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

Guillermo Aguilera1 | Tomas Roslin1 | Kirsten Miller1,2 | Giovanni Tamburini1,3 | Klaus Birkhofer4 | Berta Caballero-Lopez5 | Sandra Ann-Marie Lindström1,6,7 | 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

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.
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 service-providing 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 (Holzscheuh 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, & Ekborn, 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

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
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.

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

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...
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 semi-natural 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...
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

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Crop diversity</th>
<th>% Semi-natural habitats</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Effect size</td>
<td>p-value</td>
<td>Effect size</td>
</tr>
<tr>
<td>Diversity (Shannon index)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.031 ± 0.024</td>
<td>0.187</td>
<td>0.049 ± 0.024</td>
</tr>
<tr>
<td>Carabids</td>
<td>0.059 ± 0.039</td>
<td>0.130</td>
<td>0.087 ± 0.038</td>
</tr>
<tr>
<td>Spiders</td>
<td>-0.003 ± 0.033</td>
<td>0.930</td>
<td>0.026 ± 0.033</td>
</tr>
<tr>
<td>Pollinators</td>
<td>0.051 ± 0.034</td>
<td>0.134</td>
<td>-0.034 ± 0.033</td>
</tr>
<tr>
<td>Diversity (Simpson index)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.010 ± 0.010</td>
<td>0.310</td>
<td>0.015 ± 0.010</td>
</tr>
<tr>
<td>Carabids</td>
<td>0.017 ± 0.014</td>
<td>0.221</td>
<td>0.037 ± 0.013</td>
</tr>
<tr>
<td>Spiders</td>
<td>0.002 ± 0.004</td>
<td>0.720</td>
<td>0.001 ± 0.005</td>
</tr>
<tr>
<td>Pollinators</td>
<td>0.028 ± 0.034</td>
<td>0.430</td>
<td>-0.035 ± 0.032</td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.037 ± 0.051</td>
<td>0.476</td>
<td>-0.009 ± 0.052</td>
</tr>
<tr>
<td>Carabids</td>
<td>-0.012 ± 0.072</td>
<td>0.983</td>
<td>-0.198 ± 0.069</td>
</tr>
<tr>
<td>Spiders</td>
<td>0.091 ± 0.057</td>
<td>0.114</td>
<td>0.089 ± 0.055</td>
</tr>
<tr>
<td>Pollinators</td>
<td>-0.180 ± 0.110</td>
<td>0.092</td>
<td>0.473 ± 0.101</td>
</tr>
</tbody>
</table>

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 non-crop 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
ites, Wamser, Dauber, Birkhofer, & Wolters, 2011) and in agricul-
tural landscapes, semi-natural patches like forests, fallows or grass-
lands 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 arthro-
pods. 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 hab-
itats sometimes fail to provide crop fields with sufficient biological
pest control is that the amount of semi-natural habitats in agricul-
tural landscapes is often too low to increase the abundance of nat-
ural 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 diver-
sity 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 intensifica-
tion can have detrimental effects for wild pollinators (Le Fèon
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 com-
pletely 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 con-
tinuity 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 pres-
ence 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 man-
agement 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 (cor-
relation 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 ar-
thropods 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 differ-
ent response in their abundances. This variability of responses be-
tween 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 polli-
nators 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 understand-
ing of the effect of crop diversity and the actual temporal and spatial
resource continuity.

Carabid abundance showed a negative response with the in-
creasing 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 pro-
portion of semi-natural habitats and we detected a non-significant
positive trend with increasing crop diversity. Such effects contra-
dict some recent results (Garratt et al., 2017; Opatovsky et al., 2017;
Pompozzi et al., 2019), but these seem to indicate that the abun-
dances of ground-dwelling spiders are affected not only by the non-
crop 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 abun-
dant in the landscape, may benefit from a lower diversity of crop
types that offer a large number of resources rather than a more di-
verse 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 hover-
flies 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.O. 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


