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Unlike woodland edges, flower strips do not act as a refuge for cabbage stem flea beetle aestivation

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ABSTRACT

Background. Semi-natural habitats are generally considered to be beneficial to natural enemies of crop pests and pollinators. However, they could also be used by pests, such as the Cabbage Stem Flea Beetle (CSFB), *Psylliodes chrysocephala*, a major pest of winter oilseed rape, *Brassica napus*. Adults emerge from pupation in late spring and move to aestivation habitats. Published reports identify forest edges as the major shelter used, but flower strips may also constitute an alternative habitat. This study aimed to: (i) determine the role of perennial flower strips in CSFB aestivation in comparison with woodland edges; (ii) determine the influence of landscape composition on the abundance of aestivating CSFB and (iii) identify the characteristics of the local habitat associated with a high abundance of aestivating CSFB.

Results. CSFB emergence from aestivation was monitored with emergence traps from mid-August to mid-October 2021, at 14 sites in France. We found that CSFB preferred woodland edges and did not aestivate in flower strips. We found a negative effect of percentage woodland cover only for the smallest scale studied (250 m radius). We also found positive effects of the percentage of litter and mean tree circumference on the number of aestivating CSFB in woodland edges.

Conclusion. The aestivation of CSFB is supported by woodland edges, but not by flower strips. This implies that the presence of flower strips near oilseed rape fields does not exacerbate the problems due to this pest. However, the crops in the vicinity of woodlands could be colonized earlier by this pest than more distant fields. © 2023 Society of Chemical Industry.

Keywords: *Psylliodes chrysocephala*; aestivation; *Brassica napus*; semi-natural habitat; local environment characteristics; landscape

1 INTRODUCTION

The intensification of agriculture has led to the simplification of landscapes in many regions of North America and Western Europe, which are now dominated by arable crop fields with few natural or semi-natural habitats (SNH) remaining.¹⁻³ Landscape simplification has negative consequences for biodiversity⁴ and affects some ecosystem services, such as biological pest control.^{2, 3} Indeed, fields are ephemeral habitats subject to frequent and intensive disturbances. Many arthropod species need more stable habitats, such as non-crop habitats^{2, 5, 6} to complete their life-cycle. As a means of mitigating the effects of this landscape simplification, agri-environment schemes, including the implementation of flower strips, are encouraged by public policies, such as the European Common Agricultural Policy.^{7, 8}

Perennial habitats enhance biodiversity and related ecosystem services, such as pollination and the conservation biological control of pests by their natural enemies.⁹⁻¹³ For example, Albrecht *et al.*¹⁴ reported that flower strips, annual and perennial, enhance pest control or have a neutral effect in adjacent crops. However, it is important to bear in mind that the response to the presence of SNH depends on the species of natural enemies and pests present in the environment.¹³ Keller and Hänni⁵ showed that nine in every 10 natural enemy species require natural habitats at some point in their lifecycle, mostly during unfavorable periods, whereas such habitats are a requirement for only five in every ten pest species.

The Cabbage Stem Flea Beetle (CSFB), *Psylliodes chrysocephala* (Linnaeus, 1758, Coleoptera: Chrysomelidae), is a major pest of winter oilseed rape (*Brassica napus*, Linnaeus, 1753). This pest is becoming increasingly difficult to control in European cropping systems, in which oilseed rape is widespread^{15, 16} and control is generally achieved by insecticides. However, an increase of the populations of pests resistant to insecticides, especially to pyrethroids, limits the efficacy of chemical control.¹⁷⁻¹⁹ Insecticide use is also harmful for biodiversity²⁰ and can cause human health problems.²¹ Conservation biological control aims to enhance pest control by supporting natural enemies naturally occurring in the environment. This implies the maintenance or the development of their habitats.^{22, 23} This method could be a good alternative to synthetic pesticides with a positive impact on biodiversity.

Indeed, Gardarin *et al.*²⁴ showed that flower strips can enhance the parasitism of CSFB larvae within the crop. However, few studies to date have evaluated the extent to which such habitats, designed to enhance predator and parasitoid communities, can also provide suitable habitats for the targeted pest.

Cabbage stem flea beetle is univoltine i.e., it completes its life cycle within one year.¹⁶ The adults arrive in the newly sown oilseed rape field in autumn. They cause damage by feeding on seedlings.^{16, 25} The larvae are also responsible damage. Females lay eggs in proximity of plants, then, the larvae migrate to oilseed rape plants and enter via a petiole. They develop inside the plants and mine them. This reduces plant vigor and exposes them to frost damage and disease, which limits the overwintering survival.^{16, 25} At the end of winter, the larvae leave the plants and pupate in the soil for a few weeks in the spring. The new adults emerge in late spring²⁶ and they feed on the leaves, stems and pods of oilseed rape and other Brassicaceae, but they do not cause damage at this time.²⁵ In mid-summer, during the hottest period of the year, CSFB move to aestivation habitats, where they hide in the vegetation or the litter to aestivate.^{25, 26} During this diapause period, their activity is minimal and their rates of metabolism decrease to very low levels.²⁶⁻²⁸ According to published studies, forest edges are the principal shelter used by CSFB for aestivation, although some individuals are found in oilseed rape crop residues in fields.^{26, 29} However, the particular characteristics rendering a site suitable for CSFB aestivation

remain largely unknown. We hypothesized that CSFB might use flower strips as shelters during aestivation because these structures have several characteristics that appear to be important for aestivation. For example, the presence of vegetation and litter may reduce temperature variations, and protect CSFB from desiccation and predation while in diapause. However, factors more complex than the simple presence or absence of vegetation and litter may be involved: the percentage of soil covered by litter and vegetation, litter thickness or the diversity of the vegetation may also play a role. Furthermore, landscape characteristics, such as winter oilseed rape cover, considered as the source of CSFB and the woodland cover (the putative principal shelter of these beetles) may also influence the distribution of CSFB between aestivation sites. Indeed, these elements could lead to dilution or concentration effects on pests.³⁰

The aim of this study was to assess the extent to which flower strips can be used by CSFB as a habitat for aestivation in an agricultural landscape. More specifically, we addressed the following issues:

1. We determined the extent to which flower strips could constitute a habitat for the aestivation of CSFB through comparison with woodland edges, the principal aestivation habitat identified in published studies.
2. We investigated whether the composition of the surrounding landscape influences the distribution of CSFB between their refuges.
3. We investigated the characteristics of the local habitat associated with a high abundance of aestivating CSFB.

2 MATERIALS AND METHODS

Study site selection

The study was conducted in the south-western part of the Paris Basin (Fig. 1) in 2021, the most important agricultural area for arable crops production in France. The landscape in this area is characterized by a large-scale mosaic of arable crops with a few, scattered semi-natural habitats, such as woodlands. We selected 14 sites all containing the three habitat types we wanted to study within a radius of 1 km.

