



Cascading effects of landscape, mediated by mesoclimate, on carabid communities and weed seed predation in winter cereals



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ABSTRACT

Agricultural intensification, landscape simplification, and climate change threaten biodiversity and ecosystem services in arable lands. Increasing semi-natural habitats and landscape heterogeneity can mitigate these impacts by providing diverse habitats, resources and modifying climate at the landscape scale. As effective natural enemies in arable lands, carabids play a key role in pest and weed seed regulation and are influenced by field management and landscape. This study hypothesized that field management directly influences carabid communities and weed seed predation, while landscape factors affect them directly and indirectly through air temperature at the landscape scale. We sampled 77 winter cereal fields across 20 landscape windows representing regional landscape heterogeneity and composition. We monitored air temperature, carabid communities, and weed seed predation during two sampling sessions in late spring and early summer 2023. Piecewise Structural Equation Models were built to test for the direct and indirect effects of field-scale factors, landscape and climate at the landscape scale on carabids and weed seed predation. For both sampling sessions, results showed that the amount of semi-natural habitats and landscape heterogeneity primarily influence carabid activity-density and composition, which in turn affect weed seed predation. Grasslands, by providing resources and refuges, favour carabids but also appear linked to higher maximum air temperature, possibly influencing carabid composition via thermotolerance traits. The study highlights the importance of semi-natural habitats and landscape heterogeneity in shaping carabid communities and their ecosystem services in arable fields. Furthermore, for the first time, we have highlighted the potential influence of landscape context on carabids mediated by air temperature, which may affect weed regulation services through seed predation.

1. Introduction

Human activities pose major threats to biodiversity and ecosystem services in agricultural-dominated landscapes. Intensive farming practices, such as the use of fertilisers and pesticides, landscape simplification with field enlargement at the expense of semi-natural habitats and land-cover diversity (Newbold et al., 2015; Tscharntke et al., 2005a), have been stressed as key drivers of biodiversity decline. More recently, climate change has also emerged as a major factor (Newbold, 2018; Sánchez-Bayo and Wyckhuys, 2019; Urban, 2015), threatening agriculture and food security (Wiebe et al., 2019). In agroecosystems, many ecological services essential to crop production rely on biodiversity (e.g.

pollination and biological pest control; Dainese et al., 2019). For instance, carabids (Coleoptera, Carabidae) are abundant generalist predators in arable fields, with many species being able to consume substantial amounts of weed seeds (Frei et al., 2019; Honk et al., 2003; Kulkarni et al., 2015). Effectively promoting carabid communities should contribute to weed regulation (Bohan et al., 2011; Carbonne et al., 2020b; Schmucki et al., 2020), and a reduction in crop yield losses (Muneret et al., 2024). Therefore, understanding the relative importance of field management, landscape and climate filters that drive carabid communities and their effect on seed predation in fields is of key importance.

The effects of field-scale factors, notably farming practices, on

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carabid communities in arable fields have been widely studied (Holland and Luff, 2000). Soil disturbances linked to tillage (notably ploughing) and sowing, as well as chemical inputs, including insecticides, but also herbicides, and fungicides, have detrimental effects on carabid communities (Geiger et al., 2010; Holland and Luff, 2000; Müller et al., 2022; Navntoft et al., 2006). Conversely, incorporating temporary grasslands for 5 consecutive years or less into crop rotations as well as the application of organic fertilizers are generally beneficial for biodiversity (Hoeffner et al., 2021; Holland and Luff, 2000). These two factors increase soil organic matter and, thereby improve soil habitat quality and soil fauna, providing alternative prey for carabids (Aguilera et al., 2021; Heinen et al., 2024; Holland and Luff, 2000). Additionally, farming practices can influence the presence of arable weeds, which can support carabid richness and activity-density and modify species composition by providing shelter, a favourable microclimate and food resources (Diehl et al., 2012; Kulkarni et al., 2017; Saska et al., 2014). Consequently, maintaining a non-detrimental weed community can help sustain biodiversity in natural enemies, thereby enhancing the ecosystem services they provide.

The effect of large-scale factors, particularly the landscape, on carabid communities has also been well studied. There is growing consensus that increasing the extent of semi-natural habitats (e.g., hedgerows, grasslands) and enhancing landscape heterogeneity—both in composition (e.g., diversity of land-cover types) and configuration (e.g., density of edges between different land-cover types; Fahrig, 2017)—generally promotes higher species richness and alters species composition. However, its effects on carabid activity-density remain more variable (Gardiner et al., 2010; Hassan et al., 2018; Purtauf et al., 2005; Rusch et al., 2016). The landscape, through these habitats, can provide food resources, overwintering refuges, and source populations. It may also promote dispersal and foraging movements of carabids, facilitating the colonization of fields from other land-cover types (i.e. cross habitat spillover; Tscharntke et al., 2012; 2005b).

The mesoclimate, defined as the climate at the landscape scale, ranging from several hundred to a few kilometres (Hess, 1974) can be influenced by landscape components (Gerits et al., 2022; Sánchez et al., 2010; Sturman and Quénol, 2024). However, these relationships between landscape, climate, and biodiversity remains poorly documented in existing research. The studies on the relationship between landscape and mesoclimate have focused on hedgerow density, showing that high amount of hedgerows increases roughness in the landscape which affect airflow, reduces wind speed and alters temperatures with leading to lower minima and higher maxima (de Parcevaux and Guyot, 1980; Guyot and Seguin, 1978; Guyot, 1997). Increasing temperatures positively influence the activity of ectothermic organisms such as carabids, and affect species composition, as some species respond to minimum temperatures while others respond to maximum temperatures (Eyre et al., 2005; Honěk, 1997; Saska et al., 2013). Lower minimum temperatures and higher maximum temperatures might lead to later and earlier emergence of carabids (Forrest, 2016; Irmler, 2022), respectively, with consequences for their field colonization.

Field- and landscape-scale management that benefits carabid communities, particularly their activity-density, is expected to promote weed seed predation at the soil surface after seed dispersal. Consequently, this predation may reduce the renewal of the soil seed bank and limit future weed emergence (Blubaugh and Kaplan, 2016; Carbone et al., 2020b; Petit et al., 2018). However, the relationship between carabid activity-density and weed seed predation is not consistently supported (Jonason et al., 2013; Mauchline et al., 2005; Saska et al., 2008), suggesting the importance of species identity within carabid communities. Carabid species exhibit differences in foraging strategies (Charalabidis et al., 2019) and seed preferences (Honěk et al., 2003; Petit et al., 2014; Saska et al., 2019), with some keystone species having a disproportional effect on seed predation (Carbone et al., 2020a). Higher seed predation rates are expected when key predator species are present in communities and/or when species richness is high (Gaines

and Gratton, 2010; Jonason et al., 2013). Although most carabid species can consume both seeds and invertebrate prey (Kromp, 1999), species display predominant feeding preferences for either seeds or invertebrates (Talarico et al., 2016). The relationship between carabid communities and seed predation may be better predicted by considering carabid richness and composition – especially for seed-eating communities - in addition to activity-density (Gaines and Gratton, 2010; Jonason et al., 2013).

This study aimed to highlight the effects of human practices at both the landscape and field levels on carabid biodiversity and an associated ecosystem service: weed seed predation. Specifically, we aimed to understand how field-scale factors (farming practices and weed cover), landscape components (semi-natural habitat amount and landscape heterogeneity), and mesoclimate (mesoscale air temperature) could affect carabid activity-density and carabid community structure (species richness and composition) and in turn weed seed predation in winter cereal fields. Specifically, we hypothesised that:

(i) Less intensive farming practices and high weed cover, along with a greater amount of semi-natural habitats, increased landscape heterogeneity, and mesoscale air temperature extremes promote activity-density and species richness of carabid communities and modify their composition.

