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Abstract

To reduce herbicide use, different avenues of biological weed regulation are currently investigated. Among these, weed seed predation by carabid beetles appears promising. Though observed in different cropping systems and conditions in fields, there was to date no demonstration that this process actually influences weed dynamics over time and reduces weed harmfulness for crop production. Consequently, the objective of the present paper was to (1) model the impact of cropping system, field margin and pedoclimate on weed seed predation by carabids to complete the FLORSYS model, which simulates weed dynamics and crop production from cropping systems, soil and weather, (2) evaluate whether including seed predation is needed to correctly predict weed dynamics in different cropping systems, (3) which components of the seed predation submodel are the most influential. The new seed-predation submodel calculates the daily predation rate for each weed species from seed traits, weather data, canopy state variables and management operations. In FLORSYS, this predation rate is applied to the newly shed weed seeds on the soil surface. The equations and parameters were based on past publications from our team and other literature. Then, simulations were run with FLORSYS over 13 years, with and without the seed predation submodel, using weather data and management operations from 10 fields from the INRAE Dijon-Epoisses experimental station. The resulting output in terms of weed and crop state variables (plant density, biomass, seed bank, yield) were compared to measurements from the 10 fields, showing that including weed seed predation in the simulations improved the model's prediction quality, by reducing the overestimation in weed-variable predictions. Finally, a sensitivity analysis to the components of the predation submodel was run, by repeating the simulations after successively switching off individual components of the submodel. This showed that daily incident radiation, light interception by plant canopy, harvest, carabid reproduction and daily temperature had the most influence on seed predation rates. The simulations showed that weed seed predation by carabids can indeed contribute to managing weeds, by reducing field infestation and improving crop yields, but with large variations among crops. However, to determine which cropping systems and field margins favour weed seed predation enough to noticeably contribute to biological weed regulation, a larger diversity of cropping systems and weather series needs to be explored by simulation.

Keywords. Biological regulation; agroecological weed management; mechanistic model; model validation; sensitivity analysis; weed seed predation

1 Introduction

Agriculture is currently undergoing a major overhaul, aiming to reduce the use of synthetic inputs, among which pesticides (Jacquet *et al.*, 2022). This is a particular challenge for managing weeds, which are today the most damaging pest for arable crop production (Oerke, 2006). To do so, integrated weed management aims to replace a single simple and highly efficient weed control technique (i.e., herbicides) by combinations of many, partially efficient, highly interacting and mostly preventive techniques (Liebman and Gallandt, 1997; Munier-Jolain *et al.*, 2008).

More recently, agroecological research has demonstrated that mobilizing beneficial biotic interactions could contribute to regulating weeds (Petit *et al.*, 2018). The predation of weed seeds by seed-eating organisms could be an interesting candidate as it is a widespread process in arable agriculture (Davis *et al.*, 2011; Sarabi, 2019). Amongst the many seed predators in temperate arable cropping systems, carabid beetles are often key players (Kjellsson, 1985; Cromar *et al.*, 1999a; Honek *et al.*, 2003; Honek *et al.*, 2005). Experiments with a predator exclusion modality indicated that seed predation by invertebrates can reduce weed emergence by up to 40%, and weed biomass by up to 80% in cover crops (Blubaugh and Kaplan, 2016). Besides, the dynamics of the soil weed seedbank from one year to the next was shown to be affected by carabid seed predator abundance, at national and European scales (Bohan *et al.*, 2011; Carbonne *et al.*, 2020).

The predation of individual weed species by carabids is first determined by the feeding preferences of the carabids (Honek *et al.*, 2007; Petit *et al.*, 2014). Carabid activity and the resulting weed seed predation depend on the in-field habitat quality, e.g., soil texture, pH and moisture, crop canopy density and structure, temperature, available food sources or presence of competitors (Lovei and Sunderland, 1996; Holland and Luff, 2000). The presence of field margins, i.e., linear semi-natural habitats that define the edge of fields (Marshall and Moonen, 2002), can also enhance the diversity and activity of carabids. Margins such as grass strips and flower strips were shown to increase the in-field abundance and fitness of seed-eating carabids (Lys and Nentwig, 1992; Zangger *et al.*, 1994; Labruyère *et al.*, 2016) and thus possibly enhance weed seed predation. Carabid activity and weed seed predation are also strongly affected by in-field management (Table 1): for instance, seed predation tends to be higher in fields under reduced tillage regimes or pesticide use. Consequently, seed predation and weed dynamics each respond to many interacting abiotic and management factors, and it is thus difficult to disentangle the highly variable seed predation among the many other factors affecting weed communities in the long term.

This is the reason why several teams proposed models that synthesized the existing knowledge of environmental factors and management techniques on seed predation, and the latter's possible effects on weed dynamics (Westerman *et al.*, 2003b; Davis *et al.*, 2004; Westerman *et al.*, 2005; Westerman *et al.*, 2006; Daouti *et al.*, 2022). However, none of these models includes sufficient weed and crop species, life-cycle processes and management techniques to actually simulate the impact of cropping systems on weed dynamics, let alone the consequences for crop production or biodiversity. Conversely, there are numerous weed dynamics models in the literature (Chantre and González-Andújar, 2020) but none of them includes weed seed predation.

The objective of the present paper was to (1) model the impact of cropping system, field margin and pedoclimate on weed seed predation by carabids to complete the comprehensive FLORSYS model, which simulates weed dynamics and crop production from cropping systems, soil and weather (Colbach *et al.*, 2021), (2) evaluate whether including seed predation is needed to correctly predict weed dynamics in different cropping systems, (3) which components of the seed predation submodel are the most influential. The new weed seed predation sub-model calculates the daily predation rate by carabids on the seed rain for 32 weed species from seed traits, weather data, canopy state variables, management operations and the presence and distance to field margins. We considered here omnivore and granivore species, as both groups consume weed seeds (Frei *et al.*, 2019) and greatly contribute to weed seed predation (Jonason *et al.*, 2013; Trichard *et al.*, 2013).

2 Material and methods

2.1 The existing FLORSYS model

FLORSYS (Gardarin *et al.*, 2012; Munier-Jolain *et al.*, 2013; Colbach *et al.*, 2014b; Munier-Jolain *et al.*, 2014; Mézière *et al.*, 2015; Colbach *et al.*, 2021; Pointurier *et al.*, 2021) is a virtual field on which cropping systems can be experimented with a large range of virtual measurements of crop, weed and environmental state variables. The following sections summarize its main characteristics, more details can be found in section *A* in supplementary material online.

2.1.1 Weed and crop life cycle

The input variables of FLORSYS consist of (1) a description of the simulated field (daily weather, latitude and soil characteristics); (2) all the crops and management operations in the field, with dates, tools and options; and (3) the initial weed seed bank. The input variables influence the annual life cycle of annual weeds and crops, with a daily time-step. Pre-emergence stages (surviving, dormant and germinating seeds, emerging seedlings) are driven by soil structure, temperature and water potential, distinguishing 30 1-cm-thick soil layers from soil surface down to 30 cm depth. Post-emergence processes (e.g. photosynthesis, respiration, growth, shade response) are driven by light availability and air temperature. At plant maturity, weed seeds are added to the surface layer of the soil seed bank; crop seeds are harvested to determine crop yield. Crop-weed competition was considered for light only in the present FLORSYS version. The model is currently parameterized for 32 frequent and contrasting annual weed species (see complete list in section *A.4* online) and 33 crop species.

2.1.2 Effect of cultural techniques

Life-cycle processes depend on the dates, options and tools of management techniques (tillage, sowing, herbicides, mechanical weeding, mowing, harvesting etc.), in interaction with weather and soil conditions on the day the operations are carried out. For instance, weed plant survival probabilities are calculated deterministically depending on management operations, biophysical environment as well as weed morphology and stage; the actual survival of each plant is determined stochastically by comparing this probability to a random probability.

2.1.3 Indicators of weed impact on crop production

FLORSYS simulates crop yield as well as a set of indicators assessing weed impacts on crop production and biodiversity (Mézière *et al.*, 2015) (for details see section *A.6* online). The present study used crop yield, field infestation by weed biomass during crop growth, wild plant biodiversity (weed species richness and evenness) and weed-based food resources for farmland birds and domestic bees to evaluate cropping systems.

2.1.4 Domain of validity

FLORSYS was previously evaluated with independent field data on short and long-term weed dynamics at French national scale, over a large range of existing arable cropping systems. It showed that crop yields, daily weed species densities and, particularly, densities averaged over the years were generally well predicted and ranked as long as a corrective function was added to keep weeds from flowering during winter at more southern latitudes (Colbach *et al.*, 2016; Pointurier *et al.*, 2021). However, weed seed densities in surface layers tended to be overestimated if fields had been untilled for several years (Colbach *et al.*, 2006).

2.2 Modelling weed seed predation by carabids

2.2.1 Data origin

The new seed-predation submodel calculates the daily predation rate for each weed species from seed traits, weather data, canopy state variables and management operations (Figure 1). In FLORSYS, this predation rate is applied to the newly shed weed seeds on the soil surface. The necessary functions were

based on past publications from our team as well as other literature on (1) weed seed predation rates measured every two weeks from May to September in fields with seed cards (*Capsella bursa-pastoris* L. and *Viola arvensis* L.) (section 2.2.2), (2) seed predation rates and/or carabid activity-density measured in fields during the days or weeks following management operations (e.g., tillage, pesticides) (section 2.2.3), (3) seed predation rates and/or carabid activity-density monitored during several years after fields were converted to no-till (section 2.2.4), (4) weed seed predation rates measured with seed cards (*Capsella bursa-pastoris* L. and *Viola arvensis* L.) along transects perpendicular to field edges, bordered by different field margins (section 2.2.5), (5) which weed seeds were preferentially eaten by carabids in seed choice experiments in field experiments (section 2.2.6).

2.2.2 Seasonal seed predation

In the model, seed predation by adult carabids is only possible in the model between 1 March and 1 October, if the daily mean temperature is above the minimum requirement for carabid activity and below the maximum acceptable temperature, and if there is some incident radiation above the canopy and some protective canopy reducing light incidence on soil surface (equation [1] in Table A.1.A). If the daily temperature is inside the acceptable range, the efficient daily temperature is calculated as the difference with the minimum needed temperature, relatively to the range of acceptable temperatures [2].

The potential seed predation rate as a function of season inside these framework conditions was derived from Petit *et al.* (2014) who monitored *Capsella bursa-pastoris* L. and *Viola arvensis* seed predation every 2 weeks from mid-May to October 2009 in three wheat fields at the INRAE Dijon-Époisses experimental station (47°36'12''N,4°35'32''E). Twenty seeds of each of the two weed species were glued onto 5×14 cm predation cards and placed on soil surface for one week under cages preventing access to vertebrate predators. There were ten measurement sessions, five during the wheat growing season and five after wheat harvest. During the time the fields were monitored, there were no management operations other than the crop harvest.

The predation rate (seeds/seeds) of each session n was calculated as $sessionPredRate_n = 1 - (number\ of\ remaining\ seeds_n / number\ of\ initial\ seeds_n)$. This was transformed into a daily predation rate corresponding to day d midway between two consecutive sessions: $dailyPredRate_d = (sessionPredRate_n - sessionPredRate_{n-1}) / (onsetDate_n - onsetDate_{n-1})$, with dates in Julian days and $d = (onsetDate_n + onsetDate_{n-1}) / 2$.

