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ORIGINAL ARTICLE

Comparing habitat and landscape effects on carabid (Coleoptera: Carabidae) traits in cereal fields and grasslands

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Abstract. Carabids are important natural biocontrol agents for pest regulation in agricultural landscapes. Their role in the ecosystem is related to functional traits, which are themselves filtered by both the degree of habitat disturbance and the landscape composition and configuration that distribute ecological resources. Here we aim at sorting out the influences of habitat and landscape context on carabid traits in permanent grasslands and winter cereal crops (wheat or barley). We sampled carabids in adjacent grasslands and cereal fields in three agricultural plains of south-eastern France. We analysed the links between carabid traits and their occurrence in the studied habitats using regression models. We also characterised the influences of habitat and landscape context on trait distribution using multivariate analyses. Polyphagous species were more likely than others to be shared by both adjacent grassland and cereal fields. Granivorous carabids were strongly related to grasslands, while predatory and polyphagous species were more often captured exclusively in cereal crops when exclusive to one habitat. Small apterous carabids were more likely to be found in grasslands only. Concerning the influence of the landscape, polyphagous species were related to cereal crops surrounded by higher grassland coverage or lower compositional heterogeneity. Smaller carabids were more likely to be found in the vicinity of high grassland coverage, and apterous carabids in grassland-dominated landscapes. Grasslands thus not only provide resource and habitat complementation for generalist carabid species from neighbouring croplands, but they also host distinctive species showing particular traits. It is therefore important to maintain or restore grasslands in agricultural landscapes to support species and functional diversity in farmland.

1. INTRODUCTION

The worldwide decline in biodiversity, particularly of insects, is closely linked to major changes in agriculture and climate over previous decades (Batáry et al., 2020; Raven & Wagner, 2021). Regarding agriculture, the intensification that has occurred since the 1950s has led to a widespread adoption of monoculture farming at the expense of grasslands, an intensive use of pesticides and fertilisers as well as the enlargement of fields through the removal of hedges and other field margins (Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020; Outhwaite et al., 2022). In temperate European regions, many lowland landscapes have been greatly simplified. Agricultural systems that were historically diversified in mixed farming quickly specialised in intensive cereal farming (mainly winter cereals and maize). At the same time, land consolidation has led to larger plots to optimise both land use planning and agricultural mechanisation. As a result, permanent grasslands have declined significantly, particularly through conversion to arable land (Peeters, 2012). By negatively impacting biodiversity, intensive agriculture also threatens ecosystem services, including those from which it benefits, such as biological control, pollination and nutrient recycling (Emmerson et al., 2016; Goulson, 2019; Jankielsohn, 2023). The principles and approaches of agroecology suggest to reduce inputs while implementing practices that valorise ecosystem services in order to alleviate the negative impact of farming activities on biodiversity and enhance the delivery of different ecosystem services, in particular biological control (Bommarco et al., 2013; Wezel et al., 2014, 2020).

Carabids are widely used as bioindicators of the impacts of farming practices and landscape on biodiversity (Winqvist et al., 2014; Gayer et al., 2019; Carbonne et al., 2022). This family of generalist predators and granivores is moreover often cited for its potential to deliver biological control on a variety of agricultural pests and weeds (Holland, 2002; Kulkarni et al., 2015).

Carabid species assemblage is mainly determined by the type and quality of the habitats (Tuck et al., 2014; Tsafack et al., 2019; Massaloux et al., 2020). According to disturbance caused by farming activities, cropland carabid beetles may alternatively spillover into and from neighbouring

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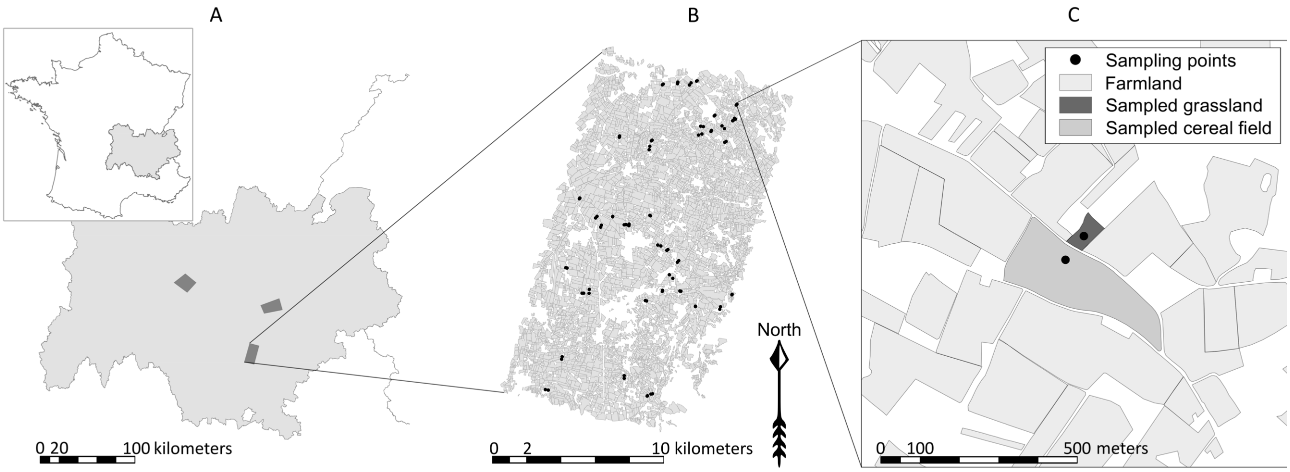

Fig. 1. Spatial locations of (a) the three study regions in the Auvergne Rhône-Alpes region, France, (b) the sampling points (either in cereal field or grassland) in the Rovaltain study region, and (c) example of neighbouring sampling points in paired cereal fields and grasslands.

habitats, such as grasslands or other crops (Schneider et al., 2016; Gallé et al., 2018).

Three carabid traits are of particular interest due to their link with dispersal ability and position in the trophic chain: size, wing development, and adult diet. Carabids in cropland and grassland show not only differences in species composition (Massaloux et al., 2020) but also some differences in the aforementioned traits. Small and winged species are, for instance, more abundant in frequently disturbed habitats, such as cereal crops, than in grasslands (Ribera et al., 2001; Pakeman & Stockan, 2014).

The landscape context is also known to act as an important filter for carabid traits. Homogeneous landscapes select against specialised traits, favouring generalist species (Gámez-Virués et al., 2015). Small species tend to dominate in croplands, whereas grassland areas support greater diversity of large and specialised predatory carabids (Duflot et al., 2014). Moreover, many carabid species found in grasslands depend on the landscape context. In landscapes dominated by grasslands, they are mostly grassland specialists, whereas more generalist species are found when the neighbouring landscape is covered by cropland (Batáry et al., 2007).

While many studies have focused on the influence of the habitat and landscape context on carabid traits, fewer have looked at species assemblages and traits in adjacent grasslands and cereal crops and their spillover between these habitats (e.g. Birkhofer et al., 2018). Moreover, landscape influence on carabid traits in adjacent crop fields and grasslands has received little attention so far.

In this study, we aimed to disentangle the effects of habitat and landscape on carabid traits in adjacent patches of two open habitats with contrasting disturbance regimes: cereal crops, with high level of agricultural disturbance, and grasslands, less frequently and intensively disturbed.

