




RESEARCH ARTICLE

Ecological requirements drive the variable responses of wheat pests and natural enemies to the landscape context

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Abstract

1. Semi-natural habitats (SNH) are considered essential for pest-suppressive landscapes, but their influence on crop pests and natural enemies can be highly variable. Instead of SNH per se, the availability of resources, such as pollen and nectar, may be more relevant for supporting pest control.
2. Here, we assessed the spatiotemporal variation of multiple insect pests (cereal leaf beetles and aphids) and natural enemies (predators and aphid parasitoids) in wheat fields and their responses to landscape context and flower availability. We combined detailed information on pollen use by natural enemies with the specific distribution of pollen-providing plants across a gradient of landscape composition and configuration.
3. The abundance of wheat pests was tightly linked to wheat development stage. Syrphids colonised the fields early in the season, while the abundance of other enemies increased later in the season. The responses of pests to landscape structure were variable and, while some pests had low abundances in landscapes with high edge density and SNH cover, *Sitobion avenae* abundance was positively associated with SNH cover. Lacewings, syrphids and cereal leaf beetles were abundant in landscapes with diverse and abundant flower resources, whereas the abundance of parasitoids and *Nabis* sp. was driven by aphid abundance. We detected no significant indirect effects of landscape on pests via natural enemies.
4. *Synthesis and applications.* Our findings highlight the need for conservation biological control to go beyond 'one size fits all' and consider the specific ecology of the involved organisms, even for a single crop type. Landscapes with high edge density and flowering woody plants may support natural enemies, in particular syrphids, which colonised the fields early in the season. Incentives for pest-suppressive landscapes should focus on tailored strategies that disfavour dominant cereal pests and simultaneously enhance natural enemies according to their ecological requirements.

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KEYWORDS

aphids, cereal leaf beetles, flower resources, parasitoids, pest-suppressive landscapes, predators, semi-natural habitats

1 | INTRODUCTION

Intensive agriculture seriously threatens farmland biodiversity via pesticide use, growing a few crop species in monocultures and the often concomitant reduction of semi-natural habitats (Raven & Wagner, 2021). Ecological intensification has been coined as a more sustainable agricultural model, which is based on strengthening the provision of ecosystem services, such as pest suppression mediated by natural enemies (Bommarco et al., 2013). Many natural enemies rely on resources provided by semi-natural habitats (hereafter SNH; Bianchi et al., 2006) and therefore the abundance and diversity of natural enemies, and associated biocontrol services, are often positively related to the proportion of SNH at the landscape scale (Martin et al., 2019; Rusch et al., 2016). However, more recently, the generality of these relationships has been questioned and there is increasing awareness that pests may benefit from SNH as well (Karp et al., 2018; Tschardt et al., 2016). This suggests that the land-use category SNH may be too broad for generalising about its potential to support pests and/or natural enemy populations. Therefore, more precise information of resource provision by different habitats may be needed to effectively design pest-suppressive landscapes (Bianchi et al., 2013).

Cereals are the dominant staple crops across the world and wheat is the most common cereal in Europe (FAOSTAT, 2021). In the northern hemisphere, cereal leaf beetles (Coleoptera; Chrysomelidae; *Oulema* spp.; Buntin et al., 2004) and aphids (Hemiptera, Sternorrhyncha) are the most important insect pests on wheat, whereby the English grain aphid (*Sitobion avenae* Fabricius), the rose-grain aphid (*Metopolophium dirhodum* Walker) and the bird cherry-oat aphid (*Rhopalosiphum padi* L.) predominate in Europe (Honěk et al., 2018). Cereal leaf beetles (hereafter CLB) can develop high abundances in landscapes with a high cereal cover, but also where overwintering woody habitats are available (Kheirodin et al., 2020). While SNH may support wheat aphid populations (Plečáček et al., 2014; Thies et al., 2005), their suppression by natural enemies may also increase in landscapes with a high proportion of SNH (Rusch et al., 2016). While aphids and cereal leaf beetles can jointly infest wheat fields, simultaneous evaluations of field and landscape-scale variables that might influence their population size are scarce (but see Redlich et al., 2021).

Both CLB and aphids are attacked by specialist parasitoids and a range of predators such as beetles, lacewings, syrphids and spiders (Kheirodin, Cárcamo, et al., 2020; Kheirodin et al., 2020; Schmidt et al., 2003). Several landscape variables, such as the cover

of SNH (Thies et al., 2005), mass-flowering crops or crop diversity (Aguilera et al., 2020; Kheirodin, Sharanowski, et al., 2020; Redlich et al., 2018), can enhance natural enemies and pest control in wheat fields. However, flowering resources can play a particularly important role as many natural enemies rely on floral food resources, which may increase their longevity and fecundity (Wäckers et al., 2005). Among aphid and CLB natural enemies, lacewing and syrphid adults feed actively on pollen and nectar (Bertrand et al., 2019; Vialatte et al., 2017), whereas aphid parasitoids and ladybeetles are facultative consumers of floral resources (Lundgren, 2009; Wäckers et al., 2005). Other predators, such as spiders or carabid beetles, do not consume floral resources at all. Therefore, flower availability can be associated with a selection of natural enemies that may enhance biocontrol of crop pests (Albrecht et al., 2020). However, given that SNH comprise a wide variety of plant species, which may or may not provide accessible floral resources for natural enemies, SNH as a general land use category has limited predictive power (Karp et al., 2018). More detailed assessment of floral resource availability at the landscape scale may improve the predictability of agricultural pests and their natural enemies, but this has been rarely evaluated (but see Vialatte et al., 2017).