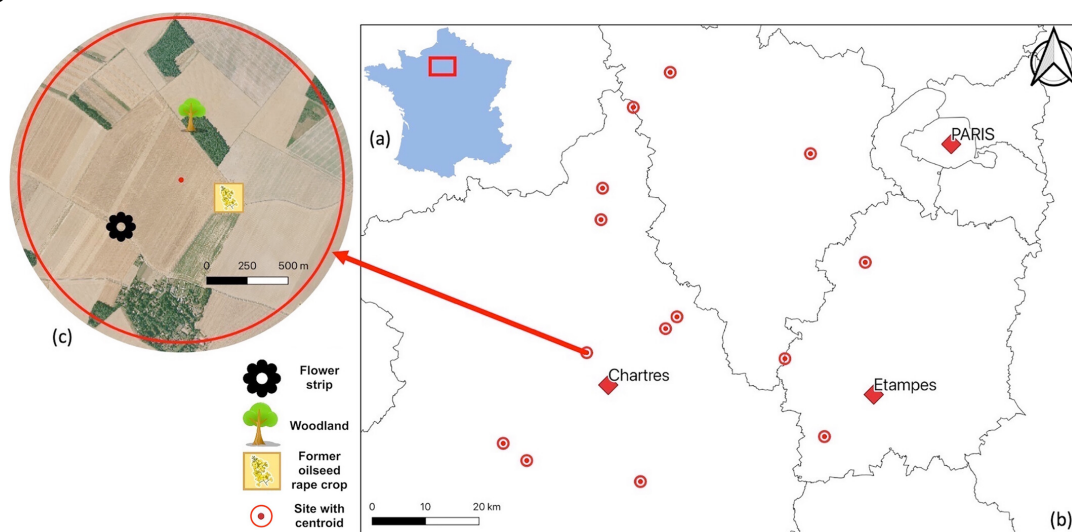


Figure 1. Location of the sampling region in northern France (a) and the 14 sites (red circles) in which the emergence of cabbage stem flea beetles was monitored (b). Magnification shows a site in more detail, to provide an example of the position of the three habitat types sampled in this study i.e., a former oilseed rape crop, a perennial flower strip and a deciduous woodland edge (c).

The three habitat types selected were: (i) fields in which a winter oilseed rape crop had recently been harvested (i.e., former oilseed rape crop) to demonstrate that CSFB leave the crop for aestivation sites after harvest; shallow tillage had recently been performed in 11 of these 14 fields; (ii) perennial flower strips sown with 42 indigenous species in late 2018 or 2019 and mown only once in winter (details Supporting Information Table [S1](#)) and (iii) a deciduous woodland edge. Within a site, the different habitat types were separated by an average of 557 ± 64 m [min: 31 m; max: 1624 m], more details are given in Supporting Information Table [S2](#). The perennial flower strip contained the flowering herbaceous plants generally promoted in environmental policies and studied across Europe.^{14, 31} Woodland edges were identified according to the definition of Matlack and Litvaitis,³² as ‘an abrupt transition between two relatively homogeneous ecosystems, at least one of which is a forest’. We considered flower strips and woodlands as semi-natural habitats as these perennial elements were not or only minimally managed.

Insect sampling

The emergence of CSFB from aestivation was monitored from mid-August to mid-October 2021. This period was chosen because adult CSFB are already present in their aestivation habitats by August and they then migrate to newly sown oilseed rape fields from late August to early September.^{25, 26} We installed 42 emergence traps (14 sites \times 3 habitat types) as illustrated in Fig. [2](#). These comprised a floorless closed tent ($60 \times 60 \times 60$ cm) with flaps at the bottom, which were buried to prevent the arthropods from escaping. An emergence trap covered a surface of 0.36 m^2 (Supporting Information Fig. [S1](#)). A collecting bottle was located at the apex of the trap, and was half-filled with 30% propylene glycol (IUPAC name: propane-1,2-diol) and soap (2 cL/L). The emergence traps were checked approximately every 3 weeks. The contents of the collecting bottle were removed and replaced at every visit. The arthropods caught were transferred to 70% ethanol solution and *P. chrysocephala* individuals were identified with the ‘Subfamily Galerucinae, keys to British species of tribe Alticini’ key adapted by Mike Hackson from the German key of Arved Lompe,³³ and counted.

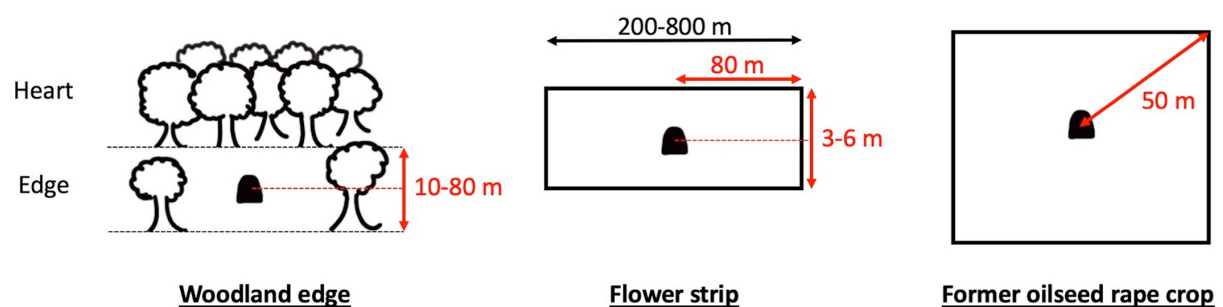


Figure 2. Placement of the emergence traps within the different habitat types studied: in woodland edges and flower strips. The trap was placed in the middle of the habitat, while in former oilseed rape crops, it was placed at 50 m in diagonal from the field corner to avoid edge effects.

Description of the habitats

In each habitat type, we recorded the characteristics of the local habitat (Table [1](#)) in a $50 \text{ cm} \times 50 \text{ cm}$ quadrat placed at 1 m from the emergence trap. We characterized the various elements of ground cover (vegetation, litter, bare soil and stones) likely to influence the microclimate or to form a hiding place for insects. We used a method inspired by Braun-Blanquet^{34, 35} to estimate the percent cover of these elements. We determined the mean vegetation height by measuring the maximum height of three plants within the quadrat. The same was done for litter thickness, by measuring the thickness at three points within the quadrat.

Table 1. Variables used to describe the local characteristics of each habitat studied, showing the mean \pm SEM and the range [min, max] measured in each type of habitat at the 14 study sites in France.