(ii) The activity-density, species richness, and composition of carabid communities influence weed seed predation intensity, with higher activity-density and species richness enhancing predation.

(iii) Field- and landscape-scale management have a cascading effect on weed seed predation mediated by carabid communities.

2. Materials and methods

2.1. Study area and large-scale sampling design

This study was conducted in 2023 in the Couesnon river watershed (1130 km²) in France (Fig. 1). This area has a flat relief, with granitic and schistose bedrock (Syndicat bassin versant du Couesnon, 2024), and the climate is temperate oceanic (mean annual temperature 11°C; mean annual precipitation 850 mm; Joly et al., 2010). The study site is characterised by a “bocage” landscape, with annual crops (mostly winter cereals and maize) and temporary and permanent grasslands interspersed with a more or less dense network of hedgerows and small post-agricultural woodlands. We selected twenty 1 km × 1 km landscape windows along four uncorrelated gradients: the amount of semi-natural habitat (grassland and hedgerow) and landscape heterogeneity (compositional and configurational heterogeneity) - for more details on the selection of windows, see Lecoq et al. (2022).

In each landscape window, we selected three to four winter cereal fields managed under conventional farming depending on their availability (three fields available for three landscape windows), resulting in 77 fields (60 grown with wheat, 11 with barley and 6 with triticale) ranging in size from 1.4 to 19.5 ha [mean ± SE (standard error of the mean): 5 ha ± 0.4]. Within each field, biological surveys (carabids, weed seed predation, and standing weeds) were conducted using three sampling points located 30 m from the edge and 15 m apart.

2.2. Carabid communities and weed seed predation

In each winter cereal field, carabid communities (Coleoptera: Carabidae) and weed seed predation were monitored over two sampling sessions aligned with crop phenology: one in late spring, during cereal growth (9–24 May), and the other in early summer, during cereal maturation, just before harvest (6–21 June).

Carabid communities were sampled using three pitfall traps consisting of a plastic container (9 cm diameter, 11.5 cm depth), half-filled with a preservative solution of salt-saturated water, and a few drops of odourless soap to reduce surface tension. Traps were buried flush with the soil surface and covered with a plastic roof (10 cm × 13.5 cm) to

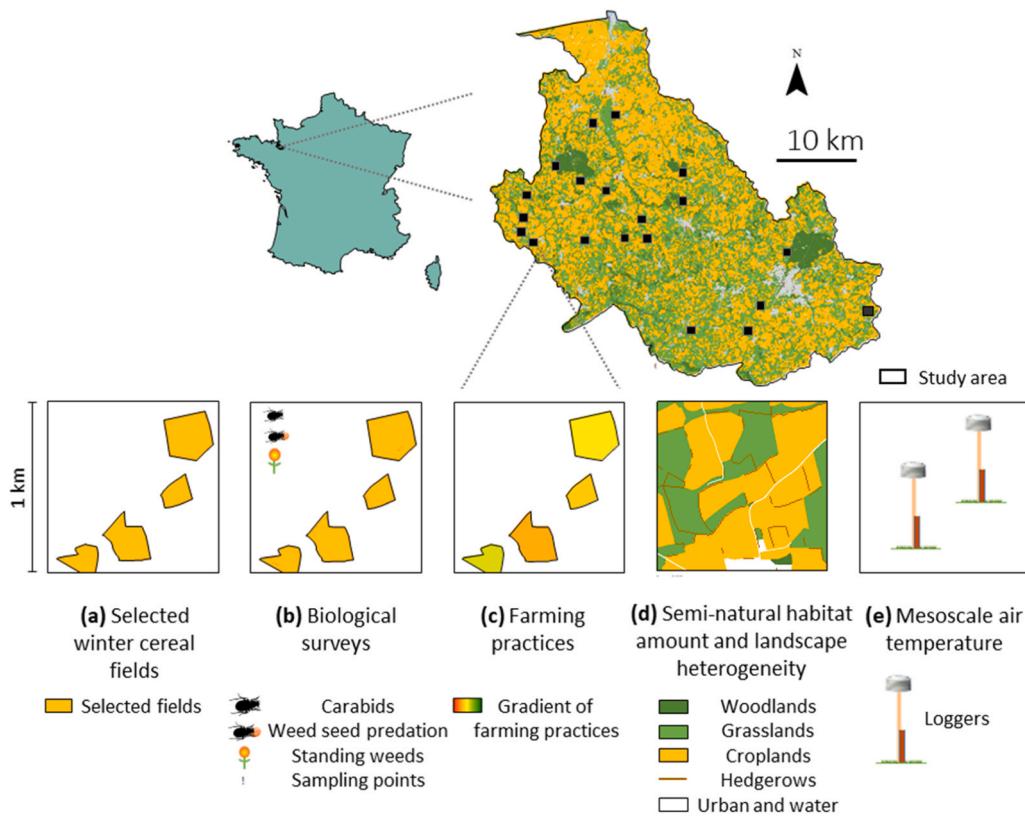


Fig. 1. Overview of the sampling design of twenty $1 \text{ km} \times 1 \text{ km}$ landscape windows along four uncorrelated gradients of semi-natural habitat amount and landscape heterogeneity in the Couesnon watershed (based on Lecoq et al., 2022). In each landscape window, (a) three to four winter cereal fields were selected. Within each field, we conducted: (b) biological surveys to describe carabid communities and weed seed predation by invertebrates (for *Poa annua* and *Viola arvensis*), and to measure weed cover, and (c) collected information about the farming practices conducted in fields. In each landscape window, we assessed: (d) semi-natural habitat amount (grassland and hedgerow amount) and landscape heterogeneity (compositional and configurational heterogeneity) and (e) mesoscale air temperature (minimum and maximum), from two loggers installed in each landscape window.

protect them from rainfall. Pitfall traps were opened for 14 days. Carabids collected in the three traps were pooled at field level for each sampling session and transferred to 70 % alcohol prior to identification. We identified and counted carabids to species level following Roger et al. (2013). Species names follow Fauna Europaea (de Jong et al., 2014). Recorded species were then classified into three trophic groups: granivorous, omnivorous or carnivorous using the online database carabids.org (Homburg et al., 2014) as the main source. For each field and each session, we described carabid activity-density, richness and composition. These descriptors were separately computed for all species and seed-eating species only (i.e. omnivorous and granivorous species). For the second sampling session, all traps were destroyed in two fields, leading to missing values, and some traps were destroyed in three other fields. This sampling imbalance between fields was taken into account in the analyses (see section Statistical analyses). Species composition was estimated using the coordinates of fields on the two first axes (hereafter referred to as “composition 1” and “composition 2”) of a Correspondence Analysis (CA) using the R package “FactoMineR” (Lê et al., 2008). Two CA were performed on the species presence-absence matrix for the first and second sampling sessions separately, after removing species present in fewer than 5 % of the fields (i.e. in fewer than four fields; McCune and Grace, 2002). As a result, 18 species (36 %) were removed from the first session dataset and 26 species (53 %) from the second session dataset. However, these removed species represented less than 0.5 % of the total activity-density in our dataset.