Here, we assessed the responses of multiple insect pests and natural enemies in wheat fields to landscape context and flower availability. We combined detailed information on the pollen use by natural enemies with the specific distribution of the pollen-providing plants across a gradient of landscape composition and configuration. Specifically, we assessed (a) the intra-field spatial distribution and population dynamics of pests and their natural enemies across wheat phenological phases; (b) the influence of landscape composition, configuration and flower availability on the abundance of pest and natural enemies in wheat fields; and (c) the direct and indirect relationships between landscape variables, natural enemies and wheat pests. Based on these objectives, we formulated three main hypotheses. First, given that the population dynamics of aphids and CLB are strongly influenced by the development stage of wheat (Buntin et al., 2004; Honěk et al., 2018), we expected pests to show marked temporal variations across wheat phases, with CLB linked to early and aphids to mid and late wheat phases, and natural enemy abundance to increase after pest populations are established. Second, given the widely known benefits of SNH on natural enemies (Bianchi et al., 2006), we expected that the abundance of natural enemies would be relatively high (a) near field edges as opposed to field interiors, (b) in landscapes with a high landscape heterogeneity (both compositional and configurational) and high flower availability.

Moreover, we expected that landscape heterogeneity and flower availability will benefit natural enemies and indirectly affect wheat pests via top-down control. Third, given the relevant role of flower resources for some natural enemies (Wäckers et al., 2005), we expected that flower availability would be more important than landscape heterogeneity for lacewings and syrphids, but not for other predators and parasitoids that are less reliant on floral resources.

2 | MATERIALS AND METHODS

2.1 | Study sites

We selected 19 winter wheat fields located in landscapes covering a gradient in landscape composition in terms of woody and herbaceous SNH cover, and floral resource availability (based on the flower resources consumed by *Bombus terrestris* L.; Eckerter et al., 2020; Figure S1a). At each field, three transects parallel to a focal field edge were established along three consecutive tractor tracks, at distances ranging between 5 and 48 m from the edge (Figure S1b) and at a minimum distance of 50 m from other field edges. The mean nearest neighbour distance between focal fields was 1.9 ± 1.0 km (range: 0.6–3.7 km). Landscape metrics were derived for circular buffers of radius 0.5 km around each focal edge (Table S1; Figure S2). We assessed the nearest distances to forest, measures of landscape composition (proportion of forest, arable land, cereals, urban areas, semi-natural habitats and Shannon–Wiener index of crop diversity) and landscape configuration (edge density, woody edge density, field size and mean field size) in QGIS 3.6.2 (QGIS Development Team, 2019). Landscapes were digitised as polygon layers using Sentinel-2 satellite imagery as base maps and ground-truthed in the field in May–July 2020. All farmers gave permission to perform sampling on their field and no further licenses were needed.

2.2 | Insect sampling

Wheat pests and natural enemies were sampled using direct counting on wheat stems and sweep netting. Direct counting entailed the visual inspection of 40 wheat stems per transect per sampling date (for a total of 120 stems per field). Sweep-net sampling consisted of taking 100 sweeps per transect at 1 m intervals using a 30 cm diameter net. Samplings were repeated three times from May to early July 2020 during three wheat phenological phases (flowering, milk ripening and dough phases).

For pests, we assessed the abundance of aphids (*Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*) and cereal leaf beetles (*Oulema* spp.). The following groups and stages of natural enemies were recorded: lacewings (*Chrysoperla* spp. eggs, larvae and adults), syrphids (eggs and larvae), ladybeetles (larvae and adults from several species of Coccinellidae), predatory bugs (i.e. adult *Nabis* sp.) and aphid parasitoids (mummies). In addition to raw abundances, we calculated aphid parasitism as the number of mummies

per transect divided by total aphid abundance. Our study did not require any ethical approval.

2.3 | Assessment of floral resources

We expressed the availability of floral resources in terms of the total area covered by flowering plants that could offer resources for natural enemies, the flower diversity of the landscapes and a specific index considering the pollen consumed by *Chrysoperla carnea*. To calculate these variables, flowering plants in each landscape were mapped during two occasions. First, woody plants were mapped in 2017–2019 (Supplementary Methods; Eckerter et al., 2020) in sampling plots of 10×10 m covering all hedgerows and forest edges of each landscape. Second, herbaceous flowering plants were mapped in May–July 2020 along transects in all the edges between landscape elements (Supplementary Methods). Both data sources were digitised in QGIS as vector layers and the total area per pollen type was calculated for each landscape. Only insect-pollinated plants were considered as these represent sources of both pollen and nectar for insects and are more likely to be actively visited by natural enemies (Wäckers et al., 2005). Plants with tubular flowers of limited accessibility were excluded from all calculations (van Rijn & Wäckers, 2016).

Total flower area was then calculated as the sum of the area covered by insect-pollinated mapped plants in each landscape. Flower diversity was calculated as the Shannon–Wiener Index of flower diversity, considering the relative cover of all insect-pollinated plants per landscape. Finally, we calculated a specific flower availability index (FAI) based on the pollen ingested by adult green lacewings collected using sticky traps in 2019 in the same study region (Supplementary Methods; Table S2). The FAI was calculated using the formula developed by Eckerter et al. (2020), which sums the relative cover of plants providing each pollen type in each landscape times their proportional use by lacewings expressed as the share of total ingested pollen volume (Supplementary Methods). Thus, the FAI allows to compare the availability of pollen between landscapes, weighing the contribution of each pollen type according to its relevance for lacewings. The index was calculated for lacewings, but should also be relevant for ladybeetles, given the similarity of the pollen diet of these two important aphid enemies (Bertrand et al., 2019).

2.4 | Data analyses

To analyse the spatiotemporal dynamics of wheat pests and enemies, the abundances of each insect group in the 40 wheat stems and the 100 sweeps in each transect were pooled to obtain one abundance value per transect, sampling period and landscape. These were used as response variables in GLMMs with Poisson error distribution or negative binomial in case of overdispersion. Wheat phenological phase (flowering, milk ripening and dough phases), distance to the edge (in meters, as a continuous variable), metrics of

landscape composition (proportion of forest, arable land, cereals, urban areas, SNH and crop diversity), landscape configuration (edge density, woody edge density, field size and mean field size), flower availability (FAI_{early} , FAI_{late} , FAI_{total} , total flower area and flower diversity) and distance to forests were included as predictor variables. In addition, abundances of natural enemies were included in the models of wheat pests to test for potential impacts of top-down control, and abundance of pests were included in enemy models to test for potential bottom-up responses (prey/host availability). We also explored models with wheat development stage \times distance and wheat development stage \times landscape metric interactions. Field ID was included as a random variable to account for the hierarchical sampling design.