Category	Variable	Scale or unit	Flower strip	Former oilseed rape	Woodland edge
<i>Local habitat characteristics (measured in a 50 cm \times 50 cm quadrat)</i>					
Soil surface	Surface covered by stones	Percentage of the area	1 \pm 1 [0, 8]	1 \pm 3 [0, 45]	0.4 \pm 0.2 [0, 2]
	Surface covered by bare soil	Percentage of the area	3 \pm 2 [0, 30]	8 \pm 9 [0, 86]	7 \pm 3 [0, 40]
Litter	Surface covered by litter	Percentage of the area	60 \pm 11 [3, 100]	17 \pm 11 [10, 100]	76 \pm 9 [15, 100]
	Litter thickness	cm	5 \pm 1 [0.1, 8]	1 \pm 0.1 [0.1, 3]	2 \pm 0.3 [0.1, 4]
Vegetation	Surface covered by moss	Percentage of the area	Not measured	Not measured	4 \pm 2 [0, 22]
	Surface covered by vegetation	Percentage of area	71 \pm 6 [30, 100]	8 \pm 7 [1, 90]	63 \pm 7 [20, 96]
	Number of species	Number of species	5 \pm 1 [1, 10]	1 \pm 0.3 [1, 4]	3 \pm 0.3 [1, 6]
	Percentage of monocotyledons	Percentage of vegetation	2 \pm 2 [0, 25]	2 \pm 7 [0, 100]	7 \pm 7 [0, 97]
	Mean height	cm	74 \pm 7 [25, 112]	2 \pm 1 [0.5, 17]	10 \pm 1 [5, 24]
<i>Characteristics of the global habitat (for woodland edges only)</i>					
Vegetation	Mean tree circumference	cm	Not measured	Not measured	59 \pm 7 [13, 107]
Openness and width	Horizontal openness	Percentage openness	Not measured	Not measured	41 \pm 10 [0, 100]
	Canopy openness	Percentage openness	Not measured	Not measured	27 \pm 6 [0, 75]
	Width of woodland edge	m	Not measured	Not measured	47 \pm 6 [10, 80]

- Note: Further details are provided in Supporting Information Tables [S3](#), [S4](#) and [S5](#).

In woodland edges, we also characterized the woodland itself in 15 m × 15 m quadrats. We measured the mean tree circumference by measuring the diameter at breast height (approximately 1.3 m above ground) of five trees. We defined two types of openness: (i) the canopy openness as the vertical openings through the top of the trees that allow light entrance; (ii) the horizontal openness as the ease of access to the woodland, related to vegetation density. Both openness percentages were estimated as for local habitat characteristics. The width of the woodland edge was also measured; i.e., the width from the border of the edge to the beginning of woodland interior. We identified the woodland interior as a more homogenous ecosystem with a higher density of trees, compared with the edge.³²

All assessments were performed by the same observer. The variables are summarized in Table 1 and further details are given in Supporting Information Tables S3, S4 and S5.

Landscape characteristics

We investigated the effect of landscape composition on the number of CSFB emerging from aestivation and caught in the emergence traps per habitat at different scales, by describing the local landscape in four circular sectors of radius 250, 500, 750 and 1000 m (Supporting Information Fig. S2). We characterized two elements of the landscape: the proportion of fields under oilseed rape harvested in 2021 (before the beginning of the study) and the proportion of woodland. The percentage of fields formerly under oilseed rape was accessed using satellite images obtained with EO Browser from the Sentinel-hub website.³⁶ The percentage of the woodland cover was obtained with the available land cover BD TOPO (vegetation layer ver. 3.0, 2020), a vector map with a resolution of 1 m.³⁷ We did not take into account the perimeter of the woodland as it was correlated with the surface. We combined broadleaved, coniferous and mixed forests with a closed canopy, and woodlands together under the term ‘woodlands’. Landscape analyses were performed with QGIS 3.10.10-A Coruña.

Statistical analysis

All statistical analyses were performed with R statistical software version 4.0.4. Before beginning the analyses, we calculated Moran's I coefficient to evaluate the possible presence of spatial autocorrelation in the abundance of emerged CSFB. No spatial autocorrelation in the abundance of emerged CSFB between the centroids of the sites was detected (Supporting Information Table S6).³⁸

Effects of site, type of habitat and landscape composition at different scales

We first analyzed the effects of site and habitat type on the number of aestivating CSFB per trap over the sampling period with a generalized linear model assuming a negative binomial distribution, ‘nbinom2’, with ‘Template Model Builder’ (glmmTMB package³⁹) with only fixed effects. The negative binomial distribution was chosen to account for overdispersion. The fit of the model was checked using DHARMA (package ‘DHARMA’⁴⁰) to look for the presence of significant deviations in residual plots (QQ plot and residual vs. predicted). Then, the possible correlations between covariates were assessed by calculating the variance inflation factor (VIF) with the ‘vif’ function of the ‘car’ package⁴¹; all covariates with a VIF less than 2.5 were retained.⁴² Wald chi-squared tests (type II sums of squares) were performed with the ‘ANOVA’ function (package ‘car’⁴¹) to calculate *P*-values. *Post hoc* analyses were then performed, by calculating the estimated marginal means and with pairwise comparison using the CLD function (package ‘emmeans’⁴³).

We then analyzed the effect of landscape composition (percentage of woodland cover and former oilseed rape crop cover), at different scales, on the numbers of CSFB aestivating in flower strips and woodland edges. For each habitat type, we performed a generalized linear model assuming a negative binomial distribution, ‘nbinom2’, with ‘Template Model Builder’, with only fixed effects, for each radius, to avoid collinearity: in total, four models were done for each type. The models were verified and analyzed the same way than the model testing the effect of site and habitat type.

Combined effects of local habitat characteristics and landscape on CSFB abundance

We analyzed the combined effects of local habitat characteristics (Table 1) and of landscape composition (percentage of woodland cover and former oilseed rape crop cover as described in section 2.4) on the CSFB abundance within woodland edges. As suggested by Ballot *et al.* (in press), we refined the selection of variables by discarding those with limited variability: quantitative variables with variation coefficients below 20% and qualitative variables with a dominant category accounting for more than 80% of the sample. We performed univariate partial linear squares regression, PLSR1⁴⁴ (package ‘plsRglm’⁴⁵) because the number of variables exceeded the number of observations and our variables were correlated (Supporting Information Fig. S3).^{46, 47} We used two indices to validate the PLSR1: R^2Y , the proportion of the variance of the dependent variable explained by the model, and Q^2 , the proportion of the variance of the response predicted by the model, obtained by a cross-validation procedure. For a variable to be included in the model, the factor concerned had to have a $Q^2 > 0.0975$.⁴⁶ We also tested the normality of the residuals from the PLSR1 with a Shapiro–Wilk test. We ranked the variables according to their variable importance in projection (VIP) scores. This VIP criterion measures evaluates the importance of each variable for predicting the dependent variable from its importance in the building of each latent variable and the correlation between these latent variables and the dependent variable. Higher VIP values are associated with more important variables. Variables with a $VIP > 1$ were considered to be the most important variables for Y prediction.^{46, 48}

3 RESULTS

In total, we collected 304 adult CSFB between mid-August and mid-October 2022 (Supporting Information Fig. S4; detailed data in Supporting Information Table S7).

Cabbage stem flea beetles aestivate in woodland edges but not in flower strips

We found no significant difference between the 14 sites on the number of aestivating CSFB (glmmTMB: $n = 42$, $\chi^2 = 12.50$, d.f = 13, $P = 0.487$). However, type of habitat had a significant effect (glmmTMB: $n = 42$, $\chi^2 = 25.14$, d.f = 2, $P < 0.001$). A *post hoc* test showed that the mean number of aestivating CSFB was significantly lower in flower strips (with predicted mean = 2.0 ± 0.61 SEM individuals) than in woodland edges (13.54 ± 3.39 individuals). No significant difference was observed between the mean number of individuals in former oilseed rape crops (3.51 ± 1.01) and that in flower strips (Fig. 3).