Weed seed predation by invertebrates was quantified by exposing three seed cards (Westerman et al., 2003) enclosed by vertebrate exclusion cages (1.3 cm wire mesh) for two weed species: *Poa annua* (family: Poaceae) and *Viola arvensis* (family: Violaceae). We selected

these species because they are common weeds in our study area and are likely to be easily consumed by various carabids (Charalabidis et al., 2025; Gaba et al., 2019; Honěk et al., 2007; Petit et al., 2014), owing in part to their low mass (0.30 mg for *P. annua*, 0.46 mg for *V. arvensis*; Bretagnolle et al., 2016). *Viola arvensis* is a model seed widely used in in-field predation experiments, and *P. annua* is of agronomic interest due to its herbicide tolerance (McCurdy et al., 2023). Seeds were purchased from Arbiotech (Rennes, France). For each species, twenty weed seeds were glued (glue: SADER® WOOD PRO D3 diluted with two-thirds of water) onto a $5 \text{ cm} \times 5 \text{ cm}$ card of sand paper (grain size: 120) following the protocol of Westerman et al. (2003). The cards were fixed to the soil with nails and left exposed for 7 days, simultaneously with the pitfall traps. The seed predation rate was measured at field level for each session and each weed species, using the total number of seeds removed relative to the total number of seeds exposed (both pooled at the field level from the three cards). Partially eaten seeds, which occur occasionally, are counted as predated since they are no longer capable of germinating. One of the three cages enclosing the seed cards was removed in certain fields, so the predation rate for those fields was calculated based on only two cards. For the second session, the seed predation rate for both species could not be estimated in one field, as all the cages had been destroyed.

2.3. Farming practices

We collected information about the farming practices conducted in the 77 winter cereal fields selected from (i) the Graphical Parcel Register (2020, 2021 and 2022) and (ii) interviews with farmers. We collected information on the (i) presence of grassland in the rotation over the

period 2020 – 2022 (grassland/no grassland), (ii) use of ploughing (i.e. ploughing /no ploughing), (iii) number of visits for tillage (excluding ploughing) and sowing operations, (iv) number of visits for pesticide applications, including herbicides (before or after sowing), fungicides, and insecticides, (v) presence of organic fertilisation (OF/no OF), and (vi) number of visits for mineral fertiliser applications. Quantitative variables were not or not overly correlated (Spearman's correlation, $0.10 \leq |\rho| \leq 0.34$; Table S1a), and qualitative variables were not significantly associated (Fisher's Exact test for Count data, p-value > 0.05; Table S1a). We then summarised farming practices using the coordinates of fields on the two first axes of a Factor Analysis of Mixed Data (FAMD) using the R package "FactoMineR" (Lé et al., 2008). The two first axes of farming practices jointly explain 53.2 % of the total variance, with axes 1 and 2 explaining (hereafter referred to as "farming practices 1" and "farming practices 2") 27.6 % and 25.6 % of the total variance, respectively. Farming practices 1 was related to farming inputs and was positively associated with more visits for mineral fertilisation and pesticide use (i.e. chemical inputs) and negatively associated with the presence of organic fertilisation. Farming practices 2 was related to soil disturbance, and was positively associated with the absence of deep ploughing, but with more frequent shallow soil tillage operations (Figure S2, Table S2). The distribution of variables related to farming practices (before and after being summarised by the coordinates of fields on the two first axis of the FAMD) is presented in Table S3a.

2.4. Weed cover

We conducted weed surveys in 77 winter cereal fields in June 2023, concurrently with the carabid surveys, to assess the weed community as a potential refuge and source of trophic resources during this period. We identified each herbaceous species and estimated its percentage cover using a 1 m × 1 m quadrat located at the three sampling points described previously. A few closely related herbaceous species, which can be easily confused at the vegetative stage, have been grouped under the same name, and three plants could not be identified (Table S4). Nomenclature followed the French taxonomic register TAXREF (Gargominy et al., 2022). In total, 58 herbaceous species were recorded. The most common species were the *Poa annua* / *trivialis* / *pratensis* group and *Juncus bufonius* (Table S4).

For each field, we measured the total weed cover (hereafter referred to as weed cover) by summing the percent cover of all species recorded in the three quadrats. Weed cover varied between zero and 353.2 %, and was on average of 25.2 ± 7.6 %. The weed cover was then fourth-root transformed to correct for skewness (Table S3b). The fourth root transformation was preferred to the popular logarithmic transformation, as weed cover includes zero values (Osborne, 2002).

2.5. Semi-natural habitat amount and landscape heterogeneity

We digitised the land cover map of the twenty 1 km × 1 km landscape windows by combining the OSO land cover map of 2022 (raster map, pixel size = 10 m resolution), automatically produced by the French Theia Land Data Centre (<https://www.theia-land.fr/en/product/land-cover-map/>) using Sentinel-2A and Sentinel-2B data, and the Graphical Parcel Register of 2022 (vector map, 1/5000) provided by the National Institute of Geography (<https://geoservices.ign.fr/rpg>). We identified five land cover classes: grasslands, croplands, woodlands, urban (built-up areas and roads), and water (water bodies and water-courses) elements. We digitised the hedgerow network from a field-based map provided by the Syndicat bassin versant du Couesnon (<https://geocouesnon.bassin-couesnon.fr/geocouesnon/>). The amount of semi-natural habitats (grasslands and hedgerows) was quantified using the proportion of the landscape window occupied by grasslands and the total length (in meters) of hedgerows in the landscape window respectively. Compositional and configurational heterogeneities were assessed based on grasslands, woodlands, and croplands as they are habitats for

carabids. Compositional heterogeneity was quantified using Shannon's diversity index (*SHDI*), given by $SHDI = -\sum_{i=1}^c p_i \ln p_i$, where p_i is the proportion of the landscape window (including unconsidered classes) occupied by class i and c is the number of considered classes (Ingla et al., 2017). The higher the *SHDI*, the higher the compositional heterogeneity (i.e. the more land cover types and/or the more equally distributed the proportions of land cover classes; McGarigal et al., 2012). Configurational heterogeneity was quantified by the proportion of heterogeneous pairs of adjacent pixels (i.e. pairs of adjacent pixels with different land cover classes, p_{hete}), given by: $p_{hete} = \frac{\sum_{i=1, i \neq j}^c n_{ij}}{\sum_{i=1}^c n_{ij}}$, where n_{ij} is the number of pairs between adjacent pixels of class i and j , c is the number of considered classes and c_T is the total number of classes (including unconsidered classes). The higher the p_{hete} , the higher the configurational heterogeneity. The proportion of grasslands, the Shannon's diversity index (*SHDI*) and the proportion of heterogeneous pairs of adjacent pixels (p_{hete}) were computed using Chloe software (Boussard and Baudry, 2017), coding unconsidered classes (urban and water elements) as zero. The total length of hedgerows was computed using ArcGis 10.8.1. All landscape indices displayed correlations under 0.45 (Pearson's correlations, Table S1b). Their distributions are summarised in Table S3c.

2.6. Mesoscale air temperature

Two air temperature loggers were installed in each landscape window. These loggers (Tinytag Plus 2 - TGP-4017, © Tinytag) recorded air temperature every hour and were placed in shelters (ACS-5050, © Tinytag) and fixed to a wooden pole 2 m above the ground. The loggers are located in open habitats (i.e. grassland or cropland), positioned at least 20 m away from buildings to avoid local or even micro-local effects as much as possible, as recommended by the World Meteorological Organization (2023). From hourly air temperature measurements, the daily minimum (between 18 UTC the previous day and 18 UTC) and the daily maximum (between 6 UTC and 6 UTC the day after) air temperatures were calculated for each day of the two sampling sessions. Then, the daily minimum and maximum averages were calculated over all days in each of the two sampling sessions. For each sampling session and landscape window, the average daily minimum and maximum air temperatures measured by the two loggers were averaged (hereafter referred to as "minimum air temperature" and "maximum air temperature"). One of the two loggers fell to the ground in one landscape window, resulting in the minimum and maximum air temperatures being calculated from a single logger for this window. We assessed Pearson's correlations between minimum and maximum air temperatures, the geographical coordinates of landscape windows, and the mean elevation of landscape windows across both sessions. These variables were not or not overly correlated (Table S1c). The mean ± SE minimum air temperature was $7.8 \pm 0.1^\circ\text{C}$ and $14.2 \pm 0.1^\circ\text{C}$ during spring and summer sessions, respectively, and the mean maximum air temperature was $18.0 \pm 0.1^\circ\text{C}$ and $25.3 \pm 0.1^\circ\text{C}$, respectively (Table S3d).