Our first objective was to find out the probability of carabid species to be shared by both habitats according to three functional traits: size, wing status, and diet. We hypothesise that more generalist and more mobile species, meaning polyphagous and/or macropterous carabids, are more likely than other species to be sampled in both paired cereal crop and grassland (hypothesis i).

Our second objective was to determine which functional traits are favoured in each habitat. Here we hypothesise that some functional groups are more likely to be encountered in one habitat, such as granivorous species in grasslands or macropterous species, supposedly more mobile, in cereal crops (hypothesis ii).

Finally, our third objective was to analyse whether the landscape context similarly influences the trait composition of carabid communities in permanent grasslands and in cereal crops. Here we expected lower grassland coverage in the surrounding landscape to reduce the occurrence of apterous and granivorous carabids found in the surveyed grassland habitats (hypothesis iii).

2. MATERIAL AND METHODS

2.1. Study regions and landscape characteristics

We studied the carabid assemblages in three agricultural plains (hereafter referred to as study regions) of around 200 km^2, dominated by conventional intensive agriculture, in south-eastern France (Fig. 1). The regions studied and the sampling design are the same here as in a previous publication (Massaloux et al., 2020). The Bièvre and Rovaltain study regions are characterised by the dominance of crops such as maize, winter wheat, winter barley and oilseed rape, whereas in Forez livestock systems dominate and permanent grasslands are more prevalent than cropped fields. Winter cereals have the highest share among croplands when considering the three study regions: they occupy respectively 26%, 18% and 8% of the whole studied area in Rovaltain, Bièvre and Forez. Furthermore, our three study regions are representative of a gradient of grassland coverage: they account for 3% of the whole area in Rovaltain, 16% in Bièvre and 27% in Forez.

Among the three study regions, ploughing is a common practice, as well as the use of chemical inputs. Winter cereals are mostly sown in autumn and harvested in the early summer while spring crops are sown in April and May and harvested in early autumn. One precautionary application of herbicides is commonly sprayed to winter cereals, before or after winter. One preventive spraying of fungicides is done during spring to avoid major fungal diseases. The use of pesticides can be more intense and is variable according to annual and local climate conditions. Permanent grasslands are mainly mown two to three times per crop season, and sometimes grazed.

2.2. Site selection

As we aimed at studying similarities of species assemblages in winter cereals and permanent grasslands embedded in similar landscape contexts, we selected field pairs consisting of a winter cereal field and a grassland which were in most cases adjacent to each other, or close enough to be in the same landscape context.

Sampled cereal fields were in majority cropped with wheat or barley and in fewer cases with triticale or rye. They were in almost all cases ploughed and farmed with chemical inputs. Grasslands were older than five years, with a cover dominance of monocots. Most of these grasslands were managed for hay, at least in spring, only 5 of them were grazed at the time of sampling.

2.3. Carabid beetles

2.3.1. Sampling

Carabid beetles were caught using pitfall traps in cereal fields and grasslands, with agreement of farmers. We placed the traps at least at 30 m to the land parcel border to limit edge effects and potential spatial auto-correlation between the traps of both adjacent habitats studied. In 2017, 82 sites were sampled, meaning 41 cereal fields and 41 grasslands. In 2018, there were 122 sites sampled (61 cereal fields and 61 grasslands, all distinct from those sampled in 2017). The distance between two different field pairs ranged from 270 m to 20.5 km and was higher than one kilometre in 97% of the cases, such as most of study pairs landscapes were not overlapping in a 500 m radius. A total of 58, 64 and 82 sites have been sampled respectively in Forez, Bièvre and Rovaltain, each study region being sampled each year. Within each of those 204 sites, one pitfall trap (10 cm diameter, half-filled with a 50% propylene glycol solution and a drop of detergent) was used to collect the ground beetles. Plastic roofs (22 cm diameter) were set about 5 cm above each trap to prevent flooding of traps during rainfall events. Each site have been sampled for two 7-day sampling sessions (14 days of cumulated trap exposure). The first sampling session took place between late April and early May, and the second between late May and early June. Whereas this strategy does not enable an exhaustive description of the communities of the sampled plots, it makes it possible to capture the general picture of species assemblage and most information about species and trait dominance at this time of the year when ground beetles are particularly active. Species identification followed the keys of Jeannel (1941, 1942) and Coulon et al. (2011). We chose to group the sampling data of the first and the second sampling period in order to summarise the diversity of carabids present each year in spring.

2.3.2. Species traits

Species were attributed traits (diet, wing status, size) according to available literature (Jeannel, 1941, 1942; Lindroth, 1992; Ribera et al., 2001; Holland, 2002; Homburg et al., 2014). We used three different carabid traits related to feeding and dispersal ability. All the 114 sampled species were associated with a modality of the three traits (Table S4). The adult diet was categorised into three values: granivorous, predatory and polyphagous for species which can feed on both vegetal and animal resources (Table 1). Wing status relates to the development of wings on adults; we distinguished apterous, macropterous and dimorphic species with adults of both phenotypes (Kromp, 1999).

Table 1. Carabid functional traits categories and their coding in GLMMs.

	Carabid life trait	Coding
Adult diet	Granivorous	Granivorous
	Polyphagous	Polyphagous
	Predatory	Predatory
Wing status	Apterous	0
	Dimorphic	1
	Macropterous	2
Size		Continuous (mm)

2.4. Data analysis

2.4.1. Landscape parameters

All the landscape parameters are the results of field recording within a radius of 500 m around every sampled site (Fig. 2). In the following analyses, radii of 200, 300 and 500 m were tested and we kept the 500 m because it explained more variance than smaller radii. The landscape parameters were obtained by the computation of on-field records under Esri ArcGIS 10.4. To analyse the compositional heterogeneity of the landscape we applied the Shannon diversity index:

$$H' = -\sum_{i=1}^{n} p_i \ln p_i$$

where p_i is the proportional area of the i^{th} land cover among the n land covers in the corresponding radius areas around the sampling points. The habitats which were considered for the Shannon index were different crop types as well as semi-natural land covers (presented in Table S1). The field border density, called in the following edge density, was measured by extracting the edges between land parcels dividing it by the area of corresponding landscape context. The winter crop-grassland edge density was obtained similarly, though it only considered the edges between adjacent parcels of winter crops and permanent grasslands in the 500 m radius.

As a preliminary analysis, we performed a principal component analysis (PCA) with 12 landscape parameters for the 500 m

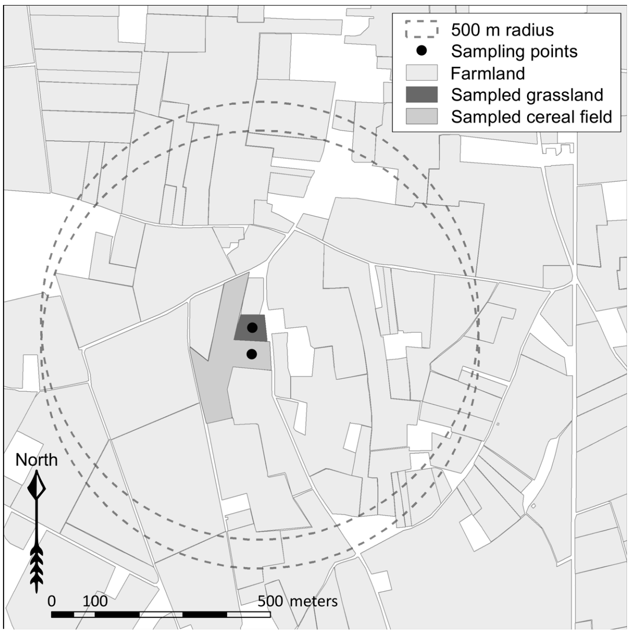

Fig. 2. Example of 500 m landscape context around a pair of sampling points.

radius areas around sampling points to explore the overall landscape structure, understand the correlation between landscape variables and identify lowly correlated predictors to use in the following models. The PCA allowed the identification of a set of variables which best described the landscape context (Table 2). The variables included in the PCA were both configurational and compositional ones: coverage ratios of annual winter crops, annual spring crops, permanent grasslands, temporary grasslands, woodlands, linear semi-natural elements; compositional diversity measures such as number of different crops, the landscape Shannon diversity, and the crop Shannon diversity; and finally configurational indicators such as the mean field area, the mean field complexity index, the overall edge density and specific winter crop-grassland and winter crop-spring crop edge densities (Table S2). The PCA thus allowed the identification of a few variables which described best the different landscape context (Table 2). We tested the Spearman's rank correlation between the different landscape variables in every study region (Table S3), in order to interpret more confidently our results.