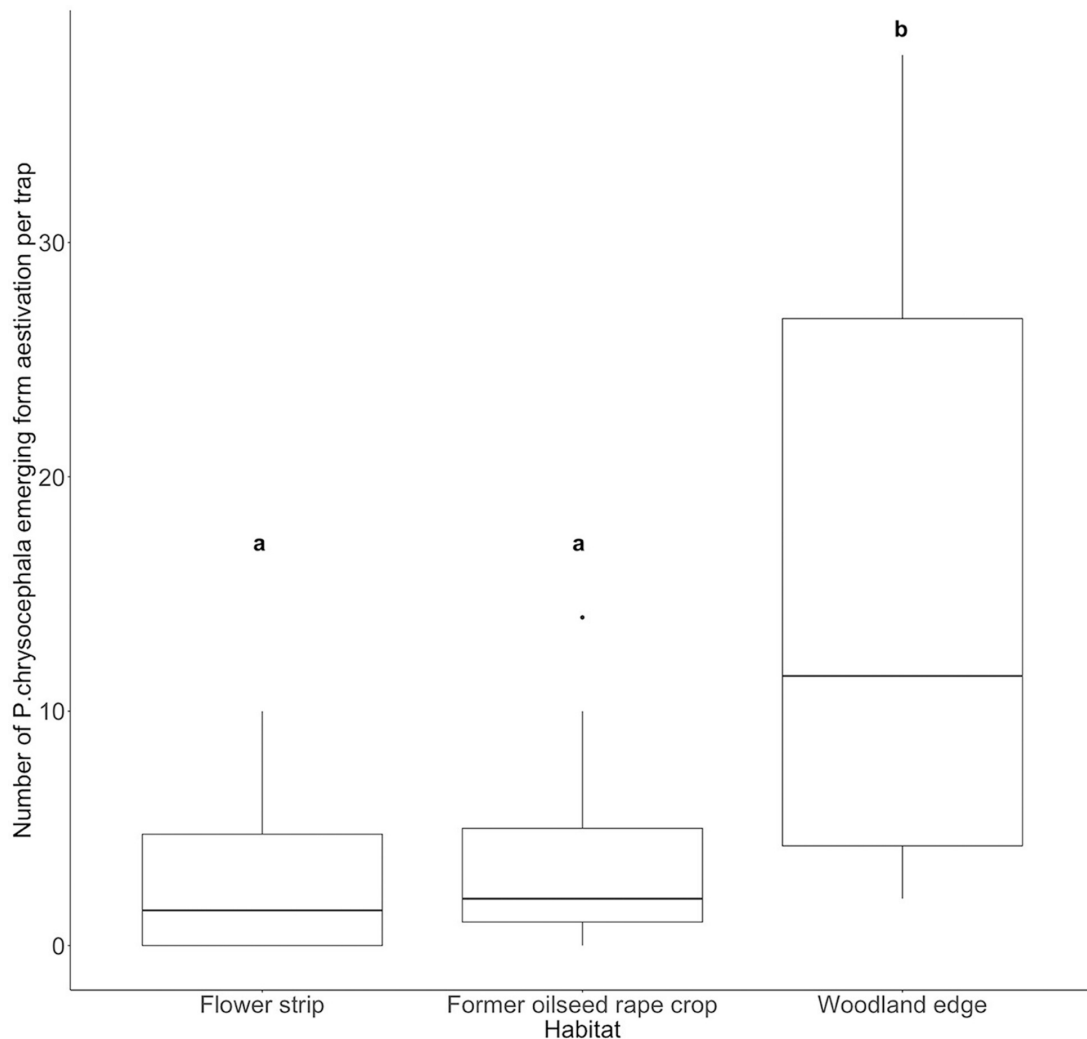


Figure 3. Mean total number of cabbage stem flea beetles (*Psylliodes chrysocephala*) emerging from aestivation in three types of habitat present in each of 14 sites sampled in France, summed over the sampling period (from August to October 2021). Different letters above the boxplot indicate groups significantly different ($P < 0.05$) in a post hoc test. The upper whisker extends from the hinge to the largest value no further than $1.5 \times$ inter-quartile range (IQR) from the hinge. The lower whisker extends from the hinge to the smallest value at most $1.5 \times$ IQR of the hinge. Data beyond the end of the whiskers are outliers.

The percentage of the landscape under woodland has an effect only at the smallest scale

The abundance of CSFB emerging from aestivation in woodland edges decreased significantly with increasing percentage woodland within a 250 m radius (Table 2). This effect was the only significant effect of landscape on the number of CSFB trapped in woodland edges and flower strips observed. In woodland edges, we also found a positive trend of the percentage of former oilseed rape cover within a 250 m radius on the abundance of CSFB. Model quality (assessed with the corrected Akaike information criterion, AICc) was highest (lowest AICc) at the smallest spatial scale (250 m radius) and decreased with increase in spatial scale to 1000 m.

Table 2. Relationships between abundance of cabbage stem flea beetles (CSFB, *Psylliodes chrysocephala*) emerging from woodland edges and the percentage former oilseed rape (OSR) cover and percentage woodland cover at different scales ('radius') within the landscape (glmmTMB: $n = 14$).

Response variable	Radius	Explanatory variable (%)	d.f.	Estimate (\pm SEM)	P-value	χ^2	AICc
CSFB in woodland edges	250 m	Former OSR	1	0.013 \pm 0.008	0.082 •	3.02	108
		Woodland	1	-0.044 \pm 0.015	0.003 **	8.87	
	500 m	Former OSR	1	0.025 \pm 0.017	0.141	2.16	114
		Woodland	1	-0.028 \pm 0.026	0.267	1.23	
	750 m	Former OSR	1	0.023 \pm 0.031	0.452	0.57	116
		Woodland	1	-0.027 \pm 0.036	0.451	0.57	
	1000 m	Former OSR	1	0.026 \pm 0.051	0.616	0.39	117
		Woodland	1	-0.004 \pm 0.044	0.932	0.01	

- *Note:* Significant results are shown in bold typeface. Significance levels: $P < 0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. The 'Estimate' corresponds to the slope of each variable in the regressions. Corrected Akaike information criterion (AICc) is also presented.

Effect of local habitat characteristics on cabbage stem flea beetle aestivation in woodland edges

The abundance of CSFB in flower strips was low, with little variability between strips (Fig. 3). However, there were differences in local characteristics between strips (Table 1 and Supporting Information Table S3). We therefore concluded that CSFB aestivate at very low densities in flower strips irrespective of their characteristics. We focused further analyses on woodland edges, in which CSFB abundance was more variable (Fig. 3), to try to identify the characteristics of the landscape or habitat favoring or reducing the likelihood of the presence of aestivating CSFB. The landscape within a radius of 250 m was also taken into account, because an effect of woodland percentage was previously detected for the smallest radius considered (250 m).

We retained only the first component of the PLSR1, as this was the only component with a $Q^2 > 0.0975$. The model had a Q^2 value of 0.51 and accounted for 75% of the variance of CSFB emergence from woodland edges. Seven variables had VIP scores above 1 (Table 3) and were considered to be the most important variables for predicting CSFB abundance. Mean tree circumference, percentage horizontal openness, percentage canopy openness, percentage litter and percentage of OSR cover within a radius of 250 m around the trap also had positive effects on CSFB abundance. This abundance was also inversely related to the percentage bare soil and percentage woodland within a radius of 250 m (Table 3).