2.7. Statistical analyses

We used piecewise Structural Equation Models (pSEM; Lefcheck, 2016) to investigate the effects of local, landscape and mesoclimatic factors on carabid communities and their cascading effects on seed predation rates for the two weed species. For each sampling session, we built two separate pSEMs, one for "all species" and another for "seed-eating species" carabid communities, resulting in four pSEMs.

With each of these pSEMs, we first investigated the effects of landscape (grassland and hedgerow amount, compositional and configurational heterogeneity) on mesoscale air temperature (minimum and maximum air temperature) using multiple Ordinary Least Square (OLS; R package "stats") regression (N = 20 landscape windows). Second, we

investigated the effects of farming practices (farming practices 1 and 2), weed cover, landscape components and mesoscale air temperature on carabid communities (activity-density, species richness, composition 1 and 2) ($N = 77$ fields for the first session, $N = 75$ fields for the second session). We used a (i) Poisson Generalised Linear Mixed Model (GLMM) with a log-link function (R package “stats”) and (ii) multiple OLS regression model to assess these effects on the (i) activity-density and species richness and (ii) composition (1 and 2), respectively. For the second session, an offset describing the number of pitfall traps used to estimate activity-density per field was added to the poisson GLMM to account for the imbalance caused by destroyed traps. For species richness, we could not correct and rarefy the data because the three traps from each field were directly pooled during collection. Third, we investigated the effects of carabid communities on the seed predation rates of *V. arvensis* and *P. annua*. These effects were tested using binomial Generalized Linear Mixed Models (GLMM; R package “glmmTMB”; Brooks et al., 2017) with a logit-link function. For models analyzing activity density and weed seed predation, we included an observation-level random effect (OLRE) to account for overdispersion (Harrison, 2015). Given the spatial structure of our sampling design, we included a random effect for the window identifier in all models conducted at the field scale, to account for the fact that several fields were nested within a single window. In addition, we tested the spatial autocorrelation of each response variable (Moran's I test) using the Moran.I function of the R package “ape” (Paradis and Schliep, 2019). For each spatially auto-correlated response variable (see Table S5), we added an autocovariate (i.e. a distance-weighted function of neighbouring response values; Dormann et al., 2013) in addition to other explanatory variables to the model, using the autocov.dist function of the R package “spdep” (Bivand, 2022; see Appendix S1 for further details). All full models were tested for multicollinearity using the variance inflation factor (VIF), and all VIF values were below three, indicating negligible collinearity (Zuur et al., 2010). VIF values were computed using the R package “car” (Fox and Weisberg, 2019) for all models, except for binomial GLMMs for which the R package “performance” (Lüdecke et al., 2021) has been used.

To reduce pSEM complexity, all of the full models were optimised using a multi-model inference based on the Akaike information criterion corrected for small sample sizes (AICc). We built all possible candidate models based on all additive combinations of up to two (for models with $N = 20$) or seven (for models with $N = 77$ or 75) explanatory variables and ranked them by the AICc using the R package “MuMI” (Bartoń, 2022). Models with the smallest AICc were retained as the most parsimonious (Burnham and Anderson, 2002). We checked all models for independence of residuals, along with equal variance and normality of residuals for multiple OLS regression models. All models were checked for spatial autocorrelation of residuals using Moran's I test (see Appendix S1 for further details). Poisson and binomial GLMMs were also checked for under- and overdispersion and zero-inflation (see Appendix S1 for further details). Model validation was performed with the R package “DHARMA” (Hartig, 2022).

Following this procedure, eight initial most parsimonious models (two for minimum and maximum temperatures, four for carabid community descriptors, and two for seed predation) were included in each pSEM using the R package “piecewiseSEM” (Lefcheck, 2016). Overall fit of pSEM was checked using Shipley's test of directed separation based on the χ^2 distributed Fisher's C statistic and AIC. This procedure checks for missing connections between unlinked variables by testing whether any omitted relationships in our initial model are significant. When Shipley's tests of directed separation suggested lack of pSEM model fit, we added significant correlated errors (non-causal relationships) and missing paths (causal relationships; see Appendix S1 for further details). The eight updated most parsimonious models and correlated errors included in each pSEM are summarised in Table S5. The method used to retrieve the summary of models included in each pSEM is described in Appendix S1. In addition to the pSEMs, we conducted paired

permutation Student's t-tests using the “RVAideMemoire” R package (Hervé, 2023) to compare *P. annua* and *V. arvensis* seed predation in late spring and early summer.

All analyses were performed using R software version 4.2.1.

3. Results

We chose to present in the main text only results for carabid communities composed of “seed-eating species”. The description of communities containing “all species”, as well as the effects of local, landscape, and mesoclimatic factors on “all species” and their cascading effects on seed predation rates are provided in Appendix S2.

3.1. Description of communities composed of “seed-eating species”

A total of 46 461 (late spring: 28 361; early summer: 18 100) seed-eating individuals belonging to 26 carabid species were found in cereal fields (late-spring: 20; early summer: 21) (Table S7). In late spring, Composition 1 of seed-eating species (CA-axis 1–16.0 % of total variance) was positively associated with *Amara plebeja*, *Amara aenea*, and *Anisodactylus binotatus* and negatively associated with *Pterostichus madidus*. Composition 2 (CA-axis 2–13.2 % of total variance) was positively associated with *Amara montivaga*, *Pseudoophonus rufipes*, and *Amara similata*, and negatively associated with *P. madidus* (Fig. 2a and Table S6c). In early summer, Composition 1 of seed-eating species (23.0 % of total variance) was positively associated with the *Amara* genus and negatively associated with *Trechus quadrifasciatus*, whereas Composition 2 (18.1 % of total variance) was positively associated with *P. madidus* and *P. rufipes* and negatively associated with *T. quadrifasciatus* (Fig. 2b and Table S6d).

3.2. Effects of local, landscape and mesoclimatic factors on “seed-eating species” carabid communities

In late spring (Fig. 3a and Table S5c), the activity-density of seed-eating species increased when grassland area ($p\text{-value} = 0.001$) increased and when hedgerow amount decreased ($p\text{-value} < 0.001$). Their richness was independent of the variables tested ($p\text{-value} > 0.05$). The “composition 1” of seed-eating species increased when configurational heterogeneity decreased ($p\text{-value} = 0.030$), and when the minimum temperature increased ($p\text{-value} = 0.015$). This suggests that lower configurational heterogeneity and higher minimum temperature favoured the presence of *A. plebeja*, *A. aenea*, and *A. binotatus*, while disfavouring *P. madidus* in fields.

In early summer (Fig. 3b and Table S5d), the activity-density of seed-eating species increased when grassland area increased ($p\text{-value} = 0.026$) and when hedgerow amount decreased ($p\text{-value} = 0.045$), and their richness increased when weed cover increased ($p\text{-value} = 0.006$). The “composition 1” of seed-eating species increased when weed cover ($p\text{-value} < 0.001$) and grassland area increased ($p\text{-value} = 0.014$) and the maximum air temperature decreased ($p\text{-value} = 0.029$). This indicates that higher weed cover and grassland area and lower maximum air temperature favoured the *Amara* genus at the expense of *T. quadrifasciatus*.

The landscape did not influence mesoscale air temperature in late spring ($p\text{-value} > 0.05$; Fig. 3a and Table S5c), but it did in early summer (Fig. 3b and Table S5d). Specifically, higher grassland area increased the maximum air temperature ($p\text{-value} = 0.044$, standardised estimate = 0.46). As maximum air temperature affected the “composition 1” of seed-eating species ($p\text{-value} = 0.029$, standardised estimate: - 0.26), we consequently observed an indirect negative effect (standardised estimate: - 0.12) of grassland area (i.e. mediated by maximum air temperature) on the composition of seed-eating species during early summer (Fig. 3b and Table S5d).