The daily predation rate was analysed with a linear model (after $\log_n$-transformation of output and most inputs) as a function of five variables, with the lme function of R {R Core Team, 2021 #18159}. The daily efficient temperature (see [2] in Table A.1) accounts for the carabids' thermal requirements (Saska *et al.*, 2013; Noroozi *et al.*, 2016) and was calculated from the daily mean temperature recorded on the experimental station. Incident radiation and the proportion of radiation intercepted by the crop canopy were used as proxies for canopy density as denser canopies protect carabids and increase predation (Gallandt *et al.*, 2005; Heggenstaller *et al.*, 2006; Meiss *et al.*, 2010). Temperature and incident radiation were provided by the local weather station via the INRAE platform CLIMATIK, managed by the AgroClim laboratory of Avignon, France, https://intranet.inrae.fr/climatik/). The radiation intercepted by the canopy was estimated with FLORSYS, using weather records and field history to mimic the experimental fields *in silico* (details in section *B.1* online). The time until or since the emergence of carabids reproducing in autumn [3] translates the drop in predation in late spring, when spring-reproducing carabids are dying and autumn-reproducing carabids have not yet emerged (Petit *et al.*, 2014). Finally, the time since wheat harvest reflects the time needed by the carabids to return after the disturbance due to the harvest operation (Petit *et al.*, 2014).

2.2.3 Short-term effect of disturbances due to management operations

The short-term effect of disturbances resulting from management techniques was based on the Ingrish & Bahn's framework to quantify resilience (Ingrisch and Bahn, 2018), with two parameters (section *B.2.1* online): the maximum impact of the disturbance is the reduction in seed predation relative to an undisturbed field and the recovery time needed for the predation to bounce back to the level of an undisturbed field (Figure 2.A). A literature analysis allowed choosing the relevant techniques to include in the model and to estimate parameter values (Table 1). We preferred studies reporting weed seed

predation response to disturbance, but we also used studies on the effect of disturbance on activity-density or mortality of carabids as a proxy of weed seed predation. The maximum impact was estimated as the variation in seed predation rates (or their proxy) in the days immediately after the disturbance relatively to the pre-disturbance level. The duration effect was estimated from studies monitoring predation (or its proxy) over a few weeks after the disturbance at the most, to avoid confusion with other factors.

Tillage and insecticides present the most straightforward adverse impact on seed predation, by directly killing carabid larvae and adults, by making the adults flee out of the field, and/or by rendering the field habitat unfavourable (Holland and Luff, 2000; Thorbek and Bilde, 2004; Kulkarni *et al.*, 2015). Inverting tillage such as mouldboard ploughing is more disturbing than non-inverting tillage, regardless of its depth. Conversely, mechanical weeding does not seem to disturb carabids sufficiently to affect seed predation (Holland and Luff, 2000), even though carabid activity/density or abundance can be reduced (Navntoft *et al.*, 2016). Consequently, only the effects of tillage and insecticides were introduced into the model. The model distinguishes mouldboard ploughing and other inverting tools from superficial tillage, but considers insecticides regardless of the applied dosage or active ingredient. Indeed, many publications do not give this information but simply report an overall negative effect on seed prediction (e.g., Trichard *et al.*, 2013).

Herbicides and fungicides do not increase the toxicity of the environment (Brust, 1990; Zhang *et al.*, 1998; Holland and Luff, 2000) and several studies observed no impact on carabids (Table 1). The rare reports on reduced seed predation or carabids are most likely due to indirect effects, e.g., a reduction in canopy density (denser canopies protect carabids, Gallandt *et al.*, 2005; Heggenstaller *et al.*, 2006; Meiss *et al.*, 2010). This canopy effect might also explain the reported increase in seed predation with increased fertilisation (Kromp, 1999). Consequently, no direct disturbance effect of these techniques was introduced into the model; any indirect effects via their impact on canopy density are already simulated by the existing FLORSYS version (section 2.1).

Finally, mowing was also reported to reduce seed predation (Table 1). This operation is similar to a harvest operation and was considered as such in the predation submodel.

2.2.4 Cumulative effect of no-till
A principle similar to Ingrish & Bahn's framework was used to include the beneficial effect of continuous no till on seed predation reported in literature (Table 1). One parameter reflects the number of years during which seed predation increases after the field was switched to continuous no-till. The other is the seed predation rate after that time relatively to the predation rate in a tilled field. Both parameters were estimated from literature reports (Cromar *et al.*, 1999b; Menalled *et al.*, 2007; Trichard *et al.*, 2014; Petit *et al.*, 2017).

2.2.5 Effect of field margins along field edges
The effect of field margins, i.e., neighbouring semi-natural linear features, on in-field on seed predation was estimated from Petit *et al.* (submitted). In that study, seed predation rates were observed on seed cards with either *Poa annua* or *Viola arvensis*, at distances ranging from 4 to 50 m along 216 transects perpendicular to the field edges. Field edges were bordered by different types of field margins, or by roads or fields.

The *P. annua* data was used to determine the shape of the effect of distance to the field edge. These data were balanced insofar as in each of the 15 survey fields, four transects with and without linear features were monitored in May and June 2018. This reduced the risk of confounding effects of distance vs weather or field history. A bell-shaped non-linear equation was fitted to the predation rate y (seeds/seeds) vs distance (m) to the field edge:

eq. 1.   If y < *maxDistInf*
              then y = $K \cdot (1 + A_{FM} \cdot x + B_{FM} \cdot x^2)$
              else y = K
              with $A_{FM} = -B_{FM} \cdot maxDistInf$

$$B_{FM} = -4 \cdot maxEffect_{FM} / maxDistInf^2$$

K (seeds/seeds) is the average seed predation rate observed in transects without field margins, $maxDistInf$ (m) is the maximum distance at which a field margin influences seed predation along a transect, and $maxEffect_{FM}$ (seeds/seeds) is the maximum effect of a field margin on seed predation on a transect perpendicular to that margin relatively to seed predation on a transect without a neighbouring field margin. The bell-shaped curve accounts for the fact that carabids do not like to stay close to the field edge where there is little protective canopy and that above a certain distance, the field-margin effect becomes negligible compared to the field-history effect. The non-linear equation was fitted with PROC NLIN (Gauss method) of SAS (version 9.4, SAS Institute Inc., Cary, NC, USA, 2002-2012).

The *P. annua* data only included two types of field margins, mostly grass strips and a few woody margins. So, to estimate the effect of the different types of field margins, the complete data set of 216 transects was used in an analysis of variance. There, log_{10}-transformed predation rates (after adding a 0.001 constant to account for nil values) were analysed as a function of field-margin type as well as tillage type, pesticide presence, weed species, year (as a factor) and log_{10}-transformed distance to field edge, using PROC GLM of SAS. Backward selection was applied to sequentially eliminate non-significant input variables (with p=0.05).

2.2.6 Carabid seed choice

Weed species were ranked according to the food preference of carabids observed in field trials. These were set up in two winter wheat fields in Côte-d'Or, France (47°36'12''N,4°35'32''E) in 2011 (Trichard, 2014). One field was managed conventionally, the other had remained untilled for four years. Six sessions were carried out between May and September, where seed cards with seeds from 26 weed species were left for 7 days. The species were chosen to be contrasted in terms of seed traits related to carabid food preference, i.e., seed length (Lundgren and Rosentrater, 2007), mass (Honek *et al.*, 2003) and lipid content (Westerman *et al.*, 2003a; Ali and Willenborg, 2021).

The 26 species used in the experiment did not cover the 32 weed species currently included in FLORSYS. Consequently, multivariate analyses were used to link the species seed predation averaged over the two fields and the six predation sessions to seed traits, i.e., seed length and width, mass, coat thickness and lipid content. First, a Principal Component Analysis followed by Hierarchical Clustering on Principal Components of the FactoMineR package (Lê *et al.*, 2008)) of R (R Core Team, 2021) was used to cluster the weed species into groups, based on their predation rates and seed traits. Then, the observed predation rates were analysed as a function of seed traits in interaction with species cluster, using the lm() function of R. Several models were tested, each testing two traits; the final model was taken from among the models with significant cluster × trait interactions, choosing the one with the highest R^2 and seed effects consistent with literature.

To estimate the predation rate of a weed species that was not used in the experiment, a Factorial Discriminant Analysis (with the lda() function of the Mass package of R) was used to predict to which cluster the new species most likely belongs, based on its seed traits. Then, the previous linear regression was used to calculate the seed predation rate from the species cluster membership and its seed traits. Finally, the seed predation rates of all species were readjusted to ensure that the average of the rates of *V. arvensis* and *C. bursa-pastoris* (i.e., the two species used in section 2.2.2) was 1.

Last, we accounted for the fact that the in-field seed consumption of individual weed species increases when the probability of carabids encountering this weed species increases, i.e., when seed availability (density) of that particular seed species increases (Diehl *et al.*, 2012; Kulkarni *et al.*, 2017b; Carbonne *et al.*, 2019). Indeed, field and lab observations concur that carabids consume seeds that are not necessarily their most preferred ones in order to limit the energy spent on foraging and/or that they are less selective in specific situations, e.g., to reduce the risk of being predated by other organisms (Blubaugh *et al.*, 2017; Charalabidis *et al.*, 2017). To reflect this, seed predation rate of individual weed species derived from seed traits was corrected by adding a function that causes carabids to prefer abundant seeds over rare seeds.

2.3 Model evaluation and sensitivity analysis

2.3.1 Principle
Simulations of cropping systems were performed with FLORSYS to (1) evaluate how much the new predation submodel improved prediction quality, by running simulations with or without the new predation submodel, and comparing the results to independent field observations (section 2.3.2), and (2) identify which components of the predation submodel influenced the prediction quality the most, by running sequential simulations where individual submodel components were switched off and then assessing how much prediction quality was affected (section 2.4).

2.3.2 Data origin
Data of ten cropping systems from the INRAE experimental station of Dijon-Époisses from 1999 to 2012 were simulated as described in Colbach et al. (2016) (section *C* online). They vary from herbicide-intensive to herbicide-free, with various rotations, tillage strategies and use of mechanical weeding. Initial weed seedbank (for 32 weed species) and soil characteristics given as inputs in the model were measured on soil samples taken in the fields. Weather data were obtained from the INRAE weather station (via the CLIMATIK platform).

Aboveground plant biomass, weed plant density, weed seed bank and crop yield were monitored in all ten fields during the 13 years of the trial. Plant density and aboveground biomass were measured in several quadrats per field several times a year, and weed seed bank was measured on ten soil samples every two years. As weed seed predation was not measured, we could not directly evaluate the prediction quality of the new submodel in our model. Instead, we checked whether including seed predation improved the prediction quality of crop and weed variables by FLORSYS.

2.3.3 Model evaluation
Each cropping system was repeated 10 times with the same inputs to take into account the stochastic effects of FLORSYS. Two series were run, with the initial FLORSYS version and then again, after including the seed predation submodel. In total, 2 series × 10 cropping systems × 10 repetitions = 200 simulation runs were carried out, each over 13 years. The simulated field sample was 6×4 m² and the actual field was simulated as an infinite repetition of this basic pattern to avoid edge effects.