Table 3. Combined effects of local habitat characteristics and landscape on cabbage stem flea beetle (*Psylliodes chrysocephala*) emerging from woodland edges following aestivation (partial linear squares regression PLSR1, $n = 14$).

Landscape parameters and habitat characteristics (explanatory variables)	Estimate	VIP
Percentage of former oilseed rape cover in 250 m radius	0.11	1.50
Mean tree circumference	0.10	1.50
Percentage of woodland cover in 250 m radius	- 0.18	1.46
Surface covered by bare soil	- 0.18	1.25
Horizontal openness	0.06	1.22
Canopy openness	0.10	1.16
Surface covered by litter (or dead plants)	0.06	1.10
Number of plant species	- 1.12	0.83
Mean vegetation height	- 0.26	0.74
Litter thickness	0.98	0.71
Surface covered by stones	1.49	0.63
Width of woodland edge	0.04	0.57
Surface covered by vegetation	0.03	0.39
Surface covered by moss	- 0.08	0.33
Percentage of monocotyledons	0.005	0.07

- *Note:* The ‘Estimate’ corresponds to the slope of the parameters in the regression. The variables are ranked by decreasing order of variable importance in projection (VIP) scores. Variables with a VIP > 1 are considered to be the most important explanatory variables.^{46, 48} The estimates with a VIP > 1 are shown in bold typeface.

4 DISCUSSION

Published studies have reported that semi-natural habitats (SNH) can support arthropod species considered beneficial for crops, such as pollinators and natural enemies by enhancing both their abundance and diversity.^{10, 13} However, there are some concerns about possible negative effects of SNH if they also benefit crop pests.^{12, 13, 49} We investigated the effect of the presence of flower strips on CSFB aestivation. We found that the perennial flower strips in our study area did not constitute a significant aestivation site for CSFB. The low density of CSFB emerging from the flower strips cannot be explained by a lack of movement of the population of CSFB during the aestivation period. Indeed, they were also less present in the fields formerly grown with oilseed rape, but emerged in high abundance from woodland edges. This implies that the CSFB had left the fields where they emerged from pupation to go to aestivation sites. The representativeness of the sampling method may be questioned in view of the small numbers of CSFB trapped. However, Sutter *et al.*⁵⁰ found similar densities in their study on the overwintering of pollen beetle (*Brassicogethes aeneus*, Fabricius, 1775): in their emergence traps (50 × 50 cm; quite similar to ours), they counted a mean of 3.2 pollen beetles from traps positioned from the end of February to the beginning of June. Furthermore, it is unlikely that some CSFB remained in the fields and flower strips but were not trapped, because the

emergence traps were left on the ground for a long time period, covering the reported period of emergence, i.e., late August to early September.^{25, 26} We observed the maximum of emergence during the first 3 weeks of September (Supporting Information Fig. S4).

Most of the CSFB emerging from aestivation were caught in traps placed in woodland edges. This result supports the findings of Bonnemaïson and Jourdheuil²⁶ that woodland edges are the main aestivation site for CSFB. However, other semi-natural habitats, such as woodland interiors or hedgerows could also constitute aestivation sites. More research is needed to explore this. We also cannot exclude the possibility that CSFB may aestivate in flower strips in larger numbers in extremely simplified landscapes devoid of woodland (unlike our study sites). However, the lack of an effect of the percentage woodland on the abundance of CSFB in flower strips, regardless of the scale considered, suggests that even if there is very little and distant woodland, CSFB nevertheless prefer to aestivate in woodlands. Similar results have been reported for another oilseed rape pest, the pollen beetle, which overwinters more rarely in sown semi-natural habitats, such as flower strips, than in forest edges or winter oilseed rape fields.⁵⁰

The population of CSFB in woodland edges varied considerably between sites. These differences probably reflect local characteristics, given the contrast between woodland edges. However, we recognize that the presence of only one trap in each habitat at each site makes it impossible to assess within-site variability. We suppose that woodland edges may have several characteristics that are essential for CSFB during their aestivation. Flower strips may have similar micro-habitat characteristics, with the presence of vegetation and litter, for example, but the global habitat differs considerably between flower strips and woodland edges, particularly due to the presence of trees.

The abundance of CSFB in flower strips was too low for us to be able to identify favorable local habitat characteristics, but it was possible for woodland edges. The most favorable woodland edge habitats for CSFB aestivation were those with the most litter, the least bare soil and the most available light (a positive effect of canopy opening). These findings suggest that vegetation density may be an important factor in aestivation site choice. In flower strips, vegetation density affects litter density (especially if mowing residues are left in place), the percentage of bare soil, and light availability. However, increasing vegetation density might result in larger amounts of litter, favoring aestivation, but lower levels of available light, which may be unfavorable for aestivation. The major impact of litter thickness may be related to the behavior of this pest, as reported by Bonnemaïson and Jourdheuil²⁶ following observations with a controlled manipulation, in which the CSFB preferred to hide in layers of muslin rather than in plants. Similar behavior was also reported by Rusch *et al.*³ for overwintering pollen beetles. Maudsley *et al.*⁵¹ found a similar effect in carabids and suggest that litter may provide a more sheltered microclimate, with bare ground providing a poor overwintering site for beetles. This is consistent with the negative effect of the percentage bare soil observed here. However, Sutter *et al.*⁵⁰ reported a negative effect of percentage litter and a positive effect of bare soil on overwintering pollen beetles.

We also observed an effect of landscape corresponding to the dilution or concentration effects on pest abundance described by Scheiner and Martin³⁰: a high percentage of woodland dilutes the population of aestivating CSFB, whereas a high percentage of fields formerly under oilseed rape, a source of the pest, creates pressure on aestivation sites. Other pests of oilseed rape are sensitive to the dilution or concentration effects, such as the pollen beetles. Schneider *et al.*⁵² also observed a decrease of the abundance of pollen beetles within the fields while the proportion of oilseed rape increased in the landscape (1 km radius). We detected no effect of

landscape at scales of more than a 250 m radius. This suggests that either this pest may have a low dispersal capability during this period or that CSFB does not disperse further than needed and aestivates in sites which are close to where they emerge from pupation. This may be because CSFB need to leave the fields and find a suitable aestivation site very rapidly.²⁶ However, these beetles are known to cover large distances when they leave their aestivation sites in search of newly sown oilseed rape, although the fields close to aestivation sites are at greater risk of attack.²⁶

In terms of the possible impact on agriculture, we show here that flower strips do not act as a shelter for CSFB under the conditions studied. This is good news, given the fears that SNH could act as a shelter for pest species reported by Tschardt *et al.*¹² and which come mainly from the farmers. The confirmation that CSFB mostly aestivate in woodland edges is also of potential importance in terms of the positioning of oilseed rape fields within the landscape. Nevertheless, additional information, concerning CSFB mortality during aestivation and rates of dispersal from aestivation sites to newly sown oilseed rape fields, will be required for the integration of this knowledge into integrated cropping system recommendations.