2.4.2. Relationship between species distribution, traits and landscape context

Statistical analyses were conducted using R 4.4.2 (R Core Team, 2024). We first performed a RLQ analysis to explore the relationship between environmental context, species distributions and species traits (Dolédec et al., 1996; Dray et al., 2003; Kleyer et al., 2012). RLQ provides double ordination between three datasets: R (environmental context), L (carabid activity-density contingency table) and Q (species traits). We standardised the carabid contingency table according to Hellinger (Legendre & Gallagher, 2001) and then performed classical Euclidean distances calculations to obtain the ecological distances matrix. Compared to Jaccard or Bray-Curtis distances, Hellinger offered the advantage to lower the dissimilarity due to rare species in the dataset. We integrated in the environmental context matrix another variable: the habitat of the sampled field, in order to investigate the potential differentiated impact of the landscape on the functional communities of grasslands and winter crops.

In RLQ it is recommended to analyse all the tables separately with the appropriate multivariate ordination method: correspondence analysis (CA) for the carabid abundance contingency table, a principal component analysis (PCA) was performed for the landscape context table and then a multiple correspondence analysis (MCA), by Hill-Smith PCA (due to categorical and numerical variables) for the trait table, weighing columns with the previous PCA species scores. Finally, the RLQ analysis provides a combination of all three independent analyses (no results of initial PCA or CA are reported here). To test the robustness of the RLQ, we performed two Monte-Carlo randomisation tests (9,999 permutations for each). For the first test, the null hypothesis was that species are distributed randomly in the environment, while for the second test the null hypothesis was that species are distributed randomly, irrespectively to their traits (Dray & Legendre, 2008; Duflot et al., 2014). The final step consisted in retaining only the highest p-value for the global environment-trait link interpreted with $\alpha = 0.05$, which avoids inflation of the false rejection rate (Braak et al., 2012). In complement we applied a fourth-corner analysis to test all possible links between specific traits and specific environment variables (Legendre et al., 1997). We used the R ade4 1.7-13 package for the RLQ analysis (Dray et al., 2018).

2.4.3. Effects of traits on carabid species exclusiveness or commonness in the paired contrasted habitats

For this analysis, we only considered presence/absence data. We studied the presence of carabid species per pair of traps: a sampled species was considered shared when it was sampled in both paired cereal field and grassland. On the contrary, a sampled species was considered as exclusive to one of the respective land cover when it was only sampled in one of the two paired land covers.

We performed two sets of generalised mixed models (GLMM) (Guisan et al., 2002; Bolker et al., 2009) to analyse the effects of the three traits (diet, wing status and size as explanatory variables) on the species commonness or exclusiveness to both land covers of each paired site (response variables). One model set predicted the species commonness (1: common, 0: exclusive). Another set of models focused on exclusive species only and predicted their observed habitat (1: cereals; 0: grassland). Since the response variables were binomial, the model error distributions were both binomial-fitted.

The tested parameters were carabid traits, as presented in Table 1. The wing status has been transformed into an integer variable (Table 1). We retained in our models the interactions of diet or wing status with size of carabids. Indeed, size could be strongly linked with prey types (DeBach & Rosen, 1991; Dainese et al., 2017) and wing status (Cole et al., 2002). We used the cereal field-grassland pair as a random effect on the intercept to account for local and regional spatial structures in our data. The year of sampling could not be included in the models as random effect since it has too few different levels and we thereby included it as a fixed effect (Bolker et al., 2009). We then fitted a set of 14 different models altogether, including a null one which was composed with the sole year of sampling parameter and the cereal field-grassland pair random effect.

Akaike information criterion corrected for small sample size (AIC_c) allowed to estimate the relative model parsimony, i.e. a compromise between goodness of fit and model simplicity (Symonds & Moussalli, 2011). For each set, we selected the most parsimonious model, i.e. the one with the lowest AIC_c, but also equivalent models whose ΔAIC_c with the best model was less than 2 (Burnham & Anderson, 2002, 2004). When there was more than one model, we averaged them in order to retain as much information as possible about the significant explanatory variables (Burnham & Anderson, 2002; Johnson & Omland, 2004). We always checked the null model ΔAIC_c to ensure the significance of our model selection (a ΔAIC_c of null models lower than 2 involved no effect of explanatory variable). We checked the absence of abnormal distribution, over-dispersion and outliers in residuals of selected models with the R package DHARMa (Hartig, 2024). We used the R lme4 1.1-18-1 package (Bates et al., 2014) and the R MuMIn 1.42.1 package (Burnham & Anderson, 2002; Barton, 2018) for the multimodel inference procedure.

Table 2. Landscape parameters selected to analyse carabid species richness with generalised linear model comparison.

Parameter	Abbreviation in graphs	Type	Values / Metric
Grassland coverage ratio	Grasslands	Continuous	Percentage of area
Hedgerows coverage ratio	Hedgerows	Continuous	Percentage of area
Landscape Shannon diversity index [a]	Shannon	Continuous	Double
Edge density	ED	Continuous	$m.ha^{-1}$

[a] The habitats accounting for landscape Shannon index are presented in Table S1.

3. RESULTS

We caught a total of 5644 carabids, corresponding to 114 different species and 1179 species occurrences. Among those species occurrences, 14% corresponded to species sampled in both fields of a given pair, 46% to species sampled only in the cereal crop and the remaining 40% to species sampled only in the grassland (Table S5).

Most of the species occurrences represented predatory, then granivorous species, polyphagous species being the least observed. Regarding the wing status, macropterous species had by far the highest number of occurrences, the apterous ones being the least frequently observed. The distribution of species occurrences between the different body size categories was more balanced, with the very large carabids showing lower species occurrence.

3.1. Small granivorous species occured less often than other functional groups in both habitats of a pair

Among the different feeding diets, polyphagous species were the most likely to be sampled in both habitats of a pair (21% of the species occurrences, Table S5), even if they were more frequently found in the cereal crop exclusively. Dimorphic as well as large species (13–22 mm, Table S5) were also more frequently observed in both habitats of a pair than the other groups of species (respectively 20% and 19% of species occurrences for the dimorphic and the large species).