Simulated aboveground plant biomass, weed plant density, weed seed bank and crop yield were compared to measurements from the ten fields, either analysed (1) at the species scale or (2) at the community scale, i.e., they were summed over all species. The prediction quality of the model was estimated with various complementary criteria described by Colbach et al. (Colbach *et al.*, 2016; Pointurier *et al.*, 2021):

The prediction bias is the mean of residuals (the difference between simulated and observed values from different fields, years and species) relatively to the range of variation of observations (equations in section *C.4* online) and determines whether the model systematically under- or overestimated variables. The relative root square of the mean squared error (RRMSEP) evaluates the relative prediction error of the model. It was calculated relatively to the standard-deviation of observed values (Coucheney *et al.*, 2015; Colbach *et al.*, 2016), and corrected for variability in observations (i.e., variability due to measurement errors) and in simulations (i.e., variability due to model stochasticity) (Wallach, 2006). If MSEP is small or smaller than the variability in observations or simulations, the difference between observed and simulated values is mostly due to observation error and/or model stochasticity, respectively.

The ability of the model to rank cropping systems and weed species correctly was calculated as the maximum between the modelling efficiency, the Pearson and the Spearman correlation coefficients between observations and predictions. Coefficients close to 1 indicate that the variables are well predicted by the model in terms of absolute values, relative values (i.e., differences between values) and ranks, respectively.

The three criteria (relative bias, RRMSEP and proportion of correctly predicted observation) were calculated from data averaged over the rotation (i.e., over all simulated values or measurements per cropping system) to check the model's ability to compare cropping systems. To assess how well the model predicts outputs on a given day, the criteria were calculated from data averaged per day (i.e. averaged over quadrats, samples and repetitions), except for daily weed density and biomass. For these two outputs, the proportion of correctly predicted observations was the proportion of observations inside the simulated 90%-confidence interval obtained over the 10 repetitions. This criterion was preferred over the three first evaluation criteria, because the latter are considerably deteriorated by a delay of a few days in the simulations vs the observations (or vice-versa), whereas such delays do not affect the prediction quality of the weed dynamics over the years (Colbach *et al.*, 2016).

All the evaluation criteria were also calculated from simulations with FLORSYS before the seed predation submodel was introduced in order to study how much the new submodel improved FLORSYS predictions.

2.4 Sensitivity analysis to submodel components

To determine how much each factor of the seed-predation submodel influenced its outcome, the same principle as in the previous section 2.3.3 was used. In addition to simulation series with predation submodel run in the previous section, 10 further series were run and their outcome compared to the same field observations. In each of these series, one of the submodel factor (e.g., light interception by crop canopy, ploughing, weed seed density) was excluded, by skipping the step in the model code. This approach was preferred to a conventional sensitivity analysis where parameters are made to vary because some effects work without parameters (e.g., the seed density effect).

Two additional series were run, where grass strips were placed around each field, even though in reality, there were no field margins surrounding these fields. In one of these series, the least well estimated parameter was halved, i.e., the maximum distance *maxDistInf* at which the field margin influences in-field predation. The aim was to assess how much field margins would change prediction outputs.

Finally, the effect of switching off submodel components (10 simulation series) or adding field margins along field edges (2 series) on crop yield as well as weed impacts on crop production and biodiversity (section 2.1.3) was assessed. The predictions errors in weed (weed density, biomass, seed bank) and crop variables (crop yield, biomass) obtained with the 12 alternative series were compared to the error obtained with the complete model. Moreover, annual predation rate, weed-impact indicators and crop yield with the complete model and the alternative series were compared with analyses of variance as a function of series, cropping system, years since simulation onset as well as double interaction, using the *lm(), Anova(,type=3)* and *eta_squared()* functions of R {R Core Team, 2021 #18159}. This was followed by comparison of means with least-difference tests with *lsmean()*.

3 Results

3.1 The seed predation submodel

Each day during a simulation, the total seed predation rate is calculated from environmental conditions and management operations (sections 3.1.1 to 3.1.4). Then, predation rates per weed species are deduced, from carabid seed preference and weed seed density (section 3.1.5). Finally, the number of predated seeds are calculated and the unpredated seeds added to the soil seed bank (section 3.1.6). The detailed equations are listed in Table A.1 in the appendix at the end of the present manuscript. Parameter values and their origin are summarized in Table A.2.

3.1.1 Seasonal seed predation rate
When the photo-thermal and seasonal conditions for predation are met during the simulation [1], the total daily potential predation rate (over all weed species) is calculated [5]. This rate increases with efficient daily temperature $Teff_d$ and the proportion of radiation intercepted by the canopy $(1 - PAR_{sol})^B$ with $B > 0$, with the radiation PAR_{sol} arriving on soil surface provided by the light

interception submodel of FLORSYS), it decreases with the daily available radiation (**PAR**$_d$ with $C < 0$). At harvest, predation is divided by nearly 2 (Figure 2.A), and then increases again during *recoveryTime*$_{Harvest}$ =18 days after harvest (time$_{Harvest}$ with $D > 0$ in [5] and calculated as days since harvest with a maximum of *recoveryTime*$_{Harvest}$ days in [4]). The shape of this effect is similar to the framework used for the effect of other disturbances (Figure 2.B), albeit with a slightly less linear recovery (Figure 2.A) using a recovery rate (i.e., parameter D) rather than a maximum impact parameter.

Seed predation also decreases during *recoveryTime*$_{Emerge}$ = 15 days prior to the emergence of autumn-reproducing carabids (with a reduction of nearly 20%) and then increases again during the *recoveryTime*$_{Emerge}$ after this key date (Figure 2.B). This results from the effect of the number of days to and since time$_{emerge}$ with $E > 0$ [5].

When fitted to field data (section 2.2.2), this equation [5] allowed estimating the regression coefficients *A-B* (Table A.2) and predicted the seasonal variation in seed predation observed in the field data (Figure 2.C).

3.1.2 *Short-term effect of disturbances due to tillage and insecticides*

On the day an inverting tillage occurs in the simulated field, seed predation is divided by 2 (*impact*$_{InvTill}$ = -0.50), and takes *recoveryTime*$_{InvTill}$ = 30 days to recover (eq [7] in in Table A.1.A, further details in section B.2 online). The same principle was used for non-inverting tillage [9] and insecticide spraying [11], except that the impact on predation is smaller (*impact*$_{othTill}$ = -0.39 and *impact*$_{Insecticide}$ = -0.43) and recovery after non-inverting tillage is faster (*recoveryTime*$_{OthTill}$ = 18 days). Except for inverting tillage, these effects are lower than the impact of crop harvest. The latter's impact on predation is larger (-0.48, (Figure 2.A) and lasts slightly longer (*recoveryTime*$_{Harvest}$ = 18 days).

The previous equations describe the direct effect of harvests, tillage and insecticides on seed predation rates. Harvest and tillage operations also influence predation rates in the longer term as they destroy or damage plants (depending on cutting heights, tillage tools and depths etc, section 2.1.2), thus reducing canopy density and seed predation for several weeks via the reduced light interception (section 3.1.1). The timing of operations is also crucial, with disturbances during weed seed rain being much more influential than earlier or late operations. As a consequence, a given operation type can have very different effects, e.g., an autumn maize harvest with its higher cutting bar impacts seed predation less than a summer wheat harvest with its lower cutting height.

3.1.3 *Cumulative effect of no till*

Seed predation is higher in continuously untilled fields. This effect is visible after one year and reaches its maximum after *upgradeTime*$_{NoTill}$ = 4 years (eq [12] in Table A.1.A). In between, the relative seed predation rate increases linearly from 1 (no variation if years$_{LastTill}$ = 1) to *impact*$_{NoTill}$ = 1.60 if years$_{LastTill}$ ≥ 4 years. So, continuous no-till can increase seed predation by up to 60 %.

3.1.4 *Effect of semi-natural habitats along field edges*

3.1.4.1 *Seed predation as a function of distance to field margins*

The non-linear equation of section 2.2.5 was successfully fitted to the seed predation as a function of the distance to the field edge and the absence or presence of a field-margin habitat along that edge (Figure 3). The effect of the field margin was visible to approximately 40 m from the field edge (*maxDistInf* = 39.8 m). At half that distance from the field edge, predation was 169% higher if there was a grass strip along that edge than there was none (*maxEffect*$_{FM}$ = 1.69). Unexplained variability was large (i.e., R² was only 0.17) because of weather, field history or location were disregarded in this analysis.

3.1.4.2 *Effect of type of field margins*

The analysis of variance of weed seed predation data in fields bordered by different types of field margins showed that grass strips increased seed predation the most (details in section B.4 online). The maximum effect *maxEffect*$_{FM}$ of habitat was estimated for each FM habitat by rescaling the

backtransformed coefficients so that the grass-strip coefficient equated *maxEffect_grass* of Figure 3 and that the one for no field margin was nil. Based on this back-transformation, the effect of flower strips was 28% lower than the effect of grass strip (*maxEffect_flower strip* = 0.763 compared to the 1.69 of grass strip). The effects of mixed strips and woody field margin were decreased even more, by 39% and 45%, respectively (*maxEffect_mixed strip* = 0.373, *maxEffect_woody* =0.182).

3.1.4.3   *Formalisation in model*
The current FLORSYS version only accepts rectangular fields for the seed predation submodel. For each of the four field edges, the first step is to calculate the parameters A_{FM} and B_{FM} of the equation computing the variation in seed predation rate with the distance to the field edge, depending on the type of the field margin (if any), as in Figure 3 (eq. [13] in Table A.1.B).
The effect of a neighbouring field margin then is the integral of eq. [13] from the field edge to the opposite field edge, or *maxDistInf*, whichever is smaller [14]. To obtain the relative effect max_v on predation rate, this amount is divided by the field size perpendicular to the field edge. The effect of all four field edges is the product of the four max_v values, which is then applied to the seed predation rate [15].

3.1.5 Carabid seed choice
3.1.5.1   *Seed traits influence carabid preferences for weed seeds*
The Principal Component Analysis of the seed predation rates and seed traits showed that high predation rates were the most associated to high seed lipid contents whereas species with long, heavy, thick-coated seeds tended to present lower predation rates (Figure 4.A). Based on this analysis, the 26 weed species were segregated into four clusters (Figure 4.B). Average seed predation rates ranged from 0.260 seeds/seeds for cluster 2 to 0.0453 seeds/seeds for cluster 4. Inside each cluster, predation rates varied with seed lipid content and seed coat thickness. In the two clusters with respectively the highest and lowest predation rates, predation increased with increasing seed lipid content and decreased with decreasing seed coat thickness. In the other two clusters, the opposite applied.

To estimate average predation rates for weed species included in FLORSYS but not used in the experiments of Figure 4, the cluster membership of the additional species was determined based on their seed traits fed to a Factorial Discriminant Analysis using the analysis of Figure 4. Once, the cluster membership of a new species was established, the regressions shown in Figure 4.B were used to predict its predation rate.