5 CONCLUSION

We show here that CSFB mostly utilize woodland edges for aestivation and far less aestivate in flower strips. CSFB abundance in woodland edges was influenced by landscape composition at a small scale (250 m radius). Aestivation CSFB densities were also positively influenced by some local and global habitat characteristics, such as the litter cover or the openness of the woodland edges. Our results confirm previous observations, which can now be taken into account in future studies on the management of CSFB. Indeed, it is important to consider the proximity of new crops of OSR to aestivation sites to limit damage due to this pest. Our principal finding — that this pest does not use flower strips for aestivation — is good news, favoring further promotion of the use of such habitats in agri-environmental schemes.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could appear to influence the work reported in this paper.

AVAILABILITY OF DATA AND MATERIALS

The datasets generated and analyzed during the current study are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.7181680>.

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Supplementary Information

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Unlike woodland edges, flower strips do not act as a refuge for cabbage stem flea beetle aestivation

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TABLE S1. List of the plant species sown in perennial flower strips sampled in our study to understand the role of flower strips in supporting aestivation of cabbage stem flea beetles. The flower strips measured 3 to 6 m wide and 200 to 800 m long (surface of the flower strips: min: 1 067 m²; max: 3 600 m²; mean: 2 044 m²).

Binomial name	Perenniality
<i>Achillea millefolium</i>	perennial
<i>Alliaria petiolata</i>	biennial
<i>Anthemis tinctoria</i>	perennial
<i>Anthriscus sylvestris</i>	perennial
<i>Barbarea vulgaris</i>	biennial
<i>Bellis perennis</i>	perennial
<i>Carum carvi</i>	biennial
<i>Centaurea cyanus</i>	annual
<i>Centaurea scabiosa</i>	perennial
<i>Cichorium intybus</i>	perennial
<i>Daucus carota</i>	biennial
<i>Echium vulgare</i>	biennial
<i>Festuca arundinacea</i>	perennial
<i>Galium mollugo</i>	perennial
<i>Geum urbanum</i>	perennial
<i>Glechoma hederacea</i>	perennial
<i>Hesperis matronalis</i>	biennial
<i>Hypericum perforatum</i>	perennial
<i>Knautia arvensis</i>	perennial
<i>Leucanthemum vulgare</i>	perennial
<i>Lotus corniculatus</i>	perennial
<i>Malva sylvestris</i>	perennial
<i>Medicago sativa</i>	perennial
<i>Melilotus officinalis</i>	perennial
<i>Onobrychis viciifolia</i>	perennial
<i>Origanum vulgare</i>	perennial
<i>Pastinaca sativa</i>	biennial
<i>Pimpinella saxifraga</i>	perennial
<i>Plantago lanceolata</i>	perennial
<i>Ranunculus acris</i>	perennial
<i>Reseda luteola</i>	biennial
<i>Securigera varia</i>	perennial
<i>Senecio jacobaea</i>	perennial
<i>Stellaria media</i>	annual
<i>Tanacetum vulgare</i>	perennial
<i>Taraxacum officinale</i>	perennial
<i>Trifolium repens</i>	perennial
<i>Trisetum flavescens</i>	perennial
<i>Veronica hederifolia</i>	annual
<i>Veronica persica</i>	annual
<i>Vicia sativa</i>	annual

TABLE S2. Average distances between the different habitat types studied within the 14 sites: flower strip, woodland edge and former oilseed rape crops (i.e., where the oilseed rape had recently been harvested). Each site comprised the three habitat types within a radius of 1 km. The average distances are presented with standard error of mean (SEM), the minimum and the maximum values (n = 14).

Distance between	Mean \pm SEM (m)	Minimum distance (m)	Maximum distance (m)
Flower strip to Former oilseed rape	288 \pm 109	32	1381
Flower strips to Woodland edge	727 \pm 105	31	1624
Woodland edge to Former oilseed rape	656 \pm 85	63	1133
Mean	557 \pm 64	31	1624

TABLE S3. Habitat characteristics of the flower strips measured at each site and used to describe the local habitat. The different characteristics were related to the soil surface, to the litter and to the vegetation.

Site	Local habitat characteristics							
	Soil surface		Litter		Vegetation			
	Surface covered by stones (%)	Surface covered by bare soil (%)	Surface covered by litter (%)	Litter thickness (cm)	Surface covered by vegetation (%)	Number of species	Percentage of monocotyledons in vegetation (%)	Mean height (cm)
A	0	0	3	0.1	80	6	25	112
B	8	10	10	0.1	90	7	0	65
C	0	0	100	0.1	95	6	1	97
D	0	0	100	8	40	1	0	25
E	0	0	30	2	70	2	0	82
F	0	3	80	0.1	30	3	0	29
G	0	0	100	0.1	30	2	s	52
H	0	0	100	0.5	60	6	0	60
I	0	0	10	0.1	99	5	2	74
J	0	2	90	0.1	65	4	0	89
K	0	0	20	0.1	100	6	0	111
L	0	30	10	0.1	65	4	0	74
M	1	0	90	0.5	90	10	0	72
N	0	0	100	0.5	75	5	0	95

TABLE S4. Habitat characteristics in former oilseed rape crops measured at each site and used to describe the local habitat. The different characteristics were related to the soil surface, to the litter and to the vegetation. At the time of the sampling, no crop was present.

Site	Local habitat characteristics							
	Soil surface		Litter		Vegetation			
	Surface covered by stones (%)	Surface covered by bare soil (%)	Surface covered by litter (%)	Litter thickness (cm)	Surface covered by vegetation (%)	Number of species	Percentage of monocotyledons in vegetation (%)	Mean height (cm)
A	0	0	100	3	35	4	8	5
B	45	0	100	0.5	75	2	0	17
C	0	0	100	3	1	1	100	13
D	0	0	100	3	45	3	0	13
E	2	60	25	0.5	8	1	0	3
F	0	0	100	3	20	4	0	7
G	0	1	99	2	30	2	0	9
H	0	78	15	0.1	7	1	0	3
I	3	5	95	0.5	90	2	0	3
J	0	80	20	0.1	2	1	0	1
K	0	5	80	0.5	45	4	0	5
L	0	55	10	0.1	45	1	0	4
M	2	30	30	0.1	40	2	1	4
N	0	86	12	0.1	2	1	0	0.5

TABLE S5. Habitat characteristics of woodland edges measured in each site and used to describe the local and the global habitat. The different characteristics were related to the soil surface, to the litter and to the vegetation and to the “openness” and width of the woodland edges. Two types of openness were defined: (i) the canopy openness as the vertical openings through the top of the trees that allowed light entrance; (ii) the horizontal openness as the ease of access to the woodland, related to vegetation density. The width of woodland edges corresponded to the width from the border of the edge to the beginning of woodland interior.