The GLMM regarding species commonness or exclusiveness showed significant effects of the diet and of the interaction between the size and the predator diet. It thus confirmed that diet and size of carabids significantly explained their commonness and exclusiveness in the sampled habitats, but did not show any significant effect of the wing status (Table 3). Concerning the effect of the diet and size, graphical observation showed no strong differences in commonness-exclusiveness patterns according to diet as most of the diets exhibited a mean commonness probability between 0.1 and 0.2 with overlapping confidence intervals (Fig. 3). The only exception is for small granivorous, which displayed a commonness probability below 0.1, which explains the significant effect of the interaction between diet and size in the model.

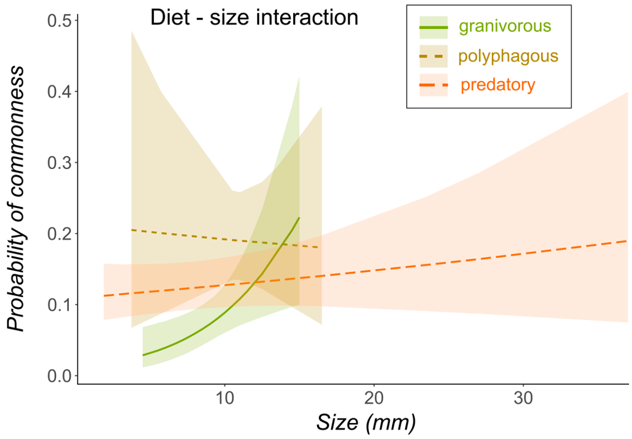

Fig. 3. Species probability of commonness according to diet - size interaction. Note: p(exclusiveness) = 1 – p(commonness). Area around the curve is the 0.95 confidence interval. The body size limits of each curve mean no smaller or larger species was sampled for the considered diet.

3.2. Exclusiveness of species occurrence to a particular habitat is related to traits or combination of traits

The GLMM model showed that when exclusive to one habitat, association with the one or the other was significantly linked to the diet, wing status, as well as the interaction between the wing status and the size, whereas the interaction between the size and the diet was only marginally significant (Table 3).

When exclusive to one habitat, granivorous species were mainly found in the grassland (276 occurrences compared

Table 3. Incidence of carabid per wing status, size and diet traits according to their commonness or exclusiveness to one sampled habitat: summary of generalised linear model averaging results.

Model[a]	Variable[b]	Importance (%)	Relative importance (%)	Multimodel estimate ± SE	z value	p value	Signif.
Species commonness and exclusiveness	(Intercept)			–2.92 +/–0.33	8.86	0.000	***
	wings	57	40	–0.08 +/–0.09	0.86	0.389	
	polyphagous	57	100	1.22 +/–0.34	3.60	0.000	***
	predatory	57	100	0.74 +/–0.29	2.52	0.012	*
	size	64	74	–0.64 +/–0.40	1.61	0.107	
	year 2018	100	100	0.37 +/–0.24	1.58	0.115	
	size*wings	21	9	–0.04 +/–0.13	0.32	0.747	
	polyphagous*size	21	59	0.69 +/–0.65	1.06	0.289	
	predatory*size	21	59	0.80 +/–0.32	2.50	0.013	*
Species exclusiveness per habitat	(Intercept)			–1.45 +/–0.20	7.33	0.000	***
	wings	57	100	0.42 +/–0.08	5.49	< 0.001	***
	polyphagous	57	100	1.83 +/–0.26	7.08	< 0.001	***
	predatory	57	100	2.04 +/–0.18	11.21	< 0.001	***
	size	64	100	0.17 +/–0.23	0.75	0.452	
	year 2018	100	100	–0.04 +/–0.19	0.21	0.835	
	size*wings	21	99	–0.36 +/–0.11	3.18	0.001	***
	polyphagous*size	21	60	–1.06 +/–0.56	1.89	0.059	.
	predatory*size	21	60	–0.35 +/–0.21	1.72	0.086	.

[a] Both models were fitted with binomial law distribution. [b] Default qualitative variables values are in intercept: phytophagous and year 2017.

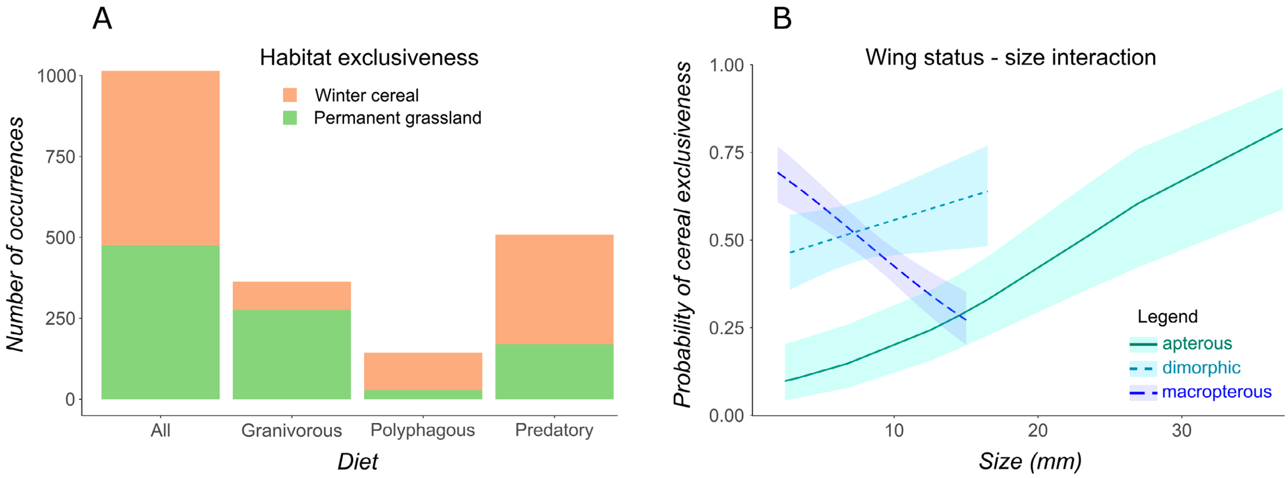

Fig. 4. Exclusiveness to one habitat type according to carabid functional traits: (a) Number of species occurrences by diet, (b) Probability of cereal exclusiveness of a species according to its wing status and body size. Note: p(PG exclusiveness) = 1 – p(WC exclusiveness). Area around the curve is the 0.95 confidence interval. The body size limits of each curve mean no smaller or larger species was sampled for the considered wing status.

to 88 in the crop only), whereas polyphagous and predatory carabids were more likely to be exclusive to the cereal crop (respectively 116 and 339 occurrences in the crop compared to 28 and 170 occurrences in the grassland only, Table S5 and Fig. 4a).

The analysis of the relationship between the body size, the wing status and the exclusive occurrence in one habitat rather than the other (Fig. 4b) shows particular effects of the interaction between those two traits.

Apterous carabids larger than 25 mm, represented only by *Carabus* spp. in our samples (Table S4), had higher probabilities to be found exclusively in the cropland, whereas smaller apterous species were more exclusive to the grassland. Small macropterous species were more likely to be caught in the cereal crop only, and macropterous species larger than 9 mm were more frequently caught in the grassland only. Dimorphic species had equivalent likelihoods to be found exclusively in the grassland or in the cropland, even though larger ones tended to be more often found in the cropland.

The analyses of the community trait values showed that the community of grasslands was more diverse regarding wing morphology compared to that of cereal fields which was dominated by macropterous species. The dispersion of wing morphology trait value was indeed higher in grasslands than in cereal fields, particularly in Bièvre and Forez regions (Rao's quadratic entropy, Table S6). On the contrary, the diet trait showed more similar dispersion in both habitats but with contrasting functional composition, grasslands harbouring more granivores and crops more polyphagous species (Table S6).