Finally, the observed and estimated seed predation rates were divided by the average predation rate of *V. arvensis* and *C. bursa-pastoris* (= (0.284 + 0.038)/2). As a result, the average species-preference coefficient of these two species was 1 and all other species were ranked relatively to these two species. As a result, among the 32 species currently included in FLORSYS, two, *Avena fatua* and *Mercurialis annua*, present a zero preference coefficient (see section *B.5* online) and are thus never eaten in the simulations. *Veronica persica* has the lowest non-zero coefficient (0.17) and *C. bursa-pastoris* the highest coefficient (1.76), meaning that at identical seed densities, *C. bursa-pastoris* seeds are 10 times more likely to be eaten by carabids than *V. persica* seeds.

3.1.5.2   *Carabids prefer abundant seeds to their favourite seeds*
To calculate the seed-predation for a given weed species, the total seed predation over all species is then multiplied by the species-preference coefficient *CP_s* (eq. [17] in Table A.1.C). It is also multiplied by the density of seeds produced by the weed species on day d relatively to the total weed seed rain. This makes it likelier that carabids concentrate on the most abundant seeds.

3.1.6 Actual seed predation and return to weed seed bank
Potentially, the number of seeds of a given species predated on a given day is the product of the species seed predation rate and the number of seeds produced on this day by the species (eq. [18] in Table A.1.D). However, if the seed rain of the preferred species is too low, or vice-versa, if carabids do not

like the most abundant weed seeds, this potential predation does not add up to the predation expected for the predation rate over all species **finalPredRate$_d$**.

To correct for this, the potential number of predated seeds of each weed species is multiplied by a corrective coefficient [20]. The latter is the ratio of the number of predated seeds summed over all species expected from **finalPredRate$_d$** divided by the potential number of predated seeds summed over all species [19]. Finally, the number of predated seeds is subtracted from the seed rain before addition to the soil seed bank [21].

3.2 Including weed seed predation improve model prediction quality

We compared simulations with the new FLORSYS version including the seed predation submodel to independent observations from the cropping-system trial to determine the prediction quality and domain of validity of the model. This showed that daily weed dynamics were well predicted, both in terms of plant density and above-ground biomass (81-85% of observations inside the simulated confidence interval, Table 2.A). There was a slight tendency to overestimate weeds (12%). Excluding weed seed predation from the simulations did not really change this satisfactory performance.

Weed variables were generally well ranked by FLORSYS in terms of cropping systems and species, with 56-69% of well-ranked observations (Table 2.B). However, these variables were somewhat overestimated, particularly weed biomass (bias = 12-17%), which resulted in large prediction errors (up to 121% for plant density). Note though that variability in observation was often so high that prediction error could not be estimated (for crop and weed biomass). Including weed seed predation was very beneficial, as the overestimation and the prediction greatly increased when predation was excluded (up to 858% for weed biomass!).

Crop variables were generally well predicted by FLORSYS, with less bias, and with 68-84% well-ranked observations, in terms of cropping systems and species (Table 2.B). Excluding weed seed predation reduced crop-yield overestimation (-5%), as there were more and larger weed plants to compete with the crop for resources.

3.3 The key factors for weed seed predation rates

3.3.1 Not all submodel components influence prediction quality and predation rates

The effect of switching off individual components of the predation submodel or adding field margin was not significant or negligible for weed species richness, weed-based food offer as well as crop yield (p<0.05 and/or partial relative Eta2 < 0.01 in analyses of variance, section *D.1.2* online). Submodel components and field margins were actually only really important for annual weed seed predation rates (partial relative Eta2 = 0.29).

The model's prediction quality depended on which individual components were switched off in the predation submodel (Table 3). Deleting the effects of daily incident radiation (i.e., **PAR$_d$**^{C} in eq. [5] in Table A.1) considerably decreased prediction error but it also increased annual predation rates by nearly 50% compared to the nominal simulation (from 0.50 seeds/seeds to 0.74 seeds/seeds per year). At the same time, it divided field infestation by more than four and increased the already overestimated yield by 15%. Weed-related biodiversity was also reduced by up to 50%. Conversely, switching off the effect of harvesting operations had the exact opposite effects, with a somewhat lesser magnitude (e.g., prediction rates decreased by only 40%, compared to the 50% increasing when switching off the radiation effect).

More generally, any reduction in simulated prediction rates led to an increase in prediction error, and vice-versa. But only three other submodel components were sufficiently influential that switching them off influenced seed predation rates significantly. Removing the effects of carabid reproduction timing and daily temperature reduced predation rates and increased prediction error whereas the opposite

occurred when the effect light interception the canopy was removed. But weed-impact indicators and crop yield did not vary significantly for any of these submodel removals. The remaining components of Table 3.B had no or only a slight effect on prediction error, and no effect on predation rates, weed impact or crop yield.

3.3.2 Field margins increase weed seed predation and crop yields
Adding grassy field margins around each field increased predation rates by approximately 20%, slightly improved weed species evenness and even increased crop yield by 5% (Table 3.C). Halving the most influential parameter driving field-margin effect, i.e., the maximum distance at which the margin influences predation, somewhat reduced these beneficial effects but not significantly.

3.3.3 Cropping system and carabids' preferences were the most influential factors
Total annual predation rates as well as weed-impact indicators and crop yield depended the most on cropping systems in interaction with time, with 83% of variability in outputs explained by linear regression in average (ranging from 53% for predation rate to 93% for weed-based bee food offer (details in section *D.1.2* online). Predation rates varied from 0.36 seeds/seeds per year for reduced-tilled sprayed A8 to 0.57 for the ploughed unsprayed A1 (section *D.2* online), with large variations according to years. Predation rates were generally lower for early-harvested crops (varying from 0.39 seeds/seeds per year on average in oilseed rape to 0.50 in barley) than for late-harvested crops, ranging from 0.51 seeds/seeds per year in sunflower to 0.63 in sugar beet (section *D.4* online).

When looking at predation rates simulated for the different weed species, almost all variation was due to species effects (94% of variability explained by linear regression was due to the species effect, section *D.3* online). The cropping system and time explained the rest. Annual predation varied from zero for eight weed species, to 0.53 for *Alopecurus myosuroides* (ALOMY) (Figure 5). The simulated species predation rates were only partially correlated to the carabids' species preference in the model (Pearson correlation coefficient = 0.51). Indeed, some species highly liked by carabids (e.g., *Abuthilon theophrasti,* ABUTH, the fourth most liked species, section 3.1.5.1) presented a near-zero predation rate (Figure 5), simply because they were extremely rare in the simulations. Conversely, a little liked species such as *Galium aparine* (GALAP, the third least liked species) was among the six most predated species in the simulation.

3.4 Weed seed predation improves crop production and reduces biodiversity

In average over all 10 cropping systems, 13 years and 10 stochastic repetitions, seed predation decreased species richness significantly but only slightly (from 59% of possible species to 57%, Table 3.A). The effect took several years to become noticeable, even in the most affected cropping system, and the difference between years and crops was more important (Figure 6.A). Predation had no significant effect on species evenness in average (Table 3.A). The predation effect depended very much on individual crops and years (Figure 6.B). Both bird and bee food offer tended to be slightly lower in the presence of seed predation (Table 3.A) even though carabids' species preference is different from birds' and bees' preferences (Pearson correlation coefficients = -0.03 and 0.11, respectively). Again, the differences in food offer with vs without predation were very small compared to the variations due to crops and years (Figure 6.C and D).

The effect of predation on field infestation and crop yield was much more important, with roughly a 50%-decrease in field infestation and a 7%-increase in yield (Table 3.A). These variations were even larger in the cropping systems with the largest impact (Figure 6.E and F), though the effect of crops and years remained more influential, even for field infestation.

4 Discussion

4.1 What is new here?

To date, the new FLORSYS is the only model that simulates weed-flora dynamics as influenced by seed predation at a daily time-step, depending on cropping systems in interaction with pedoclimate. At the onset, our model was already more complete than other weed dynamics model, in terms of processes, species and management techniques (Holst *et al.*, 2007; Chantre and González-Andújar, 2020; Colbach *et al.*, 2021). Among the few existing weed seed predation models, Westerman et al's model (Westerman *et al.*, 2006) is the closest to our approach though the mechanistic nature of FLORSYS allowed us to go more into details. For instance, Westerman et al (2006) included the impact of plant density on seed predation rates, which we translated into the proportion of light intercepted by the plant canopy. This variable is more precise insofar as it accounts for differences in plant sizes, resulting from stages and/or species, as well as indirect effects of management techniques influencing plant timing (e.g., sowing dates), location (e.g., sowing densities and patterns), size (e.g., fertilization) or destruction (e.g., harvest, mowing, herbicides, tillage, mechanical weeding), in interaction with daily soil and weather conditions.

The mechanistic nature of FLORSYS makes it akin to a virtual experimental field. As such, the present simulations represent the first long-term demonstration in contrasting cropping systems that weed seed predation by carabids actually influences weed flora dynamics and composition. To date, no such long-term empirical demonstration in real fields is available because excluding seed predation continuously over several years is next to impossible. Our results are, though, in line with annual field experiments that demonstrate the impact of seed predation on weed emergence (White *et al.*, 2007; Blubaugh *et al.*, 2016) and on the replenishment of the weed seed bank from one year to the next (Bohan *et al.*, 2011; Carbonne *et al.*, 2020). However, the signal observed in fields remains weak and highly variable and conditional to pedoclimatic and management factors.

4.2 Are the results consistent with field observations?

Another novelty of our modelling approach was that we compared model outputs with independent field observations and demonstrated that weed seed predation improved the model's prediction quality in terms of weed flora dynamics (section 3.2). To our knowledge, none of the other existing weed seed predation models mentioned in section 4.1 was ever evaluated with independent field observations. Actually, models are rarely evaluated, particularly weed dynamics models (Holst *et al.*, 2007).

Including weed seed predation in FLORSYS greatly reduced the overestimation of weed flora variables observed with earlier FLORSYS versions here and in the more complete original FLORSYS evaluation study (Colbach *et al.*, 2016). One of the outcomes of this study was that excluding weed seed predation from the model led to overestimated weed variables, particularly important in continuously untilled fields, where predation is more important compared to tillage (Table 1). Moreover, the seed predation rates simulated here (ranging from 0 to 87%) are consistent with field observations where similar ranges of variation were reported (Davis *et al.*, 2011). Including weed seed predation into FLORSYS though tended to increase crop-yield overestimation. This most likely results from disregarding plant-plant competition for nitrogen and other soil resources in the present model version, something we are currently fixing (Moreau *et al.*, 2021).

While the present model evaluation showed that weed seed predation improves the prediction of weed flora dynamics, the field data used for the evaluation was not precise enough to evaluate the different components of the seed-predation submodel and the associated parameter values. This is particularly troubling for those factors whose effects were based on carabid activity/density reported in literature rather than on actual seed predation measurements because of insufficient data. Indeed, some field studies report no correlation between weed seed predation and carabid activity/density (Mauchline *et al.*, 2005; Saska *et al.*, 2008). This was the case for short-term tillage effects (section 3.1.2) or minimum temperature for predation (section 3.1.1). However, the sensitivity analysis to submodel component found little influence for these factors (section 3.3.1).