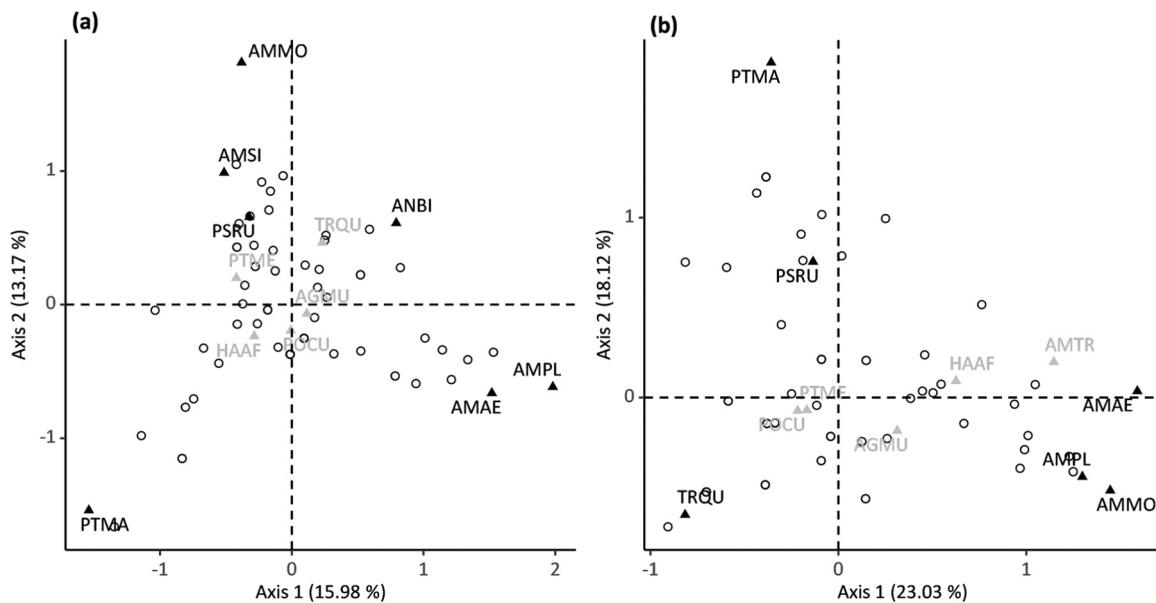


Fig. 2. Graphs describing the composition (in presence-absence) of seed-eating species in winter cereal fields for the (a) first and (b) second sessions on the two first axes of the Correspondence Analysis (CA). Only species (triangles) present in at least 5 % of fields (circles) for a given session were included. Species that contributed the most to the first and the second axes are in black (see Table S6c and d for further details). Species abbreviation: AGMU: *Agonum muelleri*, AMAE: *Amara aenea*, AMMO: *Amara montivaga*, AMPL: *Amara plebeja*, AMSI: *Amara similata*, AMTR: *Amara tricuspidata*, ANBI: *Anisodactylus binotatus*, HAAF: *Harpalus affinis*, POCU: *Poecilus cupreus*, PSRU: *Pseudocephonus rufipes*, PTMA: *Pterostichus madidus*, PTME: *Pterostichus melanarius*, TRQU: *Trechus quadrifasciatus*. Graphs were produced using the R package “factoextra” (Kassambara and Mundt, 2017).

3.3. Effects of “seed eating species” carabid communities on weed seed predation

For both sampling sessions, seed predation was higher for *V. arvensis* than for *P. annua* ($p < 0.001$ in late spring and $p = 0.011$ in early summer; Figure S4). Seed predation on *P. annua* was higher in early summer than in late spring ($p = 0.026$), whereas no seasonal difference was detected for *V. arvensis* ($p > 0.05$). In late spring, the seed predation rate of *P. annua* was positively correlated with the “composition 2” of seed-eating species ($p\text{-value} = 0.047$): the presence of the seed-eaters *A. montivaga*, *P. rufipes*, and *A. similata* in fields (at the expense of *P. madidus*) led to higher *P. annua* seed predation rates. The seed predation rate of *V. arvensis* was positively related to the activity-density ($p\text{-value} = 0.002$) and the richness of seed-eating species ($p\text{-value} = 0.004$) (Fig. 3a and Table S5c).

In early summer, the seed predation rates of *P. annua* ($p\text{-value} = 0.001$) and *V. arvensis* ($p\text{-value} = 0.001$) were negatively related to the “composition 1” of seed-eating species (Fig. 3b and Table S5d). This means that the presence of the seed-eating *Amara* genus at the expense of *T. quadrifasciatus* in fields was associated with lower seed predation rates for both plant species. The seed predation rate of *V. arvensis* was also positively correlated with the activity-density of seed-eating species ($p\text{-value} = 0.011$).

3.4. Effects of local, landscape and mesoclimatic factors on weed seed predation

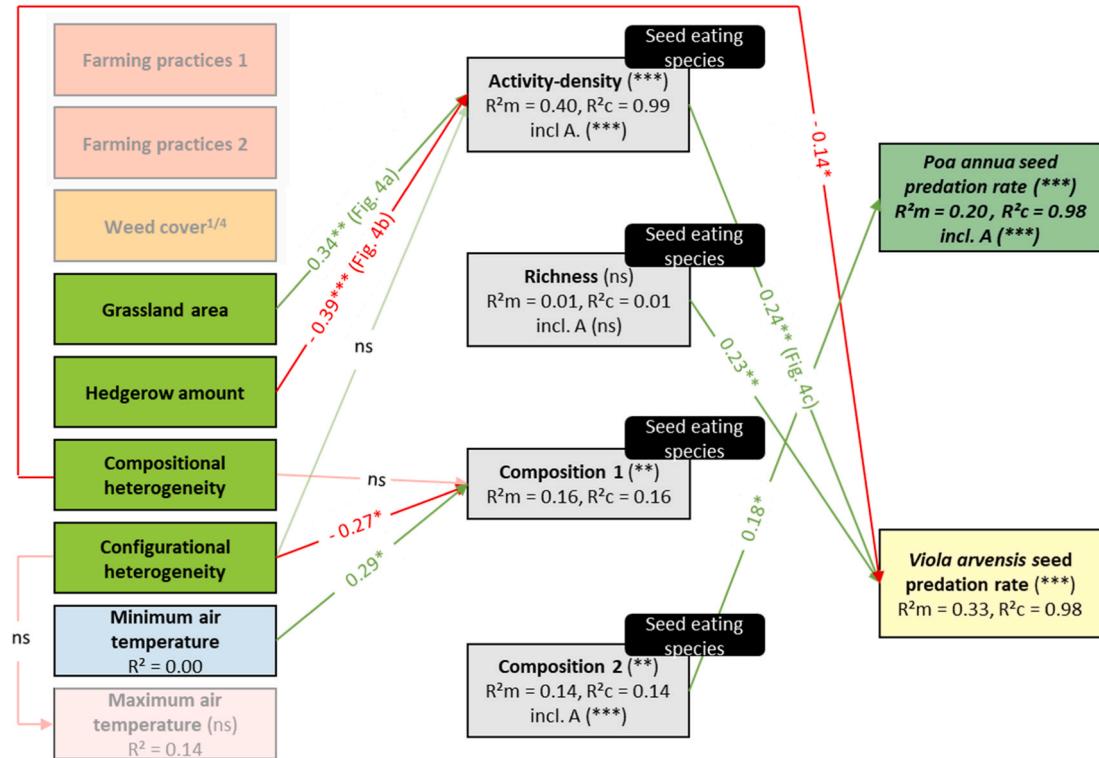
The pSEMs allowed us to identify indirect effects on weed seed predation, mediated by seed-eating carabid assemblages, resulting from weed cover and mesoscale maximum air temperature in early summer only. Additionally, the landscape influenced weed seed predation both directly and indirectly through seed-eating carabid assemblages in late spring and early summer.