Site	Local habitat characteristics									Global habitat characteristics			
	Soil surface		Litter		Vegetation					Vegetation	Openness and width		
	Surface covered by stones (%)	Surface covered by bare soil (%)	Surface covered by litter (%)	Litter thickness (cm)	Surface covered by moss (%)	Surface covered by vegetation (%)	Number of species	Percentage of monocotyledons in vegetation (%)	Mean height (cm)	Mean tree circumference (cm)	Horizontal openness (%)	Canopy openness (%)	Width of woodland edge (m)
A	0	4	15	0.1	2	96	3	97	11	39	80	25	50
B	0	0	100	4	0	92	2	0	10	107	30	0	25
C	0	2	98	1	0	35	4	0	24	45	0	25	20
D	1	30	50	0.5	0	35	3	0	6	39	60	25	60
E	0	5	20	3	10	50	3	0	17	41	0	25	35
F	0	40	20	0.1	22	40	6	5	13	84	30	25	80
G	0	0	100	2	1	70	1	0	8	88	100	75	65
H	0	0	100	2	0	20	3	0	5	54	60	25	25
I	0	0	100	2	0	40	3	0	8	84	30	23	80
J	2	3	90	0.5	3	85	2	0	8	42	30	25	40
K	2	0	90	0.5	15	85	5	0	12	84	60	50	70
L	0	0	100	0.5	0	95	2	0	7	61	0	0	40
M	0	1	99	3	0	85	3	0	11	47	100	50	55
N	0	10	80	0.5	0	55	2	0	5	13	0	0	10

TABLE S6. Summary of the Moran's Index calculated to evaluate the possible presence of spatial autocorrelation in the abundance of emerged cabbage stem flea beetles: the test for Moran's *I* coefficient was not significant.

Moran's Index	- 0.14653665
Expected Index	- 0.07692308
Variance	0.02091434
Z-score (Moran I statistic standard deviate)	- 0.48136
p-value	0.6303

TABLE S7. Total number of cabbage stem flea beetles counted in emergence traps at the various sites for each type of habitat, showing the total, the mean and the standard error of mean (SEM) per habitat type.

Site	Flower strip	Former oilseed rape crop	Woodland edge
A	6	1	17
B	0	2	26
C	10	5	5
D	1	2	2
E	0	1	4
F	2	10	6
G	4	4	38
H	0	2	29
I	0	5	27
J	5	0	29
K	2	0	23
L	0	14	2
M	5	1	6
N	0	6	2
TOTAL	35	53	216
MEAN	2.5	3.8	15.4
SEM	0.8	1.1	3.4



FIGURE S1. Emergence traps (60 x 60 x 60 cm) were placed in three habitats (here, forest edge). They were protected by three iron corners to prevent wild boars' damage.

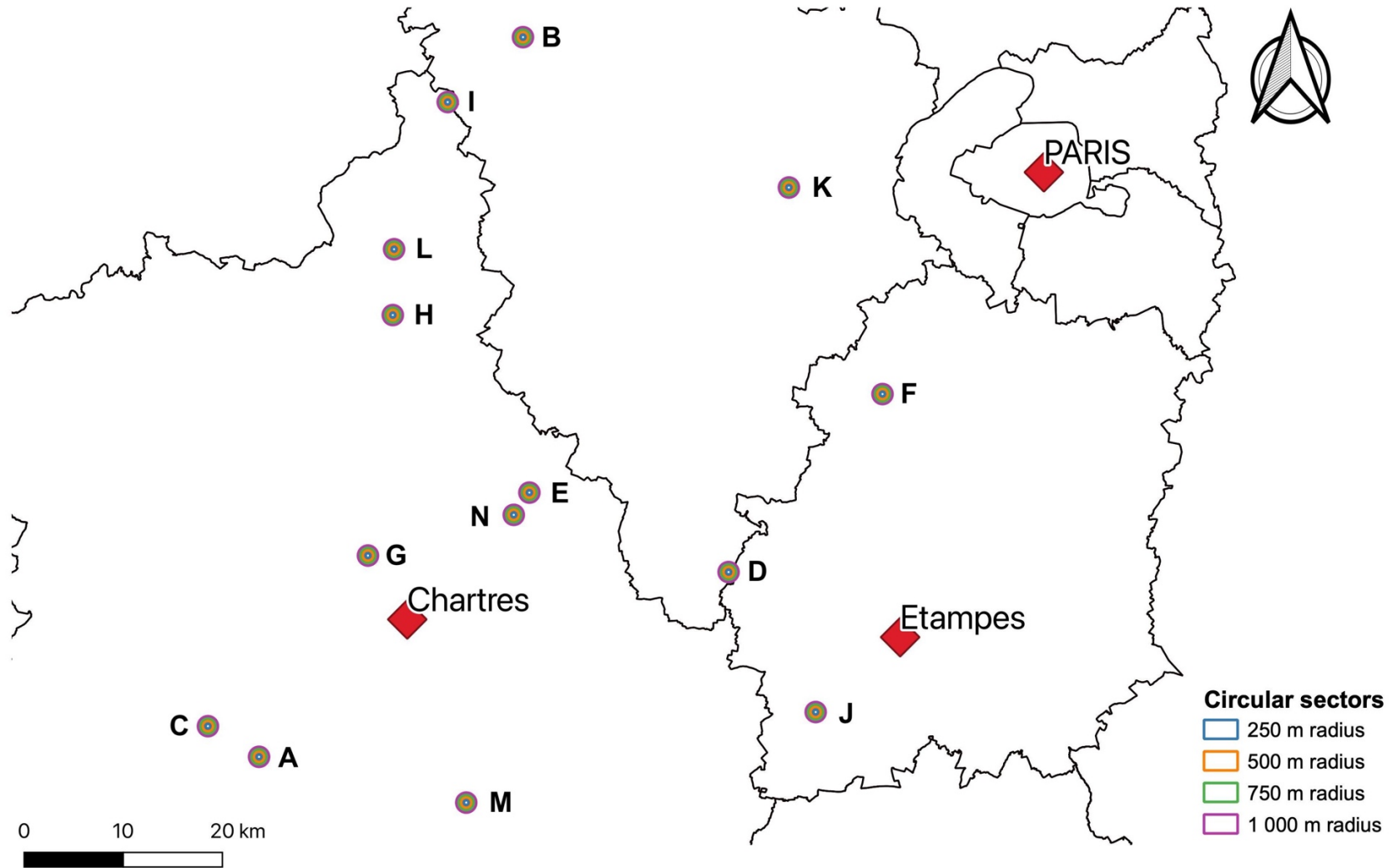


FIGURE S2. Location of the circular sectors around the traps within the woodland edges present in the 14 sites (letters), with four different radii, used for the analysis of the effect of the landscape composition on the number of cabbage stem flea beetles trapped. For the traps within the flower strips, a similar analysis was done. For the sake of clarity, the circular sectors are not represented, but the map is similar.