3.3. Interactions between habitat and landscape context influence distribution of carabid traits

The RLQ analysis showed that species composition significantly depended on sampled habitat and landscape parameters (permutation test, p-value = 0.0001). The distribution of species was also significantly linked to their functional traits (permutation test, p-value = 0.028). The projected inertia of the RLQ showed that the first axis explained 85% of the carabid traits inertia and significantly correlated with the habitat of the sample: cereal crops or permanent grasslands (Fig. 5). The second axis (9% of inertia) differentiated the landscape contexts mostly through the opposition of two compositional parameters, the Shannon landscape diversity and the grassland coverage. The third axis (5% of inertia) is also related to these two landscape composition descriptors as well as to a configurational parameter, the edge density.

The presence of granivorous species (*Amara* spp. and *Harpalus* spp.) was related to the grassland habitat. The presence of polyphagous species such as *Poecilus cupreus* was associated with the cereal crop habitat. Predatory carabids were slightly associated with cereal fields with high landscape compositional heterogeneity (Fig. 5a). Apterous species were typical of grasslands embedded in compositionally homogeneous and configurationally simple landscapes (Fig. 5a and b).

Focussing on the relationship between carabid traits and landscape context on the second and third axes of the RLQ (Fig. 5b), we observed that small body size was associated with more grasslands. Concerning the diet, polyphagous carabids were related to the vicinity of grasslands and/or low configurational complexity context, whereas predatory carabids were slightly associated with higher compositional heterogeneity. Dimorphic carabids were linked to compositionally heterogeneous landscapes. Being at the centre of both planes, the macropterous character was not related to a particular habitat or landscape context (Fig. 5a and b). The fourth corner analysis did not report any significant two-by-two link between traits and environment (habitat or landscape) variables.

4. DISCUSSION

In this study, we aimed at disentangling the influences of the habitat and that of the landscape context on the distribution of carabid traits. Despite the general trend showing a low proportion of species occurring in both paired habi-

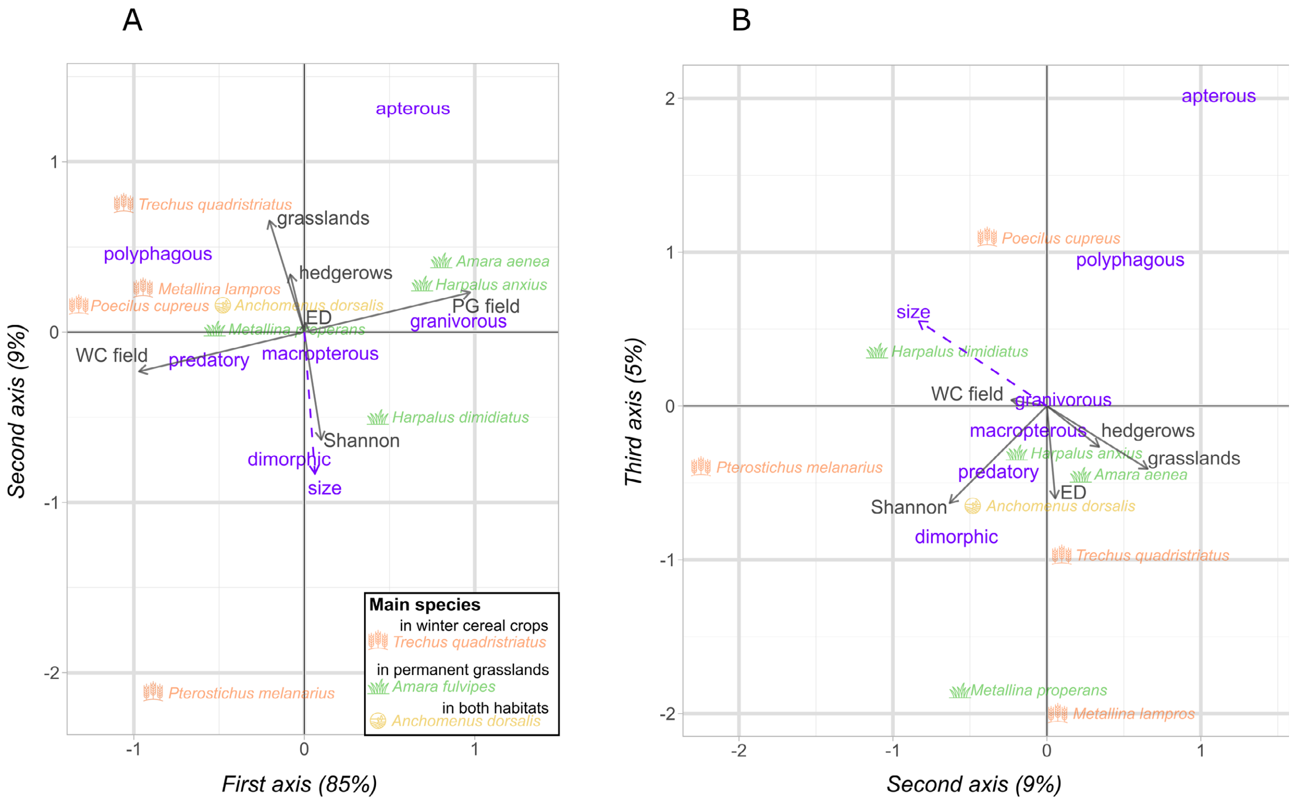

Fig. 5. Ordination of the landscape parameters and carabid species traits and projection of the most abundant species along: (a) the axes 1 and 2 and (b) the axes 2 and 3 of the RLQ analysis. Black arrows stand for sampling habitat variables (WC field – winter cereals samples; PG field – permanent grassland samples) and landscape variables in a 500 m radius (ED – edge density; grasslands – grassland coverage; hedgerows – length of hedgerows; Shannon – diversity of the land uses defined in Table S1). Blue labels represent the different species traits. Only the five main species occurring in each habitat are depicted here, among which one is common to both habitats.

tats, polyphagous species were more likely than species with other diets to be shared by paired grassland and cereal crop. Granivorous species were highly associated with grasslands, while predatory and polyphagous were more exclusively related to cereal crops. Small apterous carabids were more likely to be caught in grasslands only. Concerning the influence of the landscape, polyphagous species were more likely to be caught in landscape contexts with low compositional heterogeneity or high grassland coverage. Small body size was also associated to the presence of grasslands in the surrounding landscape. Apterous carabids were related to grasslands embedded in homogeneous landscapes. Finally, macropterous species as a whole were not influenced by the sampled habitat nor the landscape context.

4.1. Landscape homogenisation as a threat to specialised ground beetles

As we expected in our hypothesis (i), polyphagous species tended to be more often shared by both paired grasslands and cereal crops than were other species, even if this was not significant (Fig. 3). Those species can feed on invertebrate preys as well as on weed seeds, they may thereby be able to thrive more easily in a wider range of habitats. On the contrary, strictly predatory carabids were relatively more often caught exclusively in the cereal crop, and granivores in the grassland.