In late spring (Fig. 3a and Table S5c), both grassland area and hedgerow amount also affected indirectly the seed predation rate of *V. arvensis* through the activity-density of seed-eating species: higher grassland area increased the seed predation rate of *V. arvensis* by

increasing the activity-density of seed-eating species (standardised estimate: $0.34 \times 0.24 = 0.08$), whereas hedgerow amount decreased the seed predation rate of *V. arvensis* by decreasing their activity-density ($-0.39 \times 0.24 = -0.09$). In addition, compositional heterogeneity affected directly and negatively (-0.14) the seed predation rate of *V. arvensis* (Fig. 4b and c).

In early summer (Fig. 3b and Table S5d), weed cover affected indirectly and negatively the seed predation rates of both *P. annua* ($0.44 \times -0.24 = -0.11$) and *V. arvensis* ($0.44 \times -0.33 = -0.15$) by affecting the “composition 1” of seed-eating species. At larger scales, maximum air temperature affected indirectly and positively the seed predation rate of both *P. annua* ($-0.26 \times -0.24 = 0.06$; Fig. 5c and d) and *V. arvensis* ($-0.26 \times -0.33 = 0.09$; Fig. 5c and e), by reducing the “composition 1” of seed-eating species (that is by favouring the presence of *T. quadrifasciatus* at the expense of the *Amara* genus). Grassland area affected indirectly and positively the seed predation rate of *V. arvensis* by increasing the activity-density of seed-eating species ($0.22 \times 0.22 = 0.05$). In addition, grassland area indirectly affected the seed predation rates of both *P. annua* ($0.44 \times -0.24 = -0.11$) and *V. arvensis* ($0.44 \times -0.33 = -0.15$), by affecting the “composition 1” of seed-eating species. Specifically, grassland area led to a decrease in the seed predation rates of both weed species by favouring the presence *Amara* genus at the expense of *T. quadrifasciatus* in fields (Fig. 5b, d and e). Of note, grassland area also indirectly and positively affected the seed predation rates of both weed species (*P. annua*: $0.46 \times -0.26 \times -0.24 = 0.03$, *V. arvensis*: $0.46 \times -0.26 \times -0.33 = 0.04$) by increasing maximum air temperature (Fig. 5a), which decreased the “composition 1” of seed-eating species (Fig. 5c). Yet, these indirect positive (through maximum air temperature influencing seed-eating species composition) and negative (through seed-eating species composition alone) effects of grassland area on weed seed predation resulted in an overall indirect negative effect for both weed species (*P. annua*: $-0.11 + 0.03 = -0.08$ and *V. arvensis*: $-0.15 + 0.04 = -0.11$) (Fig. 5). Hedgerow amount affected directly and positively (0.21) the seed predation rate of *V. arvensis*, but also indirectly and negatively through the activity-density of seed-eating species ($-0.19 \times 0.22 = -0.04$) resulting in an overall positive effect (0.18).

(a) AIC = 2740.10, Fisher's C = 78,286, p-value = 0.997



(b) AIC = 2712.97, Fisher's C = 75.486, p-value = 0.735

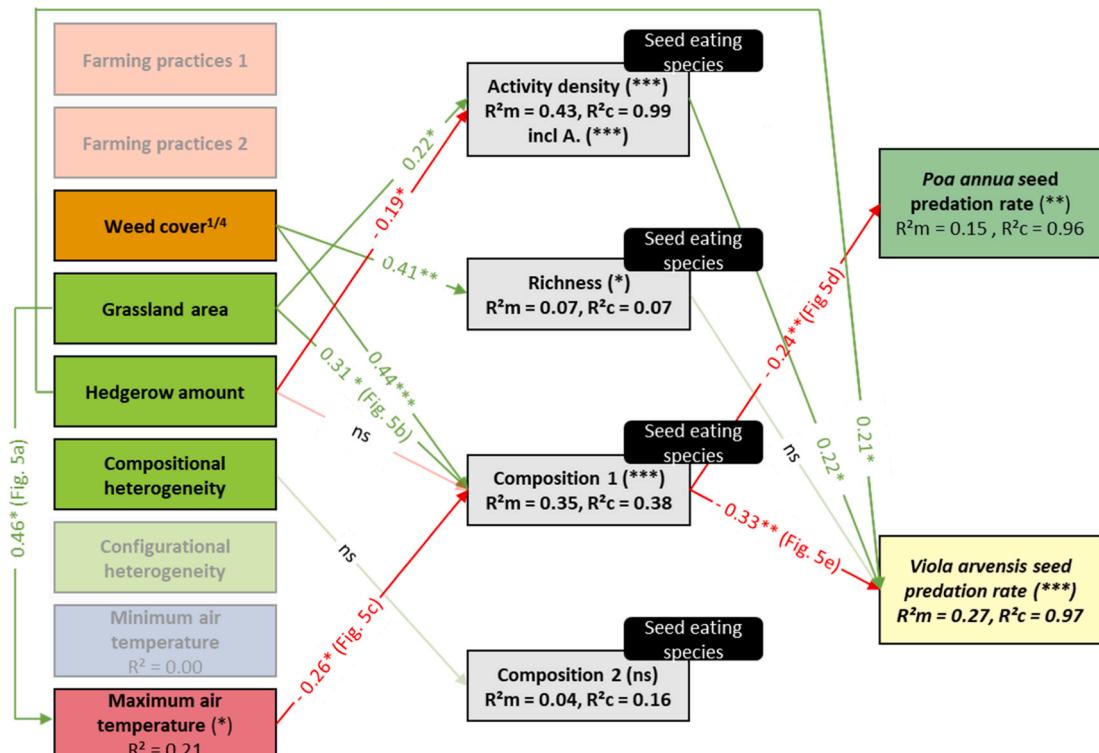


Fig. 3. Structural equation models explaining seed predation rates through seed-eating carabid communities in the (a) late spring and (b) early summer sessions. Model significance and associated R-squared are shown in the box of each response variable (model significance not shown with an associated R-squared of zero denotes model without any explanatory variables). The presence of an autocovariate (A) in the model and its significance are also shown in the box of concerned response variable. Non-transparent green and red arrows with standardised estimates denote significant positive and negative effects of explanatory variables, respectively. Transparent green and red arrows denote non-significant positive and negative effects of explanatory variables, respectively. Transparent box denotes explanatory or response variables that are not significantly involved. The significance is indicated by asterisks: ns: not significant, *: p-value < 0.05, **: p-value < 0.01, ***: p-value < 0.001. See Table S5c and d for further details on models.