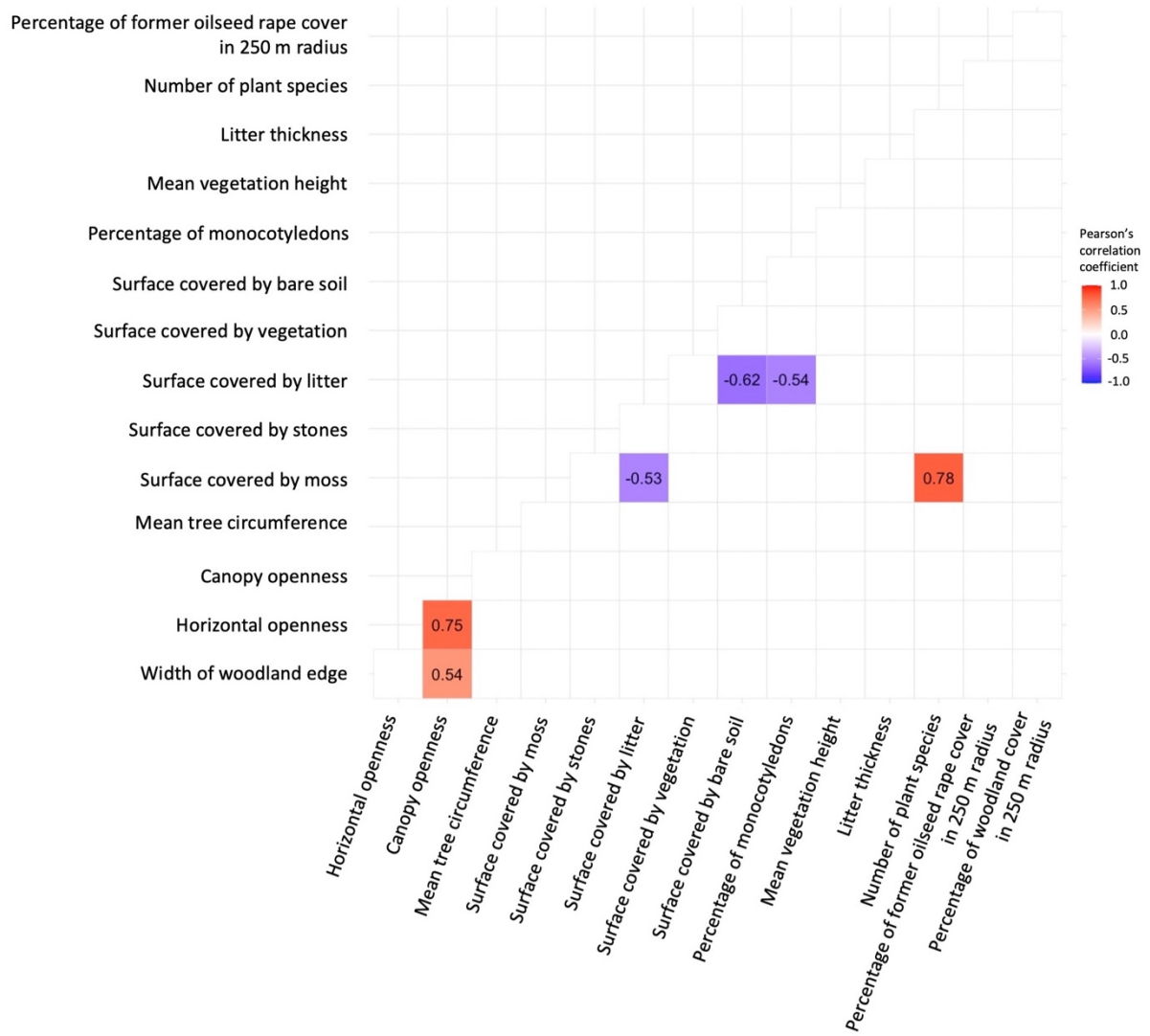


FIGURE S3. Correlation matrix between habitat and landscape characteristics. The only Pearson's correlation coefficients shown are those that were significant ($p < 0.05$). The colour represents the intensity of correlation and the sign of the correlation coefficient.

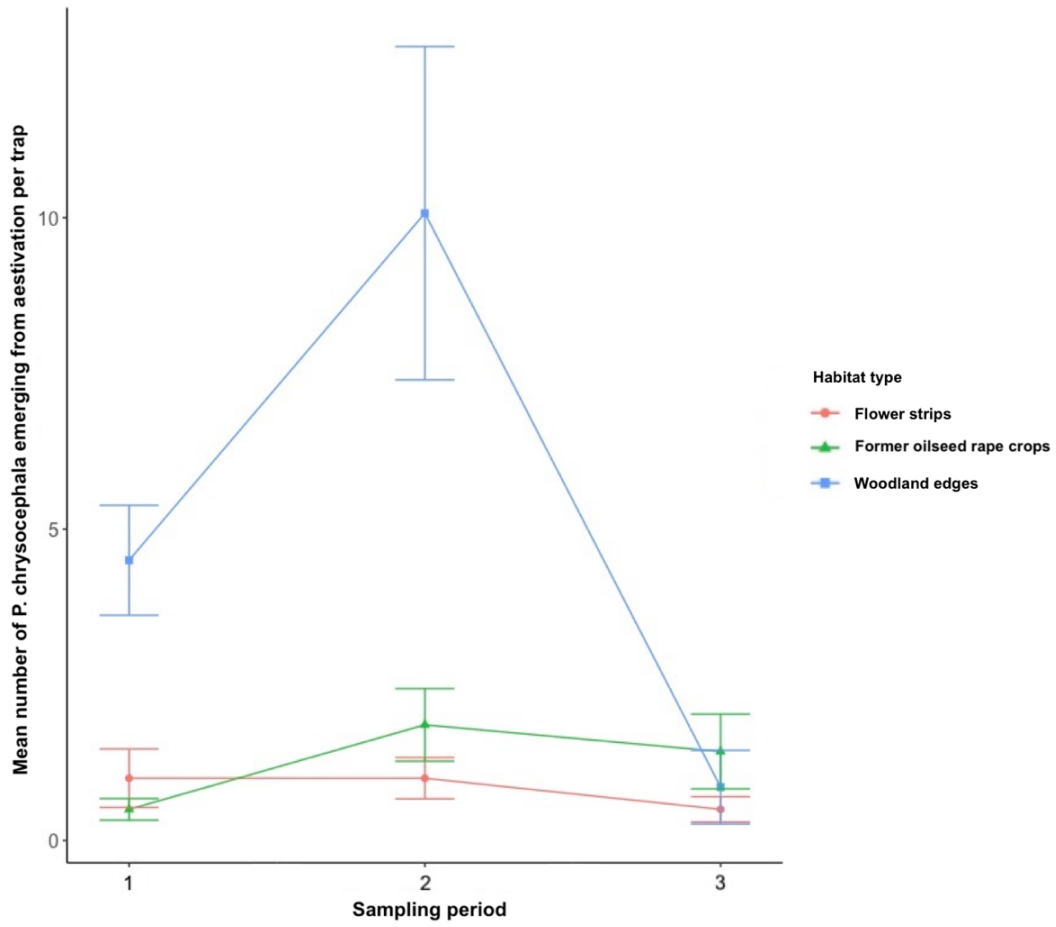


FIGURE S4. Mean number of cabbage stem flea beetles (*Psylliodes chrysocephala*) emerging from aestivation captured per trap in each type of habitat present in 14 sites sampled in France, over the sampling period from August to October (1: mid-August to beginning September; 2: to the end of September; 3: to mid-October)