flower strip farmscaping to promote natural enemies diversity and eco-friendly pest suppression in okra (Abelmoschus esculentus). Indian Journal of Agricultural Science, 89, 119–123.
- Menalled, F. D., Smith, R. G., Dauer, J. T., & Fox, T. B. (2007). Impact of agricultural management on carabid communities and weed seed predation. Agriculture, Ecosystems & Environment, 118, 1-4. https:// doi.org/10.1016/j.agee.2006.04.011
- Muneret, L., Auriol, A., Bonnard, O., Richart-Cervera, S., Thiéry, D., & Rusch, A. (2019). Organic farming expansion drives natural enemy abundance but not diversity in vineyard-dominated landscapes. *Ecology and Evolution*, 9, 13532–13542. https://doi.org/10.1002/ece3.5810
- Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44, 50–59. https://doi.org/10.1111/j.1365-2664. 2006.01250.x

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., & Wagner, H. (2019). *vegan: Community ecology package*. R package version 2.5-6. Retrieved from https://cran.r-project.org/web/packages/vegan/index.html

- Opatovsky, I., Weintraub, P. G., Musli, I., & Lubin, Y. (2017). Use of alternative habitats by spiders in a desert agroecosystem. *Journal of Arachnology*, 45, 129–138. https://doi.org/10.1636/JoA-S-16-008.1
- Palmu, E., Ekroos, J., Hanson, H. I., Smith, H. G., & Hedlund, K. (2014). Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic and Applied Ecology*, 15, 241–249. https://doi.org/10.1016/j.baae.2014.03.001
- Pollard, K. A., & Holland, J. M. (2006). Arthropods within the woody element of hedgerows and their distribution pattern. *Agricultural* and Forest Entomology, 8, 203–211. https://doi.org/10.1111/j.1461-9563.2006.00297.x
- Pompozzi, G., Marrero, H. J., Haedo, J., Fritz, L., & Torretta, J. P. (2019). Non-cropped fragments as important spider reservoirs in a Pampean agro-ecosystem. *Annals of Applied Biology*, 175(3), 326–335. https://doi.org/10.1111/aab.12537
- R Core Team. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/
- Redlich, S., Martin, E. A., & Steffan-Dewenter, I. (2018). Landscape-level crop diversity benefits biological pest control. *Journal of Applied Ecology*, 55, 2419–2428. https://doi.org/10.1111/1365-2664.13126
- Requier, F., Odoux, J. F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., & Bretagnolle, V. (2015). Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecological Applications*, 25, 881–890. https://doi.org/10.1890/14-1011.1
- Ricci, B., Lavigne, C., Alignier, A., Aviron, S., Biju-Duval, L., Bouvier, J. C., ... Petit, S. (2019). Local pesticide use intensity conditions landscape effects on biological pest control. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182898. https://doi.org/10.1098/rspb.2018.2898
- Rundlöf, M., Persson, A. S., Smith, H. G., & Bommarco, R. (2014). Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, 172, 138–145. https://doi.org/10.1016/j.biocon.2014.02.027
- Rundlöf, M., Smith, H. G., & Birkhofer, K. (2016). Effects of organic farming on biodiversity. In ELS. *American Cancer Society* (pp. 1–7). https://doi.org/10.1002/9780470015902.a0026342
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H. G., & Ekbom, B. (2014). Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia*, 175, 971–983. https://doi.org/10.1007/s00442-014-2949-z
- Rusch, A., Bommarco, R., Jonsson, M., Smith, H. G., & Ekbom, B. (2013). Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *Journal of Applied Ecology*, 50, 345–354. https://doi.org/10.1111/1365-2664.12055

- Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, 30, 524–530. https://doi.org/10.1016/j.tree.2015.06.007
- Schneider, G., Krauss, J., Boetzl, F. A., Fritze, M. A., & Steffan-Dewenter, I. (2016). Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. *Oecologia*, 182, 1141–1150. https://doi.org/10.1007/s00442-016-3710-6
- Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., ... Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proceedings of the National Academy of Sciences of the United States of America, 116, 16442-16447. https://doi.org/10.1073/pnas.1906419116
- Smith, H. G., Birkhofer, K., Clough, Y., Ekroos, J., Olsson, O., & Rundlöf, M. (2014). Beyond dispersal: The role of animal movement in modern agricultural landscapes. In L.-A. Hansson & S. Åkesson (Eds.), Animal movement across scales (pp. 51-77). Oxford, UK: Oxford University Press. ISBN: 9780199677191.
- Statistics Sweden. (2018). Retrieved from https://www.scb.se/en/Tamburini, G. (2017). [Arthropod survey]. Unpublished raw data.
- Tscharntke, T., Karp, D. S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., ... Zhang, W. (2016). When natural habitat fails to enhance biological pest control Five hypotheses. *Biological Conservation*, 204, 449–458. https://doi.org/10.1016/j.biocon.2016.10.001
- Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J. M., & Baudry, J. (2013). The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? Agriculture, Ecosystems & Environment, 166, 3-14. https://doi. org/10.1016/j.agee.2012.08.013
- Wamser, S., Dauber, J., Birkhofer, K., & Wolters, V. (2011). Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites. Agriculture, Ecosystem & Environment, 144, 235–240. https://doi.org/10.1016/j.agee.2011.08.019
- Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6, 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Aguilera G, Roslin T, Miller K, et al. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *J Appl Ecol*. 2020;00:1–10. https://doi.org/10.1111/1365-2664.13712