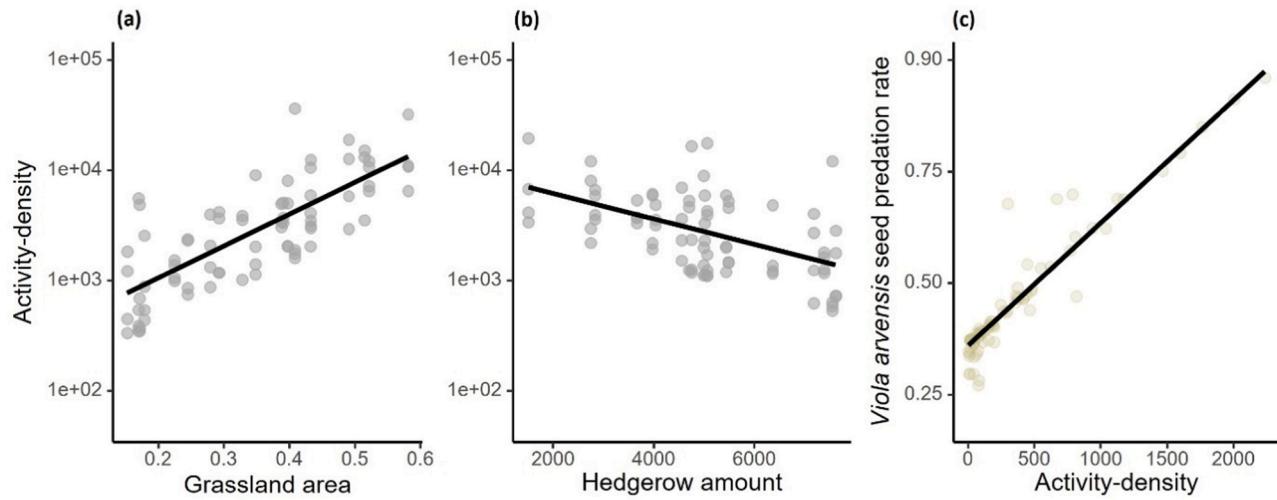


Fig. 4. Partial residual plots showing the significant indirect effects of (a) grassland and (b) hedgerow amount on the seed predation rate of *V. arvensis* through (c) the activity-density of seed-eating species in late spring. Please, note that all y-axes are on a log-scale (for activity-density) or on a logit-scale (for *Viola arvensis* seed predation rate). Partial residuals were calculated from significant linear models implemented in the pSEM conducted in late spring. See Table S5c for further details on models.

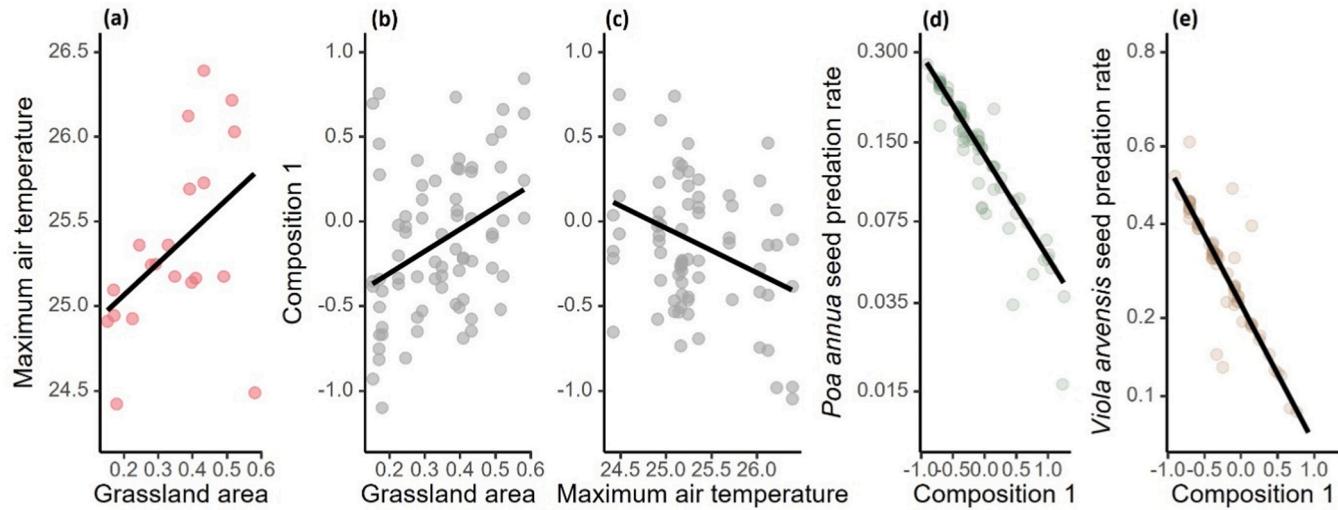


Fig. 5. Partial residual plots showing the significant indirect effects of grassland area, either through (a) maximum air temperature and (b,c) seed-eating species composition 1, on the seed predation rate of (d) *P. annua* and (e) *V. arvensis* in early summer. Please note that y-axes for the seed predation rates of both *P. annua* and *V. arvensis* are on a logit-scale. Partial residuals were calculated from significant linear models implemented in the pSEM conducted in early summer. See Table S5d for further details on models.

4. Discussion

Our study highlighted the cascading effects of local factors, landscape components and mesoclimate (air temperature) on the weed seed predation service through carabid communities. In addition, in one sampling period, we showed an indirect effect of landscape on carabids mediated by mesoscale air temperature with cascading effects on weed seed predation. Our results revealed that some of these complex cascading effects were present across both sampling periods, while others changed over time as the biotic and abiotic conditions of the fields evolved.

4.1. Field-scale factors affected carabid communities

According to our first hypothesis, high weed cover in early summer increased the carabid species richness in winter cereal fields, corroborating evidence from other studies (e.g. Diehl et al., 2012; O'Sullivan &

Gormally, 2002). This effect was observed only in early summer, coinciding with the flowering and seed dispersal of weeds. Therefore, it is likely that the effect of weed cover on the richness of carabids was partly mediated by the supply of seeds on the soil surface, favouring seed-eating carabid species in particular (Carbone et al., 2022). In addition, we found that high weed cover affected species composition by favouring the presence of the seed-eater *Amara* genus at the expense of *T. quadrivittatus* as shown in the composition analysis, in line with other studies (Holland et al., 1999; Kromp, 1990). No effect of weed cover was detected on carabids in late spring, potentially because herbicides are still applied in fields at this period and reduce the expression of weed flora.

In addition, contrary to our first hypothesis, we detected no significant effect of agricultural practices on carabid communities in our study. This absence of a management signal is likely due to the fact that the effects of farming practices on carabid communities may be mediated indirectly, primarily through their impact on weed communities

(Carbone et al., 2022). Moreover, our field selection strategy was designed primarily to span broad gradients in landscape composition rather than to maximise contrasts in local farming practices. As a result, the range of agricultural treatments represented in our dataset were likely too limited to elicit detectable responses, even for dominant species such as *P. cupreus* and *P. melanarius*, which are known elsewhere to respond to ploughing intensity (Baguette and Hance, 1997; Holland and Luff, 2000; Müller et al., 2022).

4.2. Landscape-scale factors drive carabid communities

Landscape components affected carabid communities in both sampling sessions as expected in our first hypothesis. We primarily highlighted the effect of semi-natural habitat amounts (grassland, hedgerow) on the activity-density and species composition of carabids. In contrast, the heterogeneity of composition and configuration only affected species composition. Species richness was however independent from these landscape components. Additionally, we detected an indirect effect of the landscape on carabid composition through mesoscale maximum air temperature in early summer, and a correlation between mesoscale minimum air temperature and carabid composition in late spring.

An increase in the grassland area in the landscape positively affected the activity-density of seed-eating species in late spring and early summer. However, the amount of hedgerow decreased the carabid activity-density of seed-eating species in fields in late spring and early summer. Our results may be related to the positive role of grasslands as refuges and overwintering habitats (Labruyere et al., 2016; Marrec et al., 2017), and the barrier effect of hedgerows for some dominant species such as *P. cupreus* (Mauremooto, 1995; Thomas et al., 1998).

No effect of the landscape was detected on carabid species richness, regardless of the sampling session; however, we did detect effects on species composition. Lower configurational heterogeneity was expected to act as a strong ecological filter by selecting species with high dispersal abilities, mostly by decreasing opportunities of cross-habitat spillover (Tscharntke, et al., 2005b; Tscharntke et al., 2012). We demonstrated that low configurational heterogeneity favoured the presence of winged species (*A. plebeja*, *A. aenea*, and *A. binotatus*), while disfavouring the dimorphic species *P. madidus* in fields in late spring, as evidenced by the composition analysis. The timing of this effect is likely due to these winged species using flight to migrate from overwintering habitats to reproduce in winter cereals in spring. *Pterostichus madidus* was favoured by higher configurational heterogeneity, suggesting that it uses several habitat types during its lifespan (landscape complementation; Dunning et al., 1992) and has high dispersal abilities owing to its large body size (Holland et al., 2004). In early summer, grassland area influenced species composition. Higher grassland area favoured *Amara* genus at the expense of *T. quadrivittatus*, suggesting that *Amara* species benefit from the refuges and food resources provided by grasslands. The positive role of grasslands adjacent to fields was already shown for *A. aenea* (Labruyere et al., 2016).