Other components were modelled from a single experimental study, albeit on seed predation, i.e., the carabids' species preference (section 3.1.5.1) or the impact of distance to adjacent field margins (section 3.1.4.1). The fact that the presence of a grass strip increases weed seed predation up to 40 meters into the adjacent field, compared to a situation without a field margin, is though in line with studies on the in-field spatial distribution of carabids. Several authors report an increase of carabid activity-density in the first few meters from a grass margin and then a decrease with increasing distance into the field (Thomas and Marshall, 1999; Saska *et al.*, 2007). The distance up to which such an effect exists depends on several characteristics of individual carabid species such as where they reproduce/hibernate, i.e., boundary vs. field interior (Saska *et al.*, 2007). This should though not be much of a problem insofar as our sensitivity analysis showed that the precise value of distance threshold was not very influential.

Some conclusions from the carabids' species preference are troubling at first glance. For instance, in cluster 3 whose seeds are little predated, seed predation rates increased with increasing seed coat thickness and decreasing seed lipid content (section 3.1.5.1). Conversely, previous studies reported the opposite, i.e., higher predation of thin-coated (Honek *et al.*, 2007) and high-lipid seeds (Trichard, 2014; Ali and Willenborg, 2021), which corresponds to what we found for cluster ranking as well as inside the most highly predated species cluster. If the conclusions from cluster 3 were erroneous, this should have little impact as its predation rates are low anyhow. Moreover, the impact of carabids' preferences in the sensitivity analysis was negligible compared to effects of season (incident radiation, carabid reproduction) and protection by crop cover (harvest, light interception by canopy).

4.3   What is missing?

Based on the previous section (4.2), future improvements of the seed predation submodel should focus on seasonal and crop-related effects. The hypotheses underlying the seed-predation submodel should also be analysed with care and continuously re-evaluated against new knowledge. For instance, the model shuts off seed predation on 1 Oct, based on European field reports (Honek *et al.*, 2005) though North-American studies observed predation until early November (Heggenstaller *et al.*, 2006). However, weed seed rain is rarely as late in our type of pedoclimates and cropping systems. So, even if adult carabids were not already starting to hibernate (Kromp, 1999), delaying the shutoff deadline would have little impact in our simulations. This might change if climate change and/or innovative cropping systems make weeds reproduce later and/or carabids are active longer.

Similarly, the model assumes that seeds are only predated by adult carabids, as it is widely believed most larvae species have mouthparts structure that would not allow seed consumption. Seed consumption by larvae would thus be limited to very few species from the Harpalini and Zabrini tribes. Indeed, larvae from these tribes were reported to consume weed seeds, at least in lab experiments (Hartke *et al.*, 1998; Klimes and Saska, 2010). But in field conditions, these tribes are rarely found in captures of seed-eating carabids (Trichard *et al.*, 2013; Carbonne *et al.*, 2020) so larval seed consumption would likely have little effect on model outputs. The diet of carabid larvae remains however largely undocumented and effort should be devoted to this issue.

The shutoff deadline would also become more influential if carabids predated not only freshly shed seeds in the model, but also older seeds on soil surface, including those excavated by tillage. In lab experiments, carabids showed no preference for fresh seeds vs seeds that had been previously buried in the soil for 6 months (Martinkova *et al.*, 2006). Seed burial might actually facilitate predation via chemical and/or physical changes in the seed coat (Martinkova *et al.*, 2006). Buried seeds are partially or totally imbibed and were shown to be preferred over dry freshly shed seeds, probably because they are more easily detected by carabids through higher emission of olfactory cues (Law and Gallagher, 2015; Kulkarni *et al.*, 2017a). Buried seeds could thus be consumed by adult carabids should tillage tools move these seeds back to the surface, but the proportion of such excavated seeds is actually very low across tools and lcoations (Cousens and Moss, 1990; Mead *et al.*, 1998; Colbach *et al.*, 2000; Roger-Estrade *et al.*, 2001; Colbach *et al.*, 2014a).

Some management techniques were highly simplified by the predation submodel because there were few data. For instance, the effect of insecticide spraying disregarded dosage and active ingredient. But, as the sensitivity analysis to submodel components found little impact even for the more influential tillage (section 3.3.1), this should be acceptable, particularly as the model includes the effect of the frequency and timing of spraying. Other management techniques were ignored because there were either no data or conflicting data. This was for instance the case for mineral and organic fertilizer. However, the sensitivity analysis showed that the most influential management effect was related to canopy density and that even highly disturbing operations such as inverting tillage were negligible compared to this key effect. There should then be no need to add further fertilizer effects other than the indirect effect already included in FLORSYS, i.e., the higher plant biomass production in well-fertilized crops (Moreau *et al.*, 2021). The resulting increase in weed seed predation would be consistent with field observations (Kromp, 1999). Conversely, mulching and crop-residue management might be more influential than fertilization. These plant residues lead to a more favourable microclimate, with milder temperatures and a moister soil (Kromp, 1999). But they were reported to decrease predation rates (Trichard, 2014) as they can hinder carabid movement (Cromar *et al.*, 1999a; van der Laat *et al.*, 2015).

The present model focuses on weed seed predation by carabids but there are other types of predators (e.g., rodents). But, such predators are more mobile than carabids and depend less on management techniques (Cardina and Sparrow, 1996; Winqvist *et al.*, 2011; Roos *et al.*, 2019) or crop canopy (Heggenstaller et al., 2006). As the primary objective of FLORSYS is to quantify direct and indirect effects of cropping systems on crops and weeds in order to evaluate and design agroecological weed management strategies, adding predators that depend little on cropping system would be superfluous. The same applies to other processes that potentially affect seed predation but whose correlation is either low or unknown, such as the effect of soil microflora on weed seed attractiveness to predators (Saska *et al.*, 2022).

4.4 Consequences for agroecological weed management

The simulations showed that weed seed predation indeed contributes to managing weeds, by reducing field infestation, increasing weed-flora evenness and improving crop yields (section 3.4). However, predation rates, and the consequences for crop production and biodiversity, varied greatly among the tested cropping systems, years and crops. Such variations in predation rates have also been reported from field observations (Honek *et al.*, 2003; Westerman *et al.*, 2003b; Gallandt *et al.*, 2005; Labruyère *et al.*, 2016) though these could not conclude on predation impacts on crop yields.

To determine which cropping systems and field margins favour weed seed predation enough to noticeably contribute to biological weed regulation, a higher diversity of cropping systems needs to be explored by simulation. Moreover, the present simulations were run with a single 13-year weather series, recorded during the observations for the model evaluation. To better assess the potential for biological weed regulation of cropping systems, the latter need to be simulated with different weather series. This is essential because the sensitivity analysis showed the key impact of incident radiation and, to a lesser degree, daily temperature on predation rates as well as crop yield and weed-related biodiversity.

Biological weed regulation by carabids might also be detrimental for biodiversity, particularly weed-based trophic resources for other fauna. But again, more simulations are needed to conclude in which cropping systems, this could be an issue.

5 Conclusion

The present paper presented an innovate approach to model the impact of cropping systems and weather on weed seed predation by carabids, and the resulting consequences for crop production and biodiversity. This demonstrated a key advantage of mechanistic (process-based) models, allowing to improve and add functions to existing models such as the FLORSYS model, when needed or when new knowledge becomes available. The resulting model was evaluated with independent field observations,

which is very rare, particularly for weed dynamics models. The simulations with FLORSYS showed that weed seed predation can indeed contribute to managing weeds, by reducing field infestation, increasing weed-flora evenness and improving crop yields. However, to determine which cropping systems and field margins favour weed seed predation enough to noticeably contribute to biological weed regulation, more and more diverse cropping systems and weather series must be explored by simulation. These results will be presented in a companion paper (Colbach *et al.*, in prep).

6 Acknowledgements

7 Literature

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8 Illustrations

Table 1. Main effect of disturbances related to management operations on weed seed predation as well as activity, density and/or abundance of carabids.