2.5 | Model selection

All potential models that resulted from the combination of distance, sampling period and landscape metrics (and their interactions) were run and ordered based on their AICc value. Due to large differences in the scales of some independent variables, all variables were z-transformed. Only models with up to four predictors were considered to avoid overparameterisation. A model averaging approach was used and all the models within a $\Delta AICc < 2$ were averaged and reported. To avoid multicollinearity, models including independent variables that were highly correlated ($r > 0.6$; Figure S2) were excluded. All models in the subsets met model validation criteria (Lüdecke et al., 2021) and Variation Inflation Factors were always below 3. We report conditional-averaged estimates as these are more precise than full-averaged estimates (Symonds & Moussalli, 2011). We did not use Bonferroni adjustments to our analyses because it is considered to be too conservative, especially for ecological studies where detailed assessments are performed for multiple species (Moran, 2003). Analyses were performed in the software R using the packages GLMMTMB (Brooks et al., 2017), PERFORMANCE (Lüdecke et al., 2021) and MuMIn (Barton, 2009).

2.6 | Direct and indirect influence of landscape on wheat pests

To test the relative importance of direct and indirect paths (mediated through enemies) linking landscape structure and wheat pests, we performed piecewise Structural Equation Models (pSEM). Similar to traditional SEMs, pSEMs link multiple predictor and response variables in a causal pathway. However, pSEMs evaluate each equation locally, allowing the fitting of smaller datasets (Lefcheck, 2016). All variables were z-transformed and for each insect group, landscape variables that were selected in the previous G.L.M.s were considered. We fitted a full model that included the abovementioned landscape variables and links between enemies and pests. Given that CLB eggs and larvae showed very similar responses, we kept only CLB larvae in the models, as these stages feed on wheat plants

(Buntin et al., 2004). The model was further simplified by removing non-significant paths if this improved model fit (Fisher's C with $p > 0.05$; $\Delta BIC \geq 2$; Redlich et al., 2021). Piecewise SEMs were performed with the package PIECEWISESEM (Lefcheck, 2016).

3 | RESULTS

3.1 | Wheat pests

On 6,840 wheat stems, we observed a total of 17,060 aphids and 1,164 CLB. Aphids were dominated by *S. avenae* (12,510 individuals, 73%), followed by *M. dirhodum* (4,137, 24%) and *R. padi* (413, 2.4%). The abundance of *S. avenae* peaked at the milk ripening phase (Figure S3a), significantly increased with SNH cover (Figure 1a), and decreased with cereal cover (Figure S4a; Table 1). In contrast, the abundance of *Metopolophium dirhodum* decreased over time and was negatively associated to SNH cover (Figure 1b; Figure S3b; Table 1). The abundance of *Rhopalosiphum padi* increased over time (Figure S3c) and was negatively associated with mean field size (Figure 1c) and woody edge density (Figure S4b). The averaged model for the abundance of CLB eggs (Table 1) indicated a decrease over time (Figure S2d) and a negative association with edge density and positive associations with distance to the edge and crop diversity (Figures S4c,d and S5a). Similarly, the abundance of CLB larvae also decreased over time and was negatively associated with edge density (Figure 1d) and SNH cover and positively with flower diversity and distance to the edge (Figures S4e,f and S5b,f; Table 1).

3.2 | Natural enemies

Natural enemies were numerically dominated by aphid parasitoids (2,377 mummies) and syrphids (869 eggs and 500 larvae), whereas *Nabis* sp. (337), ladybeetles (266 for all species combined) and lacewings (142) were less abundant. The number of lacewing eggs increased slightly at the dough phase (Figure S6a) and was negatively associated with FAI_{early} (Figure 2a) and positively with flower diversity (Figure 2b) and mean field size (Table 1; Figure S7a). The abundance of syrphid eggs decreased from wheat flowering towards the dough phase (Figure S6b) and was positively associated with total flower area (Figure 2c) and arable cover, and negatively with SNH cover (Figure S7b,c; Table 1). The abundance of syrphid larvae was best explained by a model including an interaction between wheat phase and FAI_{early} : the abundance of syrphid larvae slightly increased with FAI_{early} at wheat flowering, while this was no longer the case at the dough phase (Figure 2d; Table 1). The abundance of ladybeetles increased at the dough phase (Figure S6d) and with field size (Table 1; Figure S7d). The abundance of *Nabis* sp. was best explained by an interaction between wheat phase and arable cover (Table 1). During the flowering and milk ripening phases, abundances of *Nabis* decreased with arable cover, whereas at the dough phase, this pattern was no longer present (Figure S7e). The model including an