In addition, we detected an indirect effect of landscape on carabids, mediated by mesoclimate. In early summer, higher grassland area increased the maximum air temperature likely due to the reduced height of grassland vegetation during this period, after grazing or mowing (Dusseux et al., 2015). However, this link requires further investigation. Conversely to our expectation, we did not detect any effect of hedgerow amount on air temperature, which contrasts with previous studies (de Parcevaux and Guyot, 1980; Guyot and Seguin, 1978). This lack of effect may be explained by hedgerow quality variables and their orientation with the prevailing wind. As expected, minimum air temperatures influenced the composition of seed-eating species during the colder sampling session, in late spring, whereas maximum air temperatures influenced it during the warmer one, in early summer. Temperature influences carabid species composition likely as the result of species thermal niches, which differs among species (Piano et al., 2017). The effect of climate on carabid composition, partly indirectly driven by

landscape changes, is an original finding which requires further research, incorporating additional climatic parameters (such as humidity and rainfall) and conducting long-term studies to better understand the influence of landscape on mesoclimate.

4.3. Carabid communities drive weed seed predation

Following our second hypothesis, carabid communities (activity-density, species richness and composition) influenced weed seed predation. During both periods, late spring and early summer, the activity-density of carabids had a positive effect on the seed predation on *V. arvensis* corroborating previous studies using the same weed species (Carbone et al., 2020a; Petit et al., 2014). However, no effect was detected on the predation on *P. annua* contrary to previous studies (e.g. Carbone et al., 2020b). Although both seed species have low mass (Bretagnolle et al., 2016), *V. arvensis* seeds were significantly more predated than *P. annua* seeds. In addition to seed structural constraints, such as seed size or coat properties (Foffová et al., 2020), carabid seed choice/selection may rely also on lipid content, which is higher for *V. arvensis* than for *P. annua* (seed lipid content: 33.3 % vs. 4.0 % respectively) (Gaba et al., 2019). In early summer, a higher richness of seed-eating species only increased *V. arvensis* predation. These positive effects of richness could result from complementarity between species concerning for example their foraging strategies (Charalabidis et al., 2019) or ecological niche (Rouahab et al., 2024). Additionally, our results highlighted relationships between carabid species composition and weed seed predation. We observed that the presence of *A. montivaga*, *A. similata*, *P. rufipes* and *A. binotatus*, as opposed to *P. melanarius*, was associated with greater predation on *P. annua* seeds in late spring. This result was not surprising, as the previously mentioned species were known to be important seed feeders (Fawki and Toft, 2005; Talarico et al., 2016; Toft and Bilde, 2002). For example, *P. rufipes* can consume a wide variety of seeds (Foffová et al., 2020), including *P. annua* among the most consumed, with an intake of up to 20 seeds per day per individual (Deroulers et al., 2020). In early summer, seed predation on *V. arvensis* and *P. annua* was higher in the presence of *T. quadrivittatus* and the absence of *A. aenea*, *A. montivaga* and *A. plebeja*. This result is surprising given that *T. quadrivittatus* is a small species that consumes few seeds, unlike the *Amara* genus, which is recognised for its granivory. However, the consumption of *V. arvensis* and *P. annua* seeds by species of the genus *Amara* is relatively low, in contrast to highly preferred Brassicaceae seeds (Deroulers and Bretagnolle, 2019; Foffová et al., 2020). Furthermore, our metrics of species composition only considered the presence/absence of species and did not integrate their respective activity-density, which may have complicated the interpretation of the relationship between species composition and seed predation. Additionally, in early summer, we detected an indirect negative effect of weed cover on seed predation rates through carabid composition. Important weed cover appears to favor certain granivorous carabid species, such as the genus *Amara*, likely due to increased availability of refuge and seeds on the ground. However, this greater availability of seeds could negatively affect the seed predation rate measurements on the seed cards due to a dilution effect (Gardarin et al., 2023).

4.4. Cascading effect of local management, landscape and mesoscale air temperature on weed seed predation

As expected, we detected a cascading effect of landscape on weed seed predation, mediated by carabid communities, during both sampling sessions. In late spring and early summer, grassland and hedgerow amounts affected indirectly *V. arvensis* seed predation through their effect on carabid activity-density. In early summer, we also detected cascading effects of grassland area on weed seed predation through seed-eating carabid composition. Changes in relationships over time might be related to different factors including changes in cereal phenology, temperature, or landscape characteristics (e.g. change due to the

phenology of the different land-covers), while we were unable to disentangle these effects. In addition, in early summer, when temperatures increased, we detected a double cascading effect of grassland area on weed seed predation via an increase in maximum air temperature, which affected seed-eating carabid composition.

In addition to these cascading effects, we also detected direct effects of the landscape on seed predation that was not mediated by carabid activity-density, richness nor composition. In late spring, compositional heterogeneity negatively and directly affected *V. arvensis* seed predation, while hedgerow amount affected it positively in early summer. It is very likely that the heterogeneity of composition, as well as the quantity of semi-natural habitat, affects other invertebrate seed predators (e.g. slugs, ants, crickets) that were able to access our seed cards. The contribution to seed predation by these organisms (Sarabi, 2019), which were not included in our study, may have resulted in the detection of such direct effects of the landscape on seed predation. Further work should integrate the whole invertebrate compartment in the analysis of small-and large-scale environmental factors on seed predation.

5. Conclusion

The use of piecewise SEM enabled us to account for the complexity of the system by integrating a set of explanatory and response variables across different spatial scales, with cascading effects. Although this method can be complex and requires us to limit the number of variables and summarize some through multivariate analyses, it allowed us to test the significance of the expected relationships while ensuring that unmodeled relationships were not significant. As a result, this study highlights the importance of local and landscape effects on carabid communities and their cascading effects on the provision of ecosystem functions related to weed regulation, a major challenge in agriculture. The findings emphasize the critical importance of biodiversity in cultivated fields for weed regulation and suggest potential strategies to favour carabids and enhance this ecosystem service. Agricultural practices operating both at a field-scale, by maintaining a community of weeds, and at the landscape scale, by increasing the area of grassland surrounding the field were demonstrated as key drivers favouring carabids, and therefore weed seed predation. Moreover, our study highlights for the first time an effect of the landscape on mesoscale air temperature with implications for carabid species composition and levels of weed seed predation. It stresses more especially the additional role of semi-natural habitats in ecological processes driving biodiversity linked with local mesoclimate regulation. Our findings suggest that landscape composition and configuration can modulate local mesoclimate, potentially playing a significant role in mitigating the impacts of climate change on biodiversity and associated ecosystem services.

CRediT authorship contribution statement

Carbone Benjamin Jacques: Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition. **Aude Ernoult:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Léa Uroy:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Olivier Jambon:** Writing – review & editing, Resources, Methodology, Investigation. **Cendrine Mony:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Hervé Quénot:** Writing – review & editing, Validation, Conceptualization. **Caroline Le Maux:** Resources, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109776.

Data availability

Data and the R code are published on the platform “Data INRAE”: <https://doi.org/10.57745/6GJBIB>

Data for: Cascading effects of landscape, mediated by mesoclimate, on carabid communities and weed seed predation in winter cereals (Data INRAE)

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