| Technique	Decrease in		No effect on
	Seed predation	Carabid activity/density or abundance	Carabid activity/density or abundance
Mouldboard ploughing	(Brust and House, 1988; Menalled *et al.*, 2007)	(Thorbek and Bilde, 2004; Shearin *et al.*, 2014)	
Deep (> 10 cm) non-inverting tillage	(Cromar *et al.*, 1999b)	(Thorbek and Bilde, 2004)	(Shearin *et al.*, 2014)
Superficial tillage	(Sanguankeo and Leon, 2011)	(Thorbek and Bilde, 2004)	
Mechanical weeding		(Navntoft *et al.*, 2016)	(Kromp, 1999; Holland and Luff, 2000; Thorbek and Bilde, 2004)
Insecticide	(Trichard *et al.*, 2013; Cutler *et al.*, 2016; DiTommaso *et al.*, 2017)		
Herbicide	(Sanguankeo and Leon, 2011)	(Zhang *et al.*, 1998; Taylor *et al.*, 2006)	(Brust, 1990; Holland and Luff, 2000)
Fungicide	(Trichard *et al.*, 2013)		(Zhang *et al.*, 1998; Holland and Luff, 2000)
Mowing	(Meiss *et al.*, 2010)		(Thorbek and Bilde, 2004)
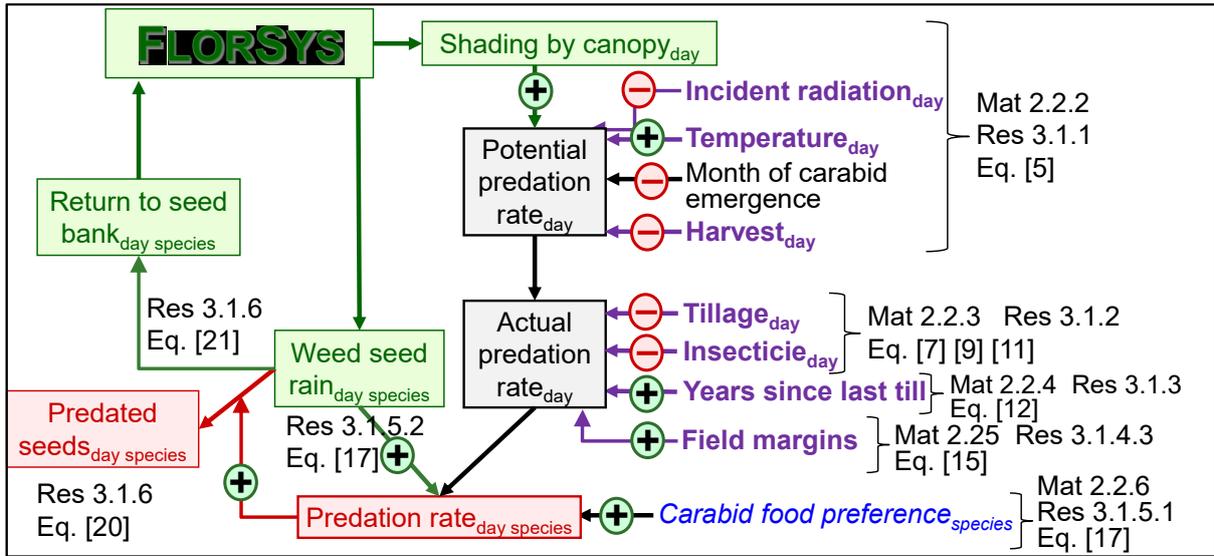
Figure 1. The main daily steps of the weed seed predation submodel to be included in the crop-weed dynamics model FLORSYS (Colbach *et al.*, 2021), with **Input variables**, *Species parameters*, FLORSYS state variables, and submodel state variables and output variables. Mat and Res numbers refer to sections of Material & methods and results, respectively. Equation numbers refer to equations in Table A.1 (Nathalie Colbach 2023).
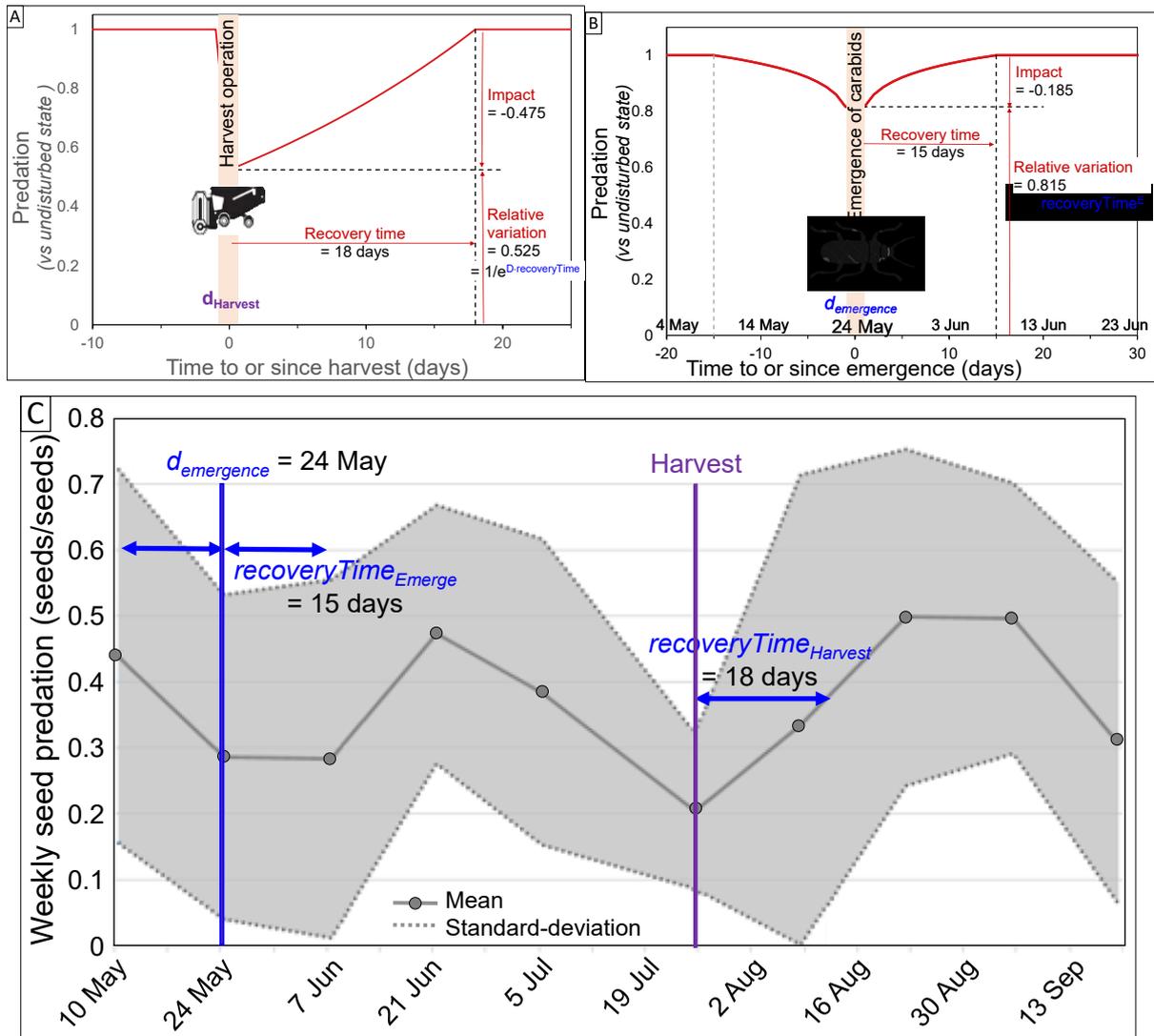
Figure 2. Variation in weed seed predation by carabids due to harvest (A) and emergence of autumn-emerging carabids (B) in the seed predation submodel, estimated by fitting non-linear equation [5] of Table A.1 accounting for these disturbances as well as effects of daily temperature, incident radiation and canopy density (C) on seed predation (symbols) monitored in three wheat fields at the INRAE Dijon-Epoisses experimental station in 2009 (Laurène Perthame 2017)

23
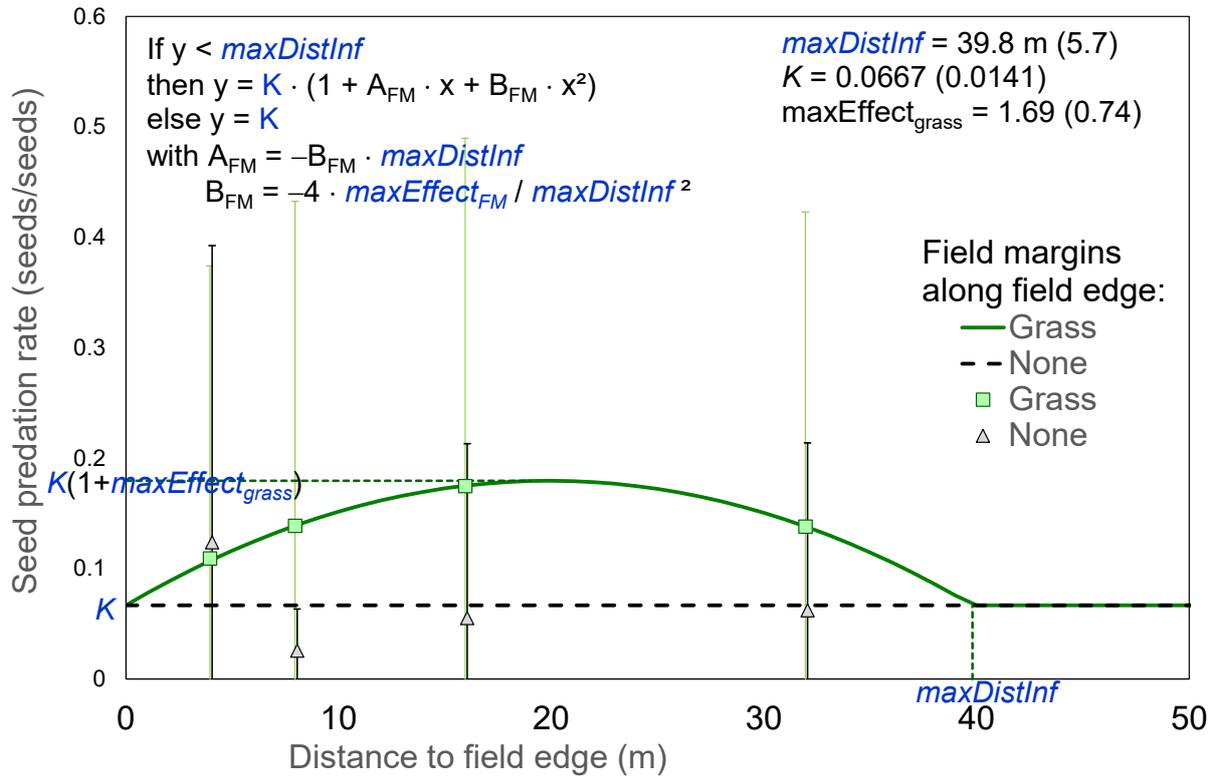
Figure 3. Seed predation rates of *Poa annua* L. as a function of distance to field edge, depending on the presence or absence of a grassy field margin along that edge. Symbols and vertical bars show mean and standard-variation of observed data (N=454), averaged per distance and presence/absence of intrastructure, lines show non-linear regression fitted to predation as a function of distance and presence/absence of field margin with PROC NLIN of SAS ($R^2 = 0.17$, p<0.0001). Data points for given distance were slightly shifted to make it easier to distinguish the standard-deviation bars. Data taken from Petit *et al.* (submitted) (Nathalie Colbach 2023)
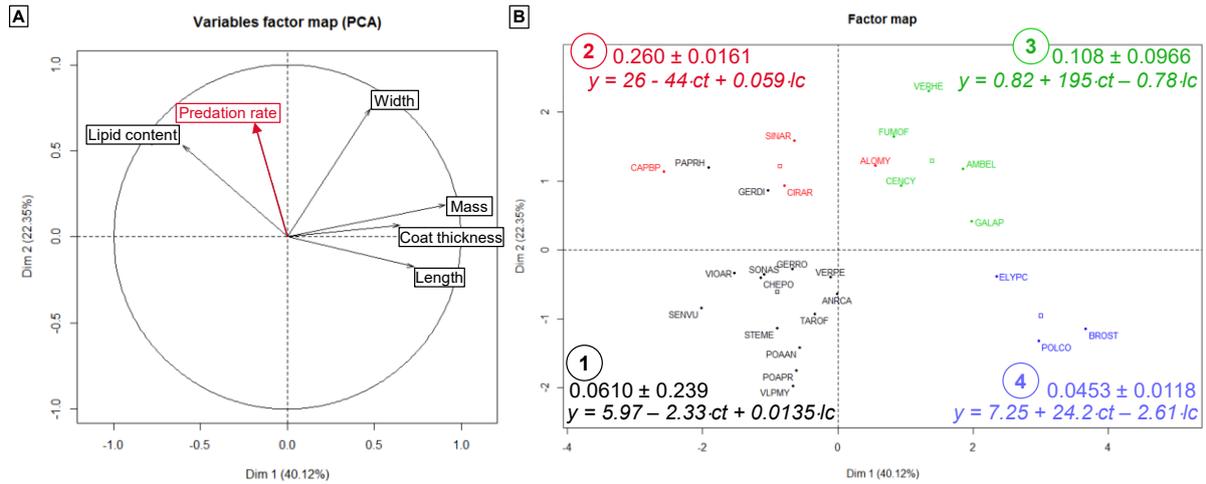
Figure 4. Carabid preference for weed seeds, depending on seed traits, based on Principal Component Analysis of seed predation rates recorded by Trichard (2014) and seed traits. A. Seed traits and seed predation rates. B. Weed species (represented by their EPPO codes, see species names in section *B.5* online) and segregated into four clusters (identified by colours and numbers) based on Hierarchical Classification on Principal Components, with average predation rates (± standard-deviation) per cluster. Equations show linear regressions ($R^2 = 0.83$) linking seed predation rates y to seed coat thickness ct and seed lipid content lc in each cluster (Laurène Perthame)

24 Table 2. FLORSYS ability to predict weed dynamics and to rank cropping systems and weed species
25 asses by comparing simulations to observations from a 12-year cropping system trial in Burgundy. Crop
26 and weed variables are given per species or at the community scale (summed over all simulated species).
27 Values in italics shows variations compared to simulations without the weed seed predation submodel.
28
29 A. Daily weed dynamics

| Variable | Daily dynamics[x] | | | | | |
| | Correct | | Over-estimated | | Under-estimated | |
	With predation	*Variation[†] if no predation*	With predation	*Variation[†] if no predation*	With predation	*Variation[†] if no predation*
Weed biomass (aboveground) (g m⁻²)	0.81	*-0.01*	0.12	*+0.01*	0.07	*-0.01*
Weed plant density (plants m⁻²)	0.85	*0*	0.12	*+0.01*	0.03	*0*