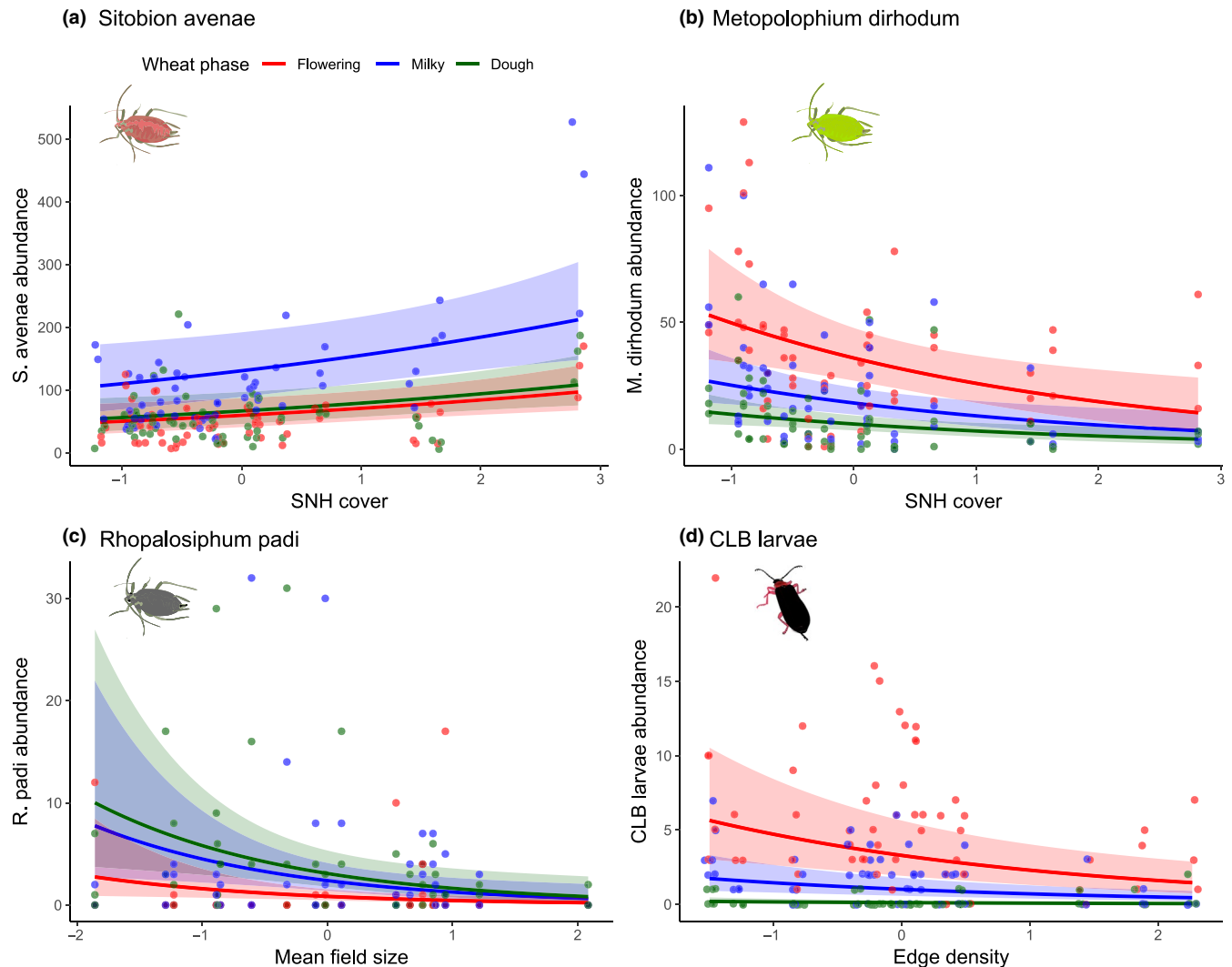


FIGURE 1 Selection of relationships between wheat pests and landscape variables. Fitted relationships based on GLMMs (lines and 95% confidence bands) and raw data (points) are shown for each pest group. Wheat development phases are indicated in colours (red: flowering; blue: milk ripening; green: dough). The x-axis shows standardised values of predictors. Solid lines represent significant landscape effects on abundances

interaction between wheat phase and mean field size best explained the abundance of aphid parasitoids (Figure S7f; Table 1); mummy abundance was low across all landscapes during wheat flowering, increased with mean field size during the milk ripening phase, and was relatively high across all landscapes during the dough phase. Aphid parasitism, on the other hand, decreased on fields with high aphid abundance and high edge density (Figure S8; Table 1).

3.3 | Direct and indirect relationships between landscape, natural enemies and wheat pests

The piecewise SEMs revealed that responses of wheat pests were heterogeneous, but in all cases direct links with landscape variables were stronger than indirect links via natural enemies (Figure 3; Table S4). At the same time, natural enemies showed variable responses to landscape variables, and aphid parasitoids

and *Nabis* sp. were positively associated with the availability of the most abundant hosts/prey. The abundance of *S. avenae* increased with SNH cover and decreased with mean field size. In contrast, *M. dirhodum* was negatively associated with SNH cover and syrphid larvae abundance, although the latter link was only marginally significant. The abundance of *R. padi* was only influenced by landscape configuration, with negative responses to edge density and mean field size. The abundance of CLB larvae was negatively linked to edge density and SNH cover, and positively linked to flower diversity.

4 | DISCUSSION

Pest-suppressive landscapes should provide enough alternative resources to support natural enemies that provide biocontrol services in crops. While SNH are generally associated with the provision of

TABLE 1 Averaged models for the influence of wheat development phase, distance to the field edge, landscape, flower availability and enemies, prey or host on pest and natural enemy abundance in wheat fields. Each model represents the conditional average of all the models within a $\Delta AICc$ of 2 (see Table S3). For each model, the independent variables are listed and the parameter estimates, their 95% confidence interval (CI) and p -values are shown. The importance of each independent variable (sum of model weights including that variable) is shown in parentheses. Significant estimates are highlighted in bold