Moreover, we found that polyphagous species were associated with cereal crops in grassland rich landscapes. One possible explanation is that some of these species need complementary resources, animal preys and seeds, for which they need to forage in both habitats (Carbonne et al., 2022). Another possibility is that polyphagous carabids can move between both habitats in case of disturbance or lack of resources in one of them because their diet allows more flexibility. They could thus spillover into nearby grasslands after crop harvest, overwinter there (Geiger et al., 2009; Alignier et al., 2014) and then migrate back into cereal crops during spring, when the vegetative cover of the crops is more developed and offers more potential preys than grasslands do (Schneider et al., 2016).

At the same time, polyphagous carabids in our study were also associated with landscapes with low heterogeneity, either compositional and configurational. This is consistent with the results of several studies which concluded that the simplification of the landscape leads to the homogenisation of functional traits towards generalist species, especially polyphagous ones (Purtauf et al., 2005; Gámez-Virués et al., 2015; Deppe & Fischer, 2023). With the more homogeneous landscapes of Bièvre and Rovaltain areas, characterised by higher proportion of crop fields, our result is also in line with the study of Marrec et al. (2017) which showed that polyphagous species like *Poecilus cupreus* could be favoured by higher crop coverage, as a possible result of higher resource concentration in such landscapes.

4.2. Trait presence is primarily determined by the habitat

Our second objective was to disentangle the effects of habitat and landscape parameters in the occurrence of carabid traits. The performed RLQ indicated that the main factor influencing carabid traits was the habitat, which is consistent with many previous studies (Tuck et al., 2014; Caro et al., 2016; Gayer et al., 2019).

We found that some functional groups of species were more likely to be associated to a particular habitat and could in particular confirm the first part of our hypothesis (ii). For instance predatory and polyphagous species were related to cropland, possibly due to the higher availability of pest preys such as aphids in this habitat (Holland et al., 2004; Winqvist et al., 2014; Hanson et al., 2016; Tamburini et al., 2022). Furthermore, we found more granivorous species in grasslands, like Hanson et al. (2016), which can be explained by the higher availability and diversity of seeds in grasslands (Klimeš & Saska, 2010; Diehl et al., 2012).

Small granivorous species were very likely to be exclusive to grasslands, emphasising their preference for this habitat relatively to cropland. Indeed, we sampled in conventionally farmed cereal fields, where the weed cover was very low, being strongly controlled by herbicides. This might explain why fewer granivorous species were found there, since their food resource was scarce compared to grasslands (Labruyere et al., 2016).

However, contrarily to the second part of our hypothesis (ii), we did not evidence more frequent occurrence of winged species in crops. Indeed, we observed that macropterous species were indifferently found in both habitats, contrarily to other studies finding more macropterous species or species with better flight ability in more intensively used lands (Ribera et al., 2001; Hanson et al., 2016). This discrepancy could be explained in part by the huge diversity of macropterous species in our study, with quite heterogeneous flight ability among them (Hendrickx et al., 2009).

Wingless species, for their part, were more likely to be found in grasslands only. This is consistent with previous studies showing a negative correlation between management intensity and/or level of disturbance and the amount of wingless carabids (Ribera et al., 2001; Pedley & Dolman, 2014). Moreover, apterous species tend to rely more widely than others on a single habitat (den Boer, 1990; Cole et al., 2002). Since apterous carabids were caught here in grasslands surrounded by grassland-rich landscapes, it is likely that they were grassland specialists according to Batáry et al. (2007).

These findings are fully compatible with the higher functional dispersion of wing morphology in grasslands than in crops. Even if we did not observe the same trend on the other traits studied, this result is partly in line with the study of Feng et al. (2021) who found higher general functional diversity of ground beetles in old fallows (a permanent grassy habitat sharing some features with our permanent grasslands) compared to crop fields.

4.3. Influence of landscape on species traits in grasslands

The trait assemblages of carabids were secondarily determined by landscape descriptors, according to two gradients. The first gradient was linked to landscape composition, considering both land use diversity and grassland coverage, while the second one was related to edge density.

Our results only partially confirmed hypothesis (iii) since we did not find any influence of the landscape context on the occurrence of granivorous carabids. This result echoes with a study showing no effect of the landscape composition on granivorous carabid diversity nor on weed seed predation rate (Ortis et al., 2025). On the other hand, we observed that apterous species were correlated with landscape contexts of low heterogeneity, dominated by a low diversity of habitats and large fields. We already pointed out that apterous species were more typical of grasslands in our study. Grasslands embedded in homogeneous landscapes can mean they are surrounded by many other grasslands, as it is the case in Forez study region (Table S4). This result is fully compatible with the study of Toivonen et al. (2024) who found that abundance of carabids with poor flight abilities decreased with proportion of arable land in the landscape. This implies that species unable to fly are favoured when they have easy access to grassland patches in their surroundings. Otherwise, if these grasslands are surrounded by a more homogeneous mosaic of annual crops, as it is the case in some areas of Rovaltain, the apterous carabids they shelter are more likely to be isolated from other grassland patches. There may be here a conservation concern for these grassland specialists, in particular when there are no or few refuges and corridors (like permanent vegetation strips or grassy margins) in their neighbouring environment. They can face local extinction in case of disturbance of their habitat (Hendrickx et al., 2009). This conservation issue is even amplified by the fact isolated grasslands are subject to the spillover of more ubiquitous species from neighbouring cropped fields, which then might put at risk specialised grassland carabids to extinction because of strong competition on their resource (den Boer, 1990; Hendrickx et al., 2009; Wamser et al., 2012). Batáry et al. (2007), for instance, observed higher generalist species richness in grasslands surrounded by crops. Another study described a higher abundance of generalist species in grasslands adjacent to crop fields than in grasslands adjacent to meadows (Madeira et al., 2016).

These results underline the importance of taking into account functional diversity and not solely activity-density or species richness to understand the ecological processes behind the spatial patterns and to better guide landscape planning in the preservation of specialist and potentially endangered species (Makwela et al., 2023). In addition to this conservation aspect, further studies monitoring ecosystem services would also enable to determine how these services are influenced by habitat and landscape management.

5. CONCLUSION

Using a sampling strategy targeting adjacent and contrasted farmland habitats, our research emphasises the need for grassland preservation or restoration in agricultural landscapes to conserve carabid functional diversity. We found that grasslands hosted functionally diverse species in terms of wing morphology. For many of these species, survival is likely to depend on this habitat as they cannot disperse due to limited mobility. Besides, our study found that grasslands are also interesting for generalist species from neighbouring cropped fields since they can possibly find refuge habitats in the event of of agricultural disturbance in cropland, and continuous food resources. In this case, polyphagous carabids can be good examples of landscape complementation between cropland and grassland. Our results involving landscape composition suggest that this trade-off will largely depend on the amount of grasslands in the landscape, isolated grasslands being less susceptible to support grassland specialists or species with low dispersal power.

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Table S1. Land cover types accounted for the landscape Shannon diversity index.

Land cover type
Winter cereal
Maize
Rapeseed
Sunflower
Soybean
Permanent grassland
Temporary grassland
Orchard
Vineyard
Fallow
Other leguminous and oleaginous crop
Other crops: market gardening, horticulture etc.
Woodland

Table S3. Significant Spearman's rank correlations (ρ) between landscape variables within a 500 m radius around the sampling point of the three study areas.

Landscape variables		ρ	P-value
Bièvre			
Landscape Shannon index	Edge density	0.39	*
Forez			
Landscape Shannon index	Grasslands	–0.55	**

Table S2. Landscape parameters included in the preliminary PCA.