30
31
32 B. Annual and multiannual crop and weed variables

| Variable | Relative bias (%) [§] | | Relative prediction error (%)[$] | | Proportion of correctly predicted observations | | |
| | | | | | Proportion [&] | | In terms of[#] |
	With predation	*Variation[†] if no predation*	With predation	*Variation[†] if no predation*	With predation	*Variation[†] if no predation*	
Crop yield (t ha⁻¹)	12%	-5%	126%	-3%	0.84	-0.01	Absolute values
Crop biomass (g m⁻²)	-1%	0%	~0	0%	0.68	-0.04	Rank
Weed seed bank at a given date	17%	+5%	74%	+5%	0.56	+0.01	Rank
Multiannual weed biomass	16%	+14%	~0	+858%	0.69	-0.01	Rank
Multiannual weed plant density	12%	+5%	121%	+20%	0.60	0	Rank

33 [x] Proportion of observations inside the simulated confidence interval. Colours: from red (0) to green (1) for the first column,
34 from green (0) to red (1) for the two other columns.
35 [†] Coloured from red (deterioration in prediction quality when disregarding weed seed predation in simulations) to green
36 (improvement in prediction quality).
37 [§] Relatively to the range of variation of observations ½[max-min observed values]. Colours: from green (0%) to red (|50%|),
38 grey (too much variability in observations to conclude).
39 [$] Corrected for variability in observations and in simulations, relatively to the standard deviation of observations. Colours: red
40 (bad, > 120%), yellow (satisfactory, 60-90%), light green (good, 30-60%), green (very good, < 30%) and grey (too much
41 variability in observations to conclude), with thresholds based on Colbach et al (2016).
42 [&] Maximum of the modelling efficiency, the Pearson and the Spearman correlation coefficients. Colours: from red (0) to green
43 (1).
44 [#] Cells were coloured from yellow for the worst case (model only ranks situations correctly) to green (model also predicts
45 absolute values correctly).
46
47

48

49 Table 3. Sensitivity analysis of model prediction quality and model outputs to the components of the weed seed predation submodel. Columns for predation rate, weed-impact indicators and crop yield show ls-means calculated
50 after analyses of variance; means of a given column followed by the same letter are not significantly different at p=0.05 (in grey those that are not different from the nominal predation scenario). Cells were coloured from white
51 (0) to red (highest variation in absolute values) for the prediction bias, from red (lowest value) through yellow to green (highest value) for indicators, except field infestation coloured vice-versa. In each subsection, the scenarios
52 were sorted with increasing total predation rate. Additional results in section *D.1* in supplementary material online.

Scenario	Variation in prediction error (weed density over rotation)	Annual predation rate (seeds/seeds per year)	Wild plant biodiversity		Food offer (no unit) for……		Field infestation (t/ha)	Crop yield (MJ/ha)
			Species richness [0,1]§	Species evenness [0, 1]$	Birds	Domestic bees		
A. Including weed seed predation submodel								
No predation	See Table 2	None	0.59 d	0.27 a	2.22 b	0.18 e	1.30 f	118 916 a
Predation		0.50 de	0.57 bc	0.28 abc	2.09 b	0.14 bc	0.86 bcd	127 222 ab
B. Predation submodel without the effect of …								
Harvest	11%	0.31 a	0.59 de	0.28 abcd	2.2 b	0.17 ef	1.10 g	121 230 ab
Carabid reproduction	3%	0.41 b	0.58 cde	0.28 abcd	2.14 b	0.15 de	0.96 ef	124 362 abc
Daily temperature	2%	0.44 c	0.58 cde	0.27 abc	2.15 b	0.14 bcd	0.99 fg	124 236 abc
Weed seed density	-5%	0.49 d	0.56 b	0.27 ab	2.07 b	0.13 bc	0.85 de	127 481 abcd
No till	0%	0.49 de	0.58 bcde	0.29 abcde	2.11 b	0.14 cd	0.89 def	126 340 abcd
Non-inverting tillage	1%	0.50 de	0.58 cde	0.29 bcde	2.10 b	0.14 cd	0.85 def	127 040 abcd
Inverting tillage	1%	0.50 de	0.58 bcd	0.28 abcd	2.11 b	0.14 bcd	0.84 cde	127 831 bcd
Species preference of carabids	1%	0.52 e	0.58 bcd	0.28 abcd	2.12 b	0.15 cd	0.85 cde	127 469 abcd
Light interception by canopy	-2%	0.57 f	0.58 bcd	0.30 de	2.09 b	0.14 bcd	0.82 cd	127 501 abcd
Daily incident radiation	-41%	0.74 h	0.53 a	0.43 f	1.74 a	0.07 a	0.20 a	146 030 e
C. Adding field margins around each simulated field								
Grassland	Not tested as no	0.61 g	0.57 bc	0.31 e	1.99 ab	0.13 b	0.59 b	134 374 d
Grassland with ½ *maxDistInf*	margins in trial	0.56 f	0.57 bc	0.29 cde	2.05 b	0.13 bc	0.72 bc	130 365 cd

(Variation in prediction error column note: vs error observed with complete predation submodel)

53 § Number of species present / maximum possible number of weeds species.
54 $ Pielou's index of species evenness, with 1 = all species present the same abundance, 0 = one dominant species

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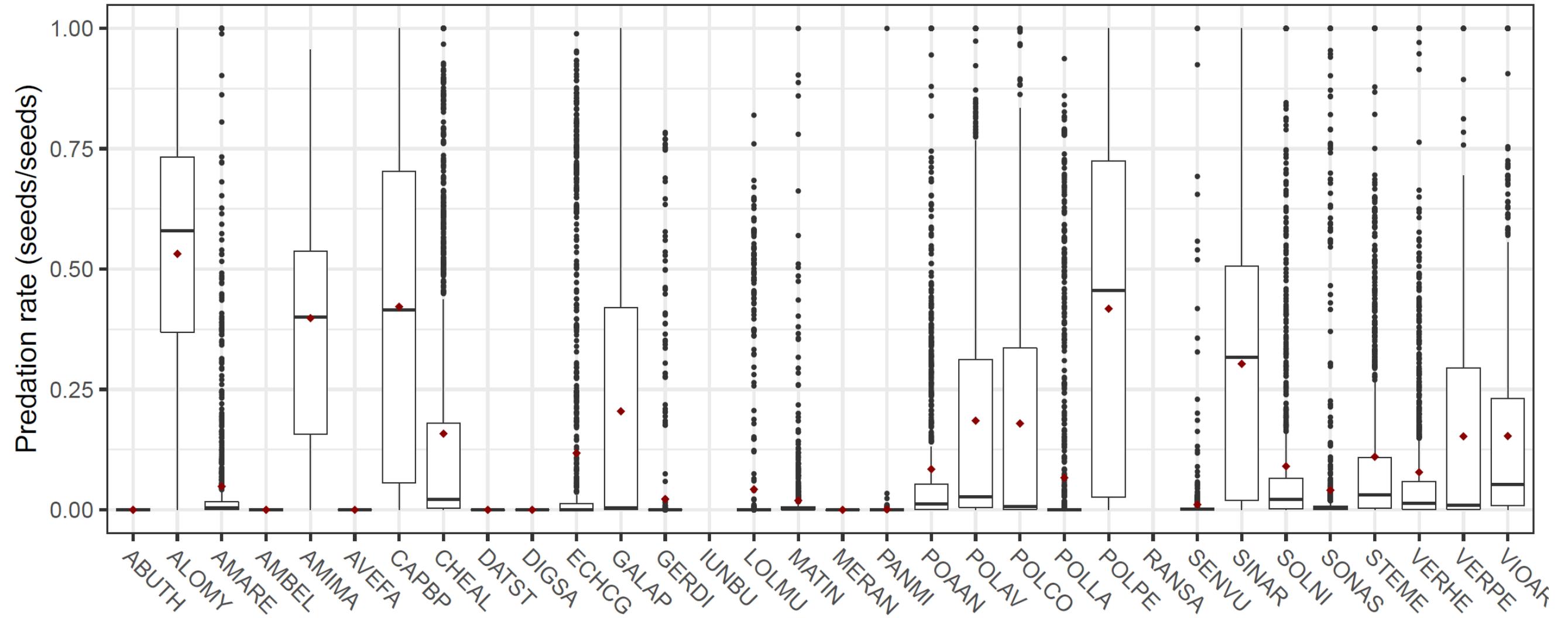
Figure 5. Annual seed predation rates per weed species averaged over all cropping systems, years and stochastic repetitions, simulated with FLORSYS. Weed species are listed with their EPPO codes, Latin names are in section A.2 in supplementary material online (Nathalie Colbach 2023 ⓒⓘⓢⓔ)
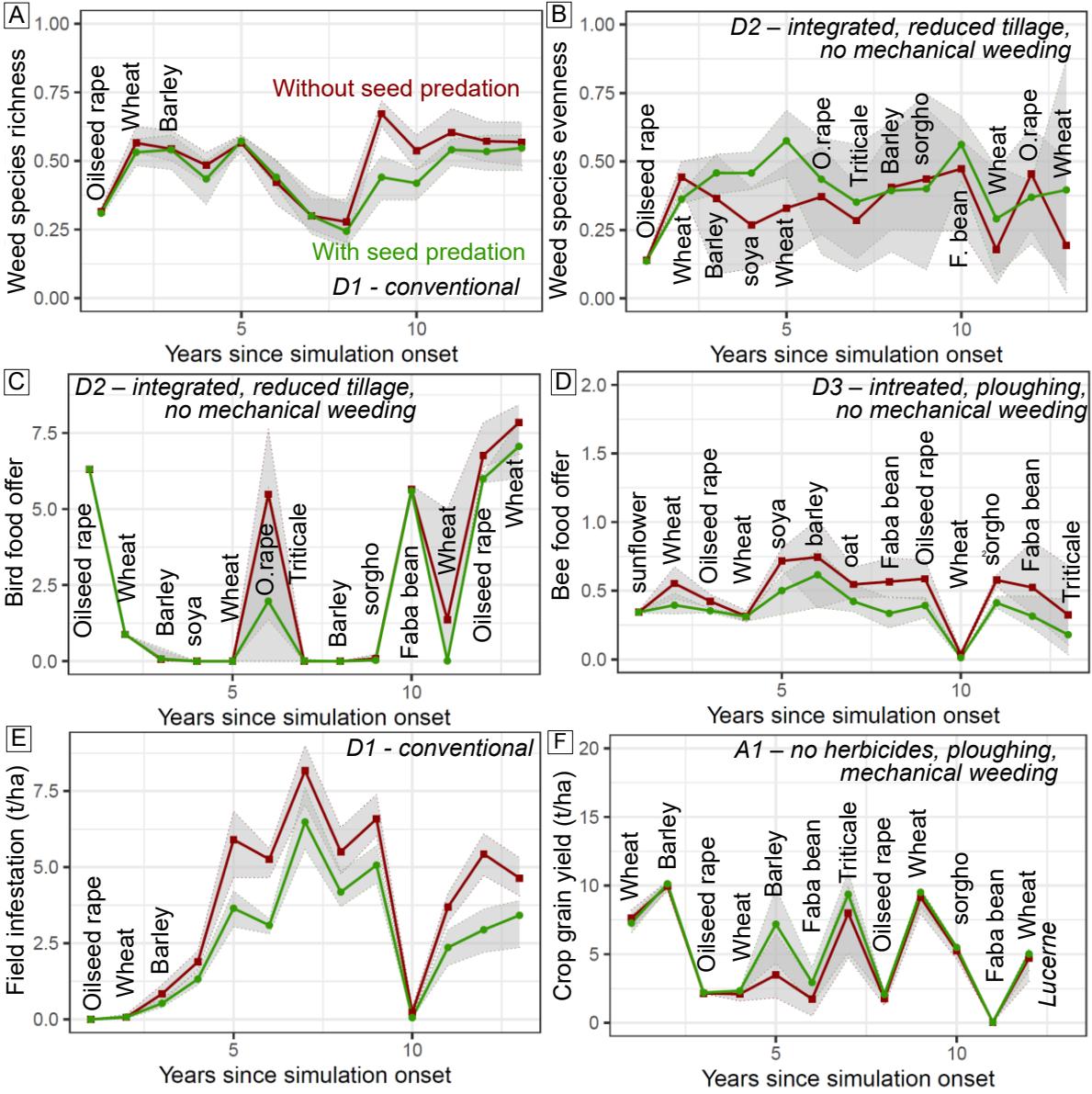
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Figure 6. Effect of weed seed predation on crop yield and weed-impact indicators simulated with FLORSYS. For each indicator, the cropping system with the largest difference between simulations with (green dots) and without predation (red squares) was shown. Grey shades show 90%-confidence intervals resulting from stochastic repetitions. Crop names show crop succession (with spring/summer crops in lower case). Y-axes were scaled to either the maximum possible value (A, B) or the 99%-percentile of values overall systems and repetitions (C-F) (Nathalie Colbach 2023 ⊚)