Group	Species	Independent variables (importance)	Estimates	CI	p
Pests	<i>Sitobion avenae</i>	Intercept (flowering)	3.85	3.68 to 4.01	<0.001
		Milk ripening phase (1.0)	0.79	0.58 to 0.99	<0.001
		Dough phase (1.0)	0.11	-0.09 to 0.31	0.286
		Cereal cover (1.0)	-0.21	-0.33 to -0.08	0.001
		SNH cover (0.57)	0.15	0.01 to 0.29	0.042
	<i>Metopolophium dirhodum</i>	Mean field size (0.61)	-0.13	-0.26 to 0.00	0.057
		Total flower area (0.59)	0.12	-0.01 to 0.26	0.063
		Intercept (flowering)	3.57	3.28 to 3.87	<0.001
		Milk ripening phase (1.0)	-0.67	-0.98 to -0.35	<0.001
		Dough phase (1.0)	-1.29	-1.61 to -0.97	<0.001
	<i>Rhopalosiphum padi</i>	SNH (1.0)	-0.33	-0.57 to -0.09	0.008
		Syrphid larvae (0.25)	-0.08	-0.22 to 0.06	0.281
		Cereal cover (0.17)	-0.07	-0.32 to 0.17	0.562
		Mean field size (0.16)	-0.07	-0.34 to 0.20	0.602
		Intercept (flowering)	-0.19	-0.78 to 0.39	0.522
	Cereal leaf beetle eggs	Milk ripening phase (1.0)	1.09	0.29 to 1.88	0.007
		Dough phase (1.0)	1.34	0.54 to 2.15	0.001
		Edge density (0.63)	0.11	-0.33 to 0.54	0.63
		Mean field size (1.0)	-0.56	-1.04 to -0.07	0.024
		Woody edge density (0.63)	-0.62	-1.08 to -0.15	0.01
		Arable cover (0.37)	0.3	-0.07 to 0.67	0.112
		Syrphid larvae (0.37)	0.26	-0.05 to 0.57	0.104
		Intercept (flowering)	2	1.73 to 2.27	<0.001
		Milk ripening phase (1.0)	-1.09	-1.35 to -0.84	<0.001
		Dough phase (1.0)	-1.89	-2.20 to -1.58	<0.001
		Crop diversity (1.0)	0.32	0.02 to 0.62	0.038
		Distance to edge (1.0)	0.15	0.03 to 0.27	0.012
		Edge density (0.50)	-0.29	-0.55 to -0.02	0.032

(Continues)

TABLE 1 (Continued)

Group	Species	Independent variables (importance)	Estimates	CI	p
Natural enemies	Cereal leaf beetle larvae	Mean field size (0.31)	0.28	−0.02 to 0.59	0.067
		Intercept (flowering)	1.59	1.39 to 1.79	<0.001
		Milk ripening phase (1.0)	−1.17	−1.44 to −0.91	<0.001
		Dough phase (1.0)	−3.36	−3.97 to −2.74	<0.001
		Distance to edge (1.0)	0.18	0.05 to 0.31	0.006
		Edge density (0.61)	−0.36	−0.55 to −0.17	<0.001
		Flower diversity (1.0)	0.34	0.14 to 0.55	0.001
		SNH cover (0.39)	−0.36	−0.58 to −0.15	0.001
		Intercept (flowering)	−0.42	−0.74 to −0.10	0.01
		Milk ripening phase (1.0)	−0.13	−0.58 to 0.32	0.572
Natural enemies	Lacewing eggs	Dough phase (1.0)	0.46	0.07 to 0.85	0.022
		FAI _{early} (1.0)	−0.4	−0.60 to −0.20	<0.001
		Flower diversity (1.0)	0.23	0.02 to 0.44	0.035
		Mean field size (0.7)	0.2	0.01 to 0.39	0.038
		Intercept (flowering)	0.66	0.33 to 0.99	<0.001
		Milk ripening phase (1.0)	1.4	1.05 to 1.75	<0.001
		Dough phase (1.0)	0.96	0.59 to 1.33	<0.001
		Total flower area (0.86)	0.16	0.01 to 0.32	0.042
		SNH cover (0.88)	−0.22	−0.39 to −0.05	0.013
		Field size (0.31)	−0.12	−0.29 to 0.05	0.159
Natural enemies	Syrphid eggs	Arable cover (0.12)	0.17	0.02 to 0.33	0.028
		Mean field size (0.10)	−0.05	−0.21 to 0.11	0.546
		Flower diversity (0.10)	0.05	−0.12 to 0.22	0.571
		Cereal cover (0.10)	0.03	−0.11 to 0.17	0.647
		Intercept (flowering)	0.8	0.40 to 1.21	<0.001
		Milk ripening phase (1.0)	0.26	−0.16 to 0.68	0.221
		Dough phase (1.0)	0.55	0.15 to 0.96	0.007
		FAI _{early} (1.0)	0.47	−0.11 to 1.05	0.111
		Milk ripening * FAI _{early} (1.0)	−0.71	−1.32 to −0.10	0.022
		Dough * FAI _{early} (1.0)	−1.06	−1.67 to −0.45	0.001
Natural enemies	Ladybeetles	Intercept (flowering)	−1.06	−1.75 to −0.37	0.003
		Milk ripening phase (1.0)	1.09	0.51 to 1.67	<0.001

(Continues)

TABLE 1 (Continued)

Group	Species	Independent variables (importance)	Estimates	CI	p
Aphid parasitism	Nabis sp.	Dough phase (1.0)	1.74	1.19 to 2.29	<0.001
		Flower diversity (0.47)	-0.52	-1.05 to 0.00	0.051
		SNH cover (0.86)	0.35	-0.17 to 0.87	0.184
		Field size (0.28)	0.53	0.02 to 1.04	0.04
		Arable cover (0.14)	-0.22	-0.76 to 0.33	0.432
		Edge density (0.13)	-0.42	-0.96 to 0.13	0.132
		Intercept (flowering)	-1.29	-1.87 to -0.71	<0.001
		Milk ripening phase (1.0)	1.32	0.73 to 1.91	<0.001
		Dough phase (1.0)	2.92	2.38 to 3.46	<0.001
		Arable cover (1.0)	-0.77	-1.17 to -0.37	<0.001
		Milk ripening * Arable (1.0)	-0.02	-0.37 to 0.33	0.906
		Dough * Arable (1.0)	0.64	0.31 to 0.96	<0.001
		Intercept (flowering)	1.6	1.42 to 1.79	<0.001
		Milk ripening phase (1.0)	0.87	0.69 to 1.06	<0.001
		Dough phase (1.0)	1.53	1.35 to 1.71	<0.001
Aphid parasitoids	Aphid parasitoids	Mean field size (1.0)	-0.06	-0.24 to 0.12	0.536
		Milk ripening * Mean field size (1.0)	0.29	0.11 to 0.48	0.002
		Dough * Mean field size (1.0)	-0.03	-0.20 to 0.15	0.756
		Intercept (flowering)	-1.16	-1.25 to -1.06	<0.001
		Milk ripening phase (1.0)	-1.7	-1.83 to -1.56	<0.001
		Dough phase (1.0)	-0.87	-0.99 to -0.76	<0.001
		Aphid abundance (1.0)	-0.45	-0.51 to -0.38	<0.001
		Edge density (0.37)	-0.1	-0.20 to -0.01	0.027
		Field size (0.57)	-0.09	-0.19 to 0.01	0.078
		Flower diversity (0.41)	-0.07	-0.15 to 0.01	0.102