Landscape parameter	Formula (always applied within the landscape radius)
Annual winter crop coverage ratio	Annual winter crop area / landscape radius area
Annual spring crop coverage ratio	Annual spring crop area / landscape radius area
Permanent grassland coverage ratio	Permanent grassland area / landscape radius area
Woodland coverage ratio	Woodland area / landscape radius area
Hedgerow coverage ratio	Hedgerow area / landscape radius area
Crop diversity	Number of different crops
Landscape Shannon diversity	$H' = -\sum_{i=1}^{n} p_i \ln p_i$ including all land cover types*
Crop Shannon diversity	$H' = -\sum_{i=1}^{n} p_i \ln p_i$ including only crop cover types*
Mean field size	Mean of the sizes of all fields
Mean field complexity	For all fields: mean of actual field perimeter / same-sized square field perimeter
Overall edge density	Edge density between all the fields
Winter crop / grassland edge density	Edge density between winter crops and permanent grasslands

* Presented in Table S1.

Table S4. Full list of sampled carabid species, their functional traits and number of individuals caught in grassland and cropland.

Species	Diet[1]	Wing status[2]	Mean body size (mm)	Overall sampled individuals in	
				Grassland	Cropland
Acinopus (Acinopus) picipes (Olivier, 1795)	grGr	m	14.5	0	1
Acupalpus (Acupalpus) meridianus (Linne, 1761)	po	m	3.75	7	2
Agonum (Olisares) hypocrita (Apfelbeck, 1904)	pr	m	8	0	1
Agonum (Agonum) muelleri (Herbst, 1784)	pr	m	7.5	38	2
Amara (Amara) aenea (De Geer, 1774)	gr	m	7.25	36	158
Amara (Zezea) anthobia A. Villa & G.B. Villa, 1833	gr	m	6	2	7
Amara (Amara) communis (Panzer, 1797)	gr	m	6.5	0	11
Amara (Bradytus) consularis (Duftschmid, 1812)	gr	m	8	1	0
Amara (Amara) familiaris (Duftschmid, 1812)	gr	m	6	15	13
Amara (Zezea) fulvipes (Audinet-Serville, 1821)	gr	m	10.5	0	58
Amara (Zezea) kulti Fassati, 1947	gr	m	9.25	2	39
Amara (Amara) lucida (Duftschmid, 1812)	gr	m	5.25	0	1
Amara (Amara) lunicollis Schiodte, 1837	gr	m	7.5	0	11
Amara (Amara) montivaga Sturm, 1825	gr	m	7.5	0	1
Amara (Amara) ovata (Fabricius, 1792)	gr	m	9	0	1
Amara (Zezea) plebeja (Gyllenhal, 1810)	gr	m	6.75	4	1
Amara (Amara) similata (Gyllenhal, 1810)	gr	m	8.5	6	11
Amara (Zezea) strenua Zimmermann, 1832	gr	m	9.25	0	27
Amara (Amara) tibialis (Paykull, 1798)	gr	m	4.5	3	16
Amara (Zezea) tricuspidata Dejean, 1831	gr	m	8	7	1
Anchomenus (Anchomenus) dorsalis (Pontoppidan, 1763)	pr	m	7	948	125
Anisodactylus (Anisodactylus) binotatus (Fabricius, 1787)	po	m	10.5	15	30
Anisodactylus (Anisodactylus) nemorivagus (Duftschmid, 1812)	po	m	8	1	0
Anisodactylus (Pseudanisodactylus) signatus (Panzer, 1796)	po	m	12.5	9	10
Asaphidion stierlini (Heyden, 1880)	pr	m	4.25	17	0
Badister (Badister) bullatus (Schrank, 1798)	pr	m	5.5	0	7
Brachinus (Brachinus) crepitans (Linne, 1758)	pr	m	8.5	9	7
Brachinus (Brachinus) elegans Chaudoir, 1842	pr	m	7.75	0	5
Brachinus (Brachynidius) explodens Duftschmid, 1812	pr	m	6.5	2	18
Brachinus (Brachynidius) sclopeta (Fabricius, 1792)	pr	a	5.75	25	41
Calathus (Calathus) fuscipes (Goeze, 1777)	pr	d	12.5	14	48
Calathus (Neocalathus) melanocephalus (Linne, 1758)	pr	m	7	0	2
Callistus lunatus (Fabricius, 1775)	pr	a	6.5	2	0
Carabus (Tachypus) auratus Linne, 1761	pr	a	23.5	59	32
Carabus (Tachypus) cancellatus Illiger, 1798	pr	a	26.5	4	0
Carabus (Procrustes) coriaceus Linne, 1758	pr	a	37	9	3
Carabus (Morphocarabus) monilis Fabricius, 1792	pr	a	27	3	0
Carabus (Megodontus) violaceus subsp. *purpurascens* Fabricius, 1787	pr	m	27	0	3
Chlaeniellus nigricornis (Fabricius, 1787)	pr	m	11	1	2
Chlaeniellus nitidulus (Schrank, 1781)	pr	m	11	0	2
Clivina (Clivina) fossor (Linne, 1758)	pr	m	6	2	0
Cylindera (Cylindera) germanica (Linne, 1758)	pr	m	9.5	0	8
Demetrias (Demetrias) atricapillus (Linne, 1758)	pr	m	5	6	0
Diachromus germanus (Linne, 1758)	gr	m	9	2	4
Dinodes (Dinodes) decipiens (L. Dufour, 1820)	pr	m	11.5	0	4
Dixus clypeatus (P. Rossi, 1790)	gr	m	9.5	0	3
Gynandromorphus etruscus (Quensel in Schonherr, 1806)	gr	m	10.5	2	0
Harpalus (Harpalus) affinis (Schrank, 1781)	po	m	10.5	117	40
Harpalus (Harpalus) albanicus Reitter, 1900	gr	m	8.5	1	9
Harpalus (Harpalus) anxius (Duftschmid, 1812)	gr	m	7.25	2	169
Harpalus (Harpalus) atratus Latreille, 1804	gr	m	12.5	1	0
Harpalus (Harpalus) dimidiatus (P. Rossi, 1790)	gr	m	12.5	42	178
Harpalus (Harpalus) distinguendus (Duftschmid, 1812)	gr	d	10	48	25
Harpalus (Harpalus) honestus (Duftschmid, 1812)	gr	m	8.5	4	0
Harpalus (Harpalus) luteicornis (Duftschmid, 1812)	gr	m	6.75	1	14
Harpalus (Harpalus) oblitus Dejean, 1829	gr	d	10.5	9	13
Harpalus (Harpalus) pumilus Sturm, 1818	gr	m	5.5	0	7
Harpalus (Harpalus) pygmaeus Dejean, 1829	gr	m	6.25	2	12
Harpalus (Harpalus) rubripes (Duftschmid, 1812)	gr	m	9	1	28
Harpalus (Harpalus) serripes (Quensel in Schonherr, 1806)	gr	m	11	0	50
Harpalus (Harpalus) tardus (Panzer, 1797)	gr	m	9.5	39	27
Leistus (Leistus) ferrugineus (Linne, 1758)	pr	m	7	0	1
Leistus (Leistus) fulvibarbis Dejean, 1826	pr	a	7.5	1	0
Licinus (Licinus) cassideus (Fabricius, 1792)	pr	m	14.5	0	1
Loricera pilicornis (Fabricius, 1775)	pr	d	7.5	8	1
Metallina (Metallina) lampros (Herbst, 1784)	pr	d	3.25	127	89
Metallina (Metallina) properans (Stephens, 1828)	pr	a	3.5	36	153
Microlestes gallicus Holdhaus, 1912	pr	m	2.9	0	3
Microlestes luctuosus Holdhaus in Apfelbeck, 1904	pr	a	2.4	3	0
Microlestes maurus (Sturm, 1827)	pr	m	2.4	1	20
Microlestes minutulus (Goeze, 1777)	pr	m	3.1	9	11
Nebria (Nebria) brevicollis (Fabricius, 1792)	pr	m	11.5	13	12
Nebria (Nebria) salina Fairmaire & Laboulbene, 1854	pr	d	11	26	20
Notiophilus biguttatus (Fabricius, 1779)	pr	d	5.25	0	1
Notiophilus palustris (Duftschmid, 1812)	pr	d	5.25	1	0
Notiophilus quadripunctatus Dejean, 1826	pr	d	5.25	17	1
Notiophilus substriatus G.R. Waterhouse, 1833	pr	d	5.25	6	2
Ocydromus (Nepha) callosus subsp. *subconnexus* (De Monte, 1953)	pr	m	3.75	7	0
Ocydromus (Peryphanes) latinus (Netolitzky, 1911)	pr	d	5.5	3	0
Ocydromus (Peryphus) tetracolus (Say, 1823)	pr	m	6	0	1
Ophonus (Ophonus) ardosiacus (Lutshnik, 1922)	gr	d	11.5	1	0
Ophonus (Hesperophonus) azureus (Fabricius, 1775)	gr	m	8	3	18
Ophonus (Hesperophonus) cribricollis (Dejean, 1829)	gr	m	8	0	6
Ophonus (Metophonus) puncticeps Stephens, 1828	gr	m	7.5	0	2
Ophonus (Ophonus) sabulicola (Panzer, 1796)	gr	m	15	0	1
Panagaeus (Panagaeus) bipustulatus (Fabricius, 1775)	pr	m	7.25	0	1
Paratachys bistriatus (Duftschmid, 1812)	pr	m	2.15	5	0
Parophonus (Parophonus) maculicornis (Duftschmid, 1812)	gr	m	6.5	2	30
Philochthus lunulatus (Geffroy in Fourcroy, 1785)	pr	d	3.6	20	3
Philorhizus notatus (Stephens, 1827)	pr	d	2.75	0	1
Phyla obtusa (Audinet-Serville, 1821)	pr	m	2.75	16	11
Phyla tethys (Netolitzky, 1926)	pr	m	3.25	1	1
Platyderus (Platyderus) depressus (Audinet-Serville, 1821)	pr	m	6.75	0	1
Poecilus (Poecilus) cupreus (Linne, 1758)	po	m	11	1331	104
Poecilus (Macropoecilus) kugelanni (Panzer, 1797)	pr	m	13	6	4
Poecilus (Macropoecilus) sericeus Fischer von Waldheim, 1824	pr	m	13	0	6
Poecilus (Poecilus) versicolor (Sturm, 1824)	pr	m	10	16	95
Pseudoophonus (Pseudoophonus) rufipes (De Geer, 1774)	po	m	13.5	13	8
Pterostichus (Pseudomaseus) anthracinus (Illiger, 1798)	pr	a	10.5	1	0
Pterostichus (Steropus) madidus (Fabricius, 1775)	po	d	16.5	12	4
Pterostichus (Morphnosoma) melanarius (Illiger, 1798)	pr	m	16.5	126	35
Pterostichus (Pseudomaseus) nigrita (Paykull, 1790)	pr	d	10.5	0	1
Pterostichus (Phonias) strenuus (Panzer, 1796)	pr	d	6.25	1	3
Pterostichus (Argutor) vernalis (Panzer, 1796)	pr	m	7	1	2
Semiophonus signaticornis (Duftschmid, 1812)	gr	m	6.5	18	4
Stenolophus (Stenolophus) teutonus (Schrank, 1781)	po	a	5.75	1	5
Stomis (Stomis) pumicatus (Panzer, 1796)	pr	a	6.75	4	1
Syntomus foveatus (Geoffroy in Fourcroy, 1785)	pr	m	3.25	26	29
Syntomus obscuroguttatus (Duftschmid, 1812)	pr	a	3.25	33	8
Syntomus truncatellus (Linne, 1761)	pr	m	3.25	2	14
Tachyura (Tachyura) parvula (Dejean, 1831)	pr	d	1.9	1	0
Trechus (Trechus) obtusus Erichson, 1837	pr	m	3.6	1	1
Trechus (Trechus) quadristriatus (Schrank, 1781)	pr	m	3.6	193	1