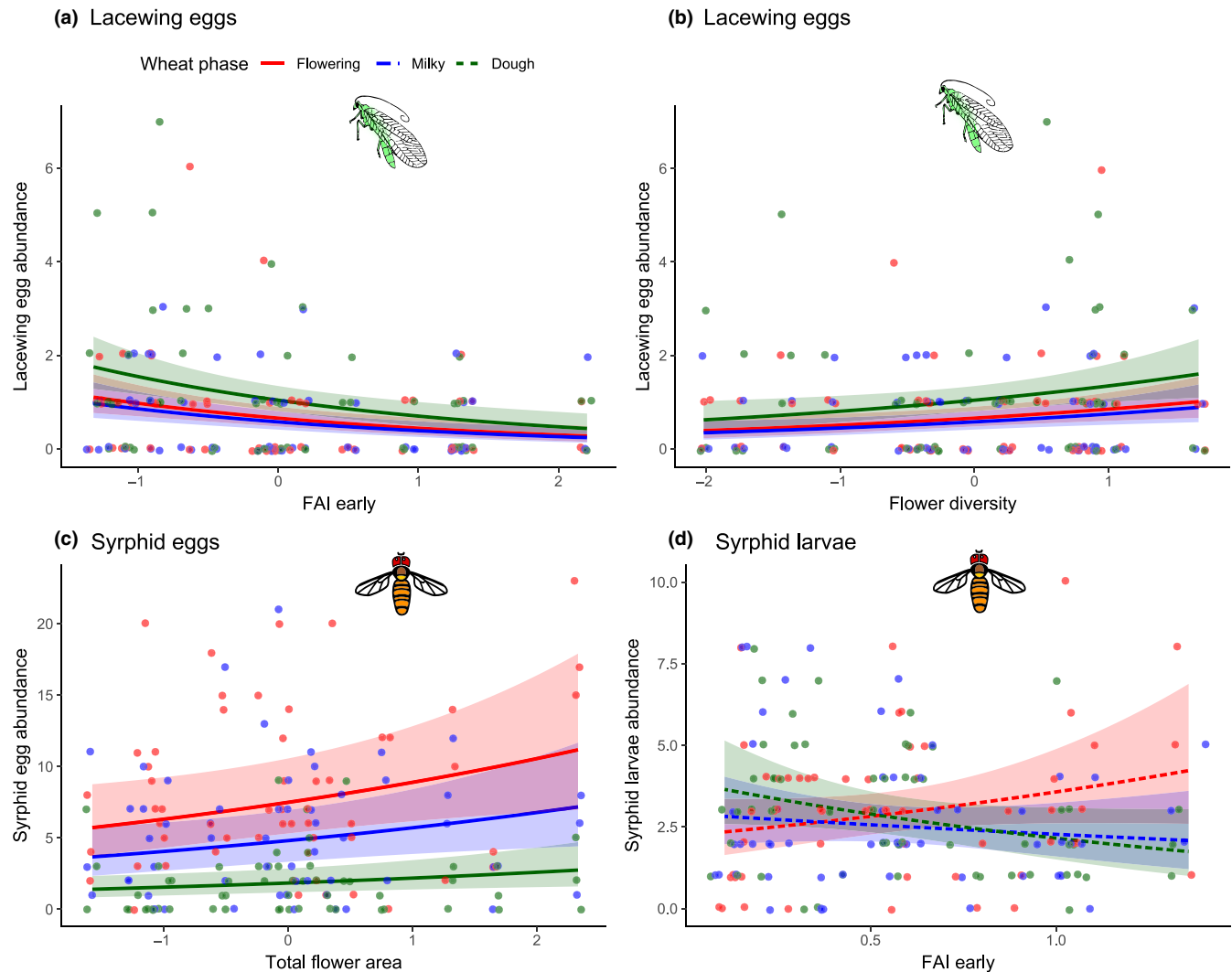


FIGURE 2 Selection of relationships between natural enemies of wheat pests and landscape-scale flower availability and SNH cover. For lacewing eggs (a, b) and syrphid eggs (c, d), the fitted relationships from the GLMMs (lines and 95% confidence bands) and raw data (points) are shown. Wheat development phases are indicated in colours (red: flowering; blue: milk ripening; green: dough). The x-axis shows standardised values of predictors. Solid lines represent significant landscape effects on abundances

floral resources, overwintering sites, refuge from disturbances, and alternative prey and hosts for natural enemies (Bianchi et al., 2006), the responses of pest and natural enemies to SNH are still poorly understood (Karp et al., 2018). Accounting for specific traits and ecological requirements of pests and natural enemies and the availability of specific resources in the landscape may offer an avenue for acquiring a better mechanistic understanding of how species respond to landscape context (Martin et al., 2019). Here we found that wheat pests and their enemies responded to landscape structure and flower availability in various ways. Landscapes with high SNH cover enhanced the dominant pest *S. avenae* and to a less extent natural enemies (*Nabis* and ladybeetles), while supporting relatively low abundances of other pests (*M. dirhodum* and CLB). Similar contrasting responses were detected for compositional heterogeneity. Flower diversity and area enhanced lacewings and syrphids, which depend on these resources, but lacewings were negatively associated to a species-specific flower availability index. CLB were the only pest

that was positively associated with flower diversity. Species-specific resource and habitat requirements, along with species interactions, are likely drivers of this variability, which highlights the importance of evaluating multiple pests and enemies simultaneously.

In agreement with our first hypotheses, temporal variation in pest abundances showed clear patterns linked to the biology of each species. CLB were most abundant in the early wheat phases, when they feed actively on leaves (Buntin et al., 2004). The relative abundances of aphid species followed the same trend as reported in other studies from central Europe, with *S. avenae* being the dominant and *R. padi* the least abundant species (Gagic et al., 2011; Roschewitz et al., 2005). *M. dirhodum* are leaf-colonising aphids and were most abundant during wheat flowering, whereas *S. avenae* aggregates in the ears and reached their highest abundance in the milk ripening phase (Honěk et al., 2018). Most natural enemies had low abundances at the early stages of wheat development and increased over time, which for *Nabis* and aphid parasitoids was linked to the increasing

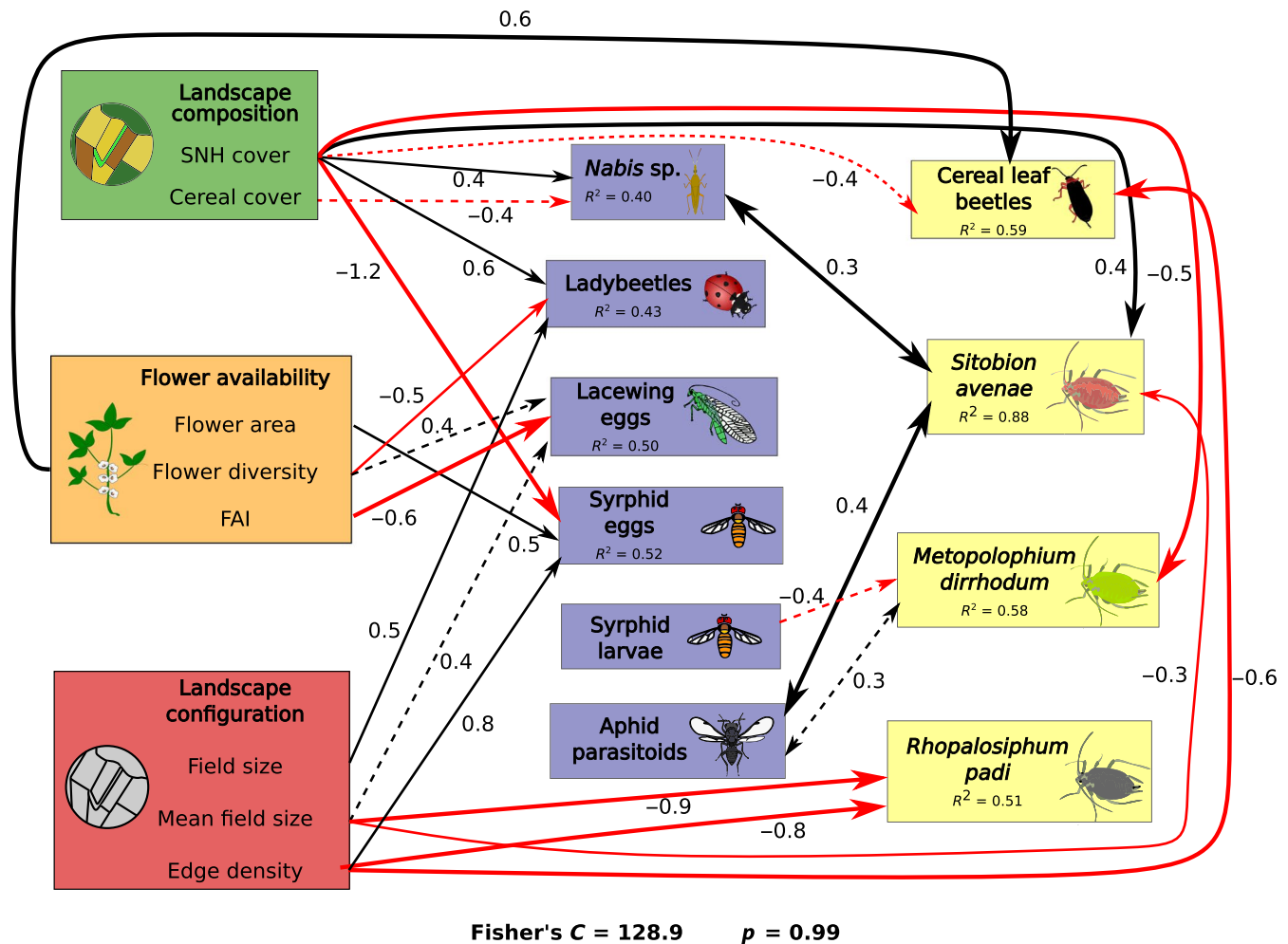


FIGURE 3 Best piecewise SEM for landscape and natural enemy effects on wheat pests. Dashed lines indicate marginally significant ($0.05 < p < 0.1$) and solid lines significant relationships (thin lines: $p < 0.05$; thick lines: $p < 0.01$). The standardised estimate for each line is shown next to each line. Black and red lines indicate positive and negative relationships, respectively. R^2 values are shown for response variables. See Table S4 for detailed statistics

density of *S. avenae*. In contrast, syrphid eggs were already abundant in the first sampling round, which indicates a high potential for pest suppression (Costamagna et al., 2015). Nevertheless, only a trend of declining *M. dirhodum* densities with increased syrphid larvae abundance was detected in the structural equation model.

Only CLB were influenced by distance to the edge, with increasing egg and larvae abundances towards the field centre, which is in line with findings of other studies (Tschumi et al., 2016; Van de Vijver et al., 2019). This spatial pattern of CLB abundances may result from high levels of pest control near the field edge due to spillover of enemies from neighbouring habitats (Martin et al., 2019). However, contrary to our expectations, the natural enemies were not concentrated near the field edge, which suggests that these flying insects have good dispersal capacities (Dunn et al., 2020; McEwen et al., 2007; Roschewitz et al., 2005). Accordingly, other enemies that are commonly more abundant near edges (e.g. ground-dwelling spiders and beetles) might be more important control agents for CLB near field edges (Safarzoda et al., 2014; Schmidt-Entling & Döbeli, 2009).