[1] gr – granivorous; po – polyphagous; pr – predatory; [2] a – apterous; d – dimorphic; m – macropterous.

Table S5. Number and percentage of carabid species occurrence caught in both paired habitats or exclusively in grassland or cropland, in relation to traits: (a) all traits, diet and wing status, (b) size (for practical reasons, species have been attributed to size classes here, whereas size is used as a continuous variable in all analyses presented, see Table S4 for exact size values).

(a)	Overall All traits		Diet						Wing status					
			Predatory		Granivorous		Polyphagous		Macropterous		Dimorphic		Apterous	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Total	1181		598		400		183		906		175		100	
Present in both	164	14	89	15	36	9	39	21	116	13	35	20	13	13
Exclusive to cropland	543	46	339	57	88	22	116	63	421	46	90	51	32	32
Exclusive to grassland	474	40	170	28	276	69	28	15	369	41	50	29	55	55

(b)	Body size									
	Very small 2–5 mm		Small 6–8 mm		Medium 9–12 mm		Large 13–22 mm		Very Large 23–40 mm	
	n	%	n	%	n	%	n	%	n	%
Total	247		370		362		172		30	
Present in both	29	12	48	13	50	14	33	19	4	13
Exclusive to cropland	147	60	149	40	163	45	65	38	19	63
Exclusive to grassland	71	29	173	47	149	41	74	43	7	23

Table S6. Community-weighted mean trait values (CWM) and functional dispersion (Q – Rao's quadratic entropy) of the communities found in each land use of each study region.

Land cover	Study region	CWM / Wing morphology			CWM / Diet			CWM / Size	Dispersion		
		Apterous	Dimorphic	Macropterous	Granivores	Polyphagous	Predators		Q (WM)	Q (Diet)	Q (Size)
Cereal fields	Bièvre	0,034	0,151	0,815	0,025	0,348	0,627	8,91	0,440	0,685	4,348
	Forez	0,046	0,043	0,911	0,104	0,565	0,331	9,45	0,234	0,792	3,057
	Rovaltain	0,029	0,062	0,909	0,102	0,343	0,555	9,00	0,240	0,798	4,048
Permanent grasslands	Bièvre	0,077	0,272	0,651	0,311	0,114	0,575	8,62	0,702	0,791	4,919
	Forez	0,091	0,177	0,731	0,395	0,144	0,462	7,78	0,601	0,863	3,899
	Rovaltain	0,067	0,050	0,883	0,714	0,047	0,239	9,36	0,302	0,609	3,188

As Rao's functional diversity is sensitive to the number of species when it is small, all the computation of the above table were made on aggregated abundance data per study area and land cover. Wing morphology and diet traits have been kept as qualitative variables (each modality being a binary variable) in all calculations to give a more detailed view of the community functional composition (WM – wing morphology).