The associations between wheat pests and landscape metrics were diverse and could be related with their biology and overwintering sites. For example, the abundance of *S. avenae* increased with SNH cover as found in other studies (Gagic et al., 2011; Plečaš et al., 2014). This response can be explained by the abundant presence of perennial grasses in SNH where this species overwinters (Vialatte et al., 2007). In contrast, *M. dirhodum* and CLB larvae were negatively associated with SNH, which is in line with findings of Gagic et al. (2011). Since both pests use woody habitats as overwintering sites (Honěk et al., 2018; Kheirodin, Cárcamo, et al., 2020), this suggests that the availability of overwintering sites may limit *M. dirhodum* and CLB abundances in landscapes with little SNH. *S. avenae* was enhanced in landscapes with low cereal cover, indicating a possible resource dilution effect, where pests abundance becomes higher at decreasing host crop area (Bosem-Baillo et al., 2017). Landscape configurational heterogeneity also had contrasting effects on pests. At increasing edge density, the abundance of both *R. padi* and CLB decreased, suggesting that edges may increase top-down pest suppression by natural enemies as in many European

agroecosystems (Martin et al., 2019). However, the abundances of *R. padi* and *S. avenae* were higher in landscapes with small fields. Despite that fine-grained landscapes tend to benefit natural enemies, also pests can be enhanced because overwintering habitats can be closer to cultivated fields (Gallé et al., 2018). However, the number of studies assessing the influence of the size of cereal fields on pest populations is still low and further work on the role of landscape configuration on pest–natural enemy interactions is needed to further elucidate these complex interactions (Haan et al., 2019).

The availability of flower resources in agricultural landscapes is considered an important driver of population dynamics for natural enemies, but assessing landscape-scale flowering resources is time-consuming and rarely done (but see Kleijn & van Langevelde, 2006; Vialatte et al., 2017). In line with our second hypothesis, we found that lacewing and syrphid eggs, which are deposited by adults that depend on flower resources (Dunn et al., 2020; McEwen et al., 2007), were enhanced by flower diversity and total flower area, respectively. Syrphid larvae were also enhanced by the flower availability index but only early in the season. More than 60% of the flower area in our sites was represented by naturally occurring plants and semi-natural orchards, highlighting the relevance of diverse landscapes with ample floral resources to enhance beneficial arthropods. Surprisingly, the abundance of lacewing eggs was negatively related to the specific index that considered the pollen resources preferred by adults. Possibly, landscapes with high concentrations of preferred resources may reduce lacewing movement and the associated colonisation of cereal fields. On the other hand, CLB were also positively associated with flower diversity, though this might reflect the availability of overwintering sites as woody plants on edges represented an important component of flower measurements. More research is needed to unravel these complex relationships between availability of floral resources and insect population responses.

Natural enemies did not always benefit from landscape heterogeneity, contrary to the predictions of our second hypothesis. The abundance of syrphid eggs was negatively associated with SNH cover, while the abundance of *Nabis* sp. and ladybeetles showed weak positive associations with SNH, reinforcing that landscapes with high SNH cover do not always support more natural enemies (Tschantke et al., 2016). On the other hand, syrphid eggs were enhanced by high edge densities, which in combination with flower availability can also drive syrphid abundance (Sarhou et al., 2005). Reversely, aphid parasitoids, lacewings and ladybeetles were most abundant in coarse-grained landscapes with larger fields. Large fields might impair the colonisation of field centres for natural enemies with poor, but not good dispersal abilities (Haan et al., 2019; Martin et al., 2019). On the other hand, aphid parasitoids and *Nabis* were enhanced by the abundance of *S. avenae* and reached high abundances at the dough phase of wheat. These bottom-up effects are common for natural enemies of aphids (e.g. Leslie et al., 2009; Thies et al., 2005), and can limit the efficiency of aphid suppression when enemies colonise crops later than pests (Safarzoda et al., 2014). Surprisingly, top-down effects of natural enemies on pests were rare

and only syrphid larvae appeared to reduce *M. dirhodum* infestation when considering pooled data across the whole season. The early oviposition of syrphids in wheat fields when aphid densities are still relatively low may explain this relationship (Costamagna et al., 2015; Safarzoda et al., 2014). Therefore, facilitating early crop colonisation by natural enemies by enhancing key resources can contribute to pest suppression, but limiting pest establishment by reducing overwintering habitats of pests and modifying landscape configuration may have even a stronger pest-suppressive effect.

5 | CONCLUSIONS

We found variable responses of pests and their natural enemies to local and landscape factors that can be grounded in the life history and ecological requirements of these species. Landscapes with high edge density and the associated floral resources provided by woody plants may support natural enemies and offer fewer grassy habitats that are used by *S. avenae* for overwintering. At the same time, flower availability was important for syrphids, which colonised the fields early in the season and showed the highest potential to control aphids in this study. Therefore, our results highlight the need for management strategies for strengthening biocontrol services that go beyond 'one size fits all', even for a single crop type. Considering the requirements of all relevant pests, enemies and pollinators in agricultural landscapes containing multiple crops will be even more challenging, and conflicts between the different management goals can be expected. In the absence of strong evidence for biological control, incentives for pest-suppressive landscapes should focus on tailored strategies that disfavour dominant cereal pests and simultaneously enhance natural enemies by incorporating detailed ecological knowledge.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

E.G., F.J.J.A.B. and M.H.E. conceived the ideas and designed the methodology; E.G., P.W.E., V.P. and S.W. conducted the fieldwork; E.G. performed the statistical analyses and led the writing of the

manuscript. All authors contributed to the manuscript and agreed on the final version.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.dz08kprzh> (González et al., 2021).

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