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9 Appendix

Table A.1. Algorithm and equations of the weed seed predation submodel of FLORSYS, running for each day d. Submodel state variables are in black, parameters are in *italic blue*, inputs are in **bold purple**, state variables provided by other FLORSYS submodels are in green, and the outputs of the predation submodel are in **bold red**.

Eq.	Objective	Equations	Explanations
A. Calculate the daily total predation rate from field history and weather, irrespective of species			
[1]	Photo-thermal and seasonal conditions for predation	If d in [1 Mar, 1 Oct] and $T_{min} < \mathbf{T_d} < T_{max}$ and $\mathbf{PAR_d} > 0$ and $1 - PARsol_d > 0$ then $pred_d = yes$ else $pred_d = no$	T_{min} and T_{max} (°C): min and max temperatures for predation $\mathbf{T_d}$ (°C): daily mean (air) temperature $\mathbf{PAR_d}$ (MJ/cm²/jour): incident photosynthetically active radiation above canopy $PARsol_d$ (MJ/MJ): proportion of PAR_d arriving on soil surface $pred_d$ (yes or no): is predation possible today?
[2]	Efficient temperature	If $T_{min} < \mathbf{T_d} < T_{max}$ then $Teff_d = (\mathbf{T_d} - T_{min}) / (T_{max} - T_{min})$ else $Teff_d = 0$	$Teff_d$ (°C): daily efficient temperature for predation
[3]	Time since and until emergence of carabids with autumnal reproduction	$time_{emerge} = |d - d_{emergence}|$ If $time_{emerge} = 0$ then $time_{emerge} = 1$ If $time_{emerge} > recoveryTime_{Emerge}$ then $time_{emerge} = recoveryTime_{Emerge}$	$time_{emerge}$ (days): time since carabid emergence in spring $d_{emergence}$ (Julian day): date of carabid emergence in spring $recoveryTime_{Emerge}$ (days): duration of emergence effect
[4]	Time since last harvest (or mowing)	$time_{Harvest} = d - \mathbf{d_{Harvest}} + 1$ If $time_{Harvest} > recoveryTime_{Harvest}$ then $time_{Harvest} = recoveryTime_{Harvest}$	$time_{Harvest}$ (days): time since last harvest $\mathbf{d_{Harvest}}$ (Julian day): date of last harvest $recoveryTime_{Harvest}$ (days): duration of harvest effect
[5]	Potential daily predation rate	If $pred_d = yes$ then $potpredRate_d$ $= e^A \cdot Teff_d \cdot (1 - PAR_{sol})^B \cdot \mathbf{PAR_d}^C \cdot e^{D \cdot time_{Harvest}} \cdot time_{emerge}^E$ else $potPredRate_d = 0$	$potPredRate_d$ (seeds/seeds): daily potential predation rate A, B, C, D, E: parameters for the impact of daily temperature, shading by canopy, incident light, harvest and carabid emergence
[6]	Time since last inverting tillage	$time_{InvTill} = d - \mathbf{d_{InvTill}} + 1$	$time_{InvTill}$ (days): time since inverting tillage $\mathbf{d_{InvTill}}$ (Julian day): date of last inverting tillage
[7]	Effect of inverting tillage on predation rate	If $time_{InvTill} < recoveryTime_{InvTill}$ then $predRate_d = potPredRate_d$ $\cdot (1 + impact_{InvTill} \cdot (1 - \frac{time_{InvTill}}{recoveryTime_{InvTill}})$	$recoveryTime_{InvTill}$ (days): duration of effect of inverting tillage $predRate_d$ (seeds/seeds): predation rate after inverting tillage (if any)

Eq.	Objective	Equations	Explanations
		else predRate$_d$ = potPredRate$_d$	$impact_{InvTill}$ (seeds/seeds)**:** maximum effect of inverting tillage
[8]	Time since last non-inverting tillage	time$_{OthTill}$ = d − **d$_{OthTill}$** + 1	time$_{OthTill}$ (days): time since last non-inverting tillage **d$_{OthTill}$** (Julian day): date of last non-inverting tillage
[9]	Effect of non-inverting tillage on predation rate	If time$_{OthTill}$ < $recoveryTime_{OthTill}$ then predRate'$_d$ = PredRate$_d$ $\cdot (1 + \text{impact}_{OthTill} \cdot (1 - \frac{\text{time}_{OthTill}}{\text{recoveryTime}_{OthTill}}))$ else predRate'$_{d=}$ PredRate$_d$	$recoveryTime_{OthTill}$ (days): duration of effect of non-inverting tillage $impact_{othTill}$ (seeds/seeds)**:** maximum effect of non-inverting tillage predRate'$_d$ (seeds/seeds): predation rate after non-inverting tillage (if any)
[10]	Time since last insecticide spraying	time$_{insecticide}$ = d − **d$_{insecticide}$** + 1	time$_{insecticide}$ (days): time since last insecticide spraying **d$_{insecticide}$** (Julian day): date of last insecticide spraying
[11]	Effect of insecticide on predation rate	If time$_{insecticide}$ < $recoveryTime_{Insecticide}$ then predRate''$_d$ = PredRate'$_d$ $\cdot (1 + \text{impact}_{Insecticidel} \cdot (1 - \frac{\text{time}_{insecticide}}{\text{recoveryTime}_{Insecticidel}}))$ else predRate''$_{d=}$ PredRate'$_d$	$recoveryTime_{Insecticide}$ (days): duration of effect of insecticide $impact_{Insecticide}$ (seeds/seeds)**:** maximum effect of insecticide spraying predRate''$_d$ (seeds/seeds): predation rate after insectide spraying (if any)
[12]	Cumulative effect of no till	If years$_{LastTill}$ > $upgradeTime_{NoTill}$ then predRate'''$_d$ = (1 + $impact_{NoTill}$)$\cdot$ predRate''$_d$ else if years$_{LastTill}$ ≤ 1 then predRate'''$_d$ = predRate''$_d$ else predRate'''$_d$ = predRate''$_d$ $\cdot \left(1 + \frac{\text{impact}_{NoTill} \cdot (\text{years}_{LastTill}-1)}{\text{upgradeTime}_{NoTill}-1}\right)$	years$_{LastTill}$ (years): years since last tillage operation $upgradeTime_{NoTill}$ (years): years needed to reach to maximum impact of continuous no till $impact_{NoTill}$ (seeds/seeds): maximum impact of continuous no till
	B. Effect of a field margin along the field edges on daily seed predation rate		
[13]	Effect of distance to field margin and type of field margin	B_{FM} = −4 $\cdot$ $maxEffect_{FM}$ / $maxDistInf^2$ A_{FM} = −B_{FM} $\cdot$ $maxDistInf$ $f(x, FM_v)$ = A_{FM} $\cdot$ x + B_{FM} $\cdot$ x^2	$maxDistInf$ (m): maximum at which there is an effect of a field margin on predation $maxEffect_{FM}$ (seeds/seeds): maximum additional predation observed at $maxDistInf$ from field margin FM (grass, flower, or woody strip), with 0 if no margin (i.e., road, neighbour field) A_{FM} and B_{FM} (seeds$\cdot$seeds$^{-1}\cdot$m^{-1}): parameters depending on type FM of field margin x (m): (perpendicular) distance from field edge

Eq.	Objective	Equations	Explanations
[14]	Effect of a given field margin	$\max_v = \min(maxDistInf, fieldLength_v)$ $effectFM_v = 1$ $\quad + \int_{x=0}^{\max_v} f(x, \mathbf{FM_v})/fieldLength_v$	$fieldLength_v$ (m): length of field perpendicular to vertix v $\max_v$ (m): distance over which the function f is integrated $effectFM_v$ (seeds/seeds): effect of field margin along field vertix v relatively to a vertix without field margin (control = 1)
[15]	Effect of all field margins surrounding the simulated field	$finalPredRate_d = predRate'''_d \cdot \prod_{v=1}^{NV} effectFM_v$ if $finalPredRate_d > 1$ then $finalPredRate_d = 1$	$finalPredRate_d$ (seeds/seeds): final seed predation rate over all species
C. Effect of seed density and predator preference on daily species predation rate			
[16]	Carabid weed-species preference	$CP_s = f(\text{weed seed traits, section 3.1.5.1})$	CP_s (no unit): Relative carabid preference for species s
[17]	Species predation rate	$speciesPredRate_{ds} = finalPredRate_d \cdot CP_s$ $\quad \cdot NSeeds_{ds}/\sum_{i=1}^{NS} NSeeds_{di}$ If $speciesPredRate_{ds} > 1$ then $speciesPredRate_{ds} = 1$	$speciesPredRate_{ds}$ (seeds/seeds): seed predation rate of species s $Nseeds_{ds}$ (seed/m²): Number of seeds produced by species s NS; number of weed species
D. Actual seed predation and return to weed seed bank			
[18]	Potentially predated seeds per species	$NpredSeeds_{ds} = speciesPredRate_{ds} \cdot Nseeds_{ds}$	$NpredSeeds_{ds}$ (seeds/m²): potential number of predated seeds of species s
[19]	Correct for insufficient seed rain of preferred species and/or carabid dislike of abundant seeds	$corrCoeff_d = finalPredRate_d \cdot$ $\sum_{i=1}^{NS} NSeeds_{di} / \sum_{i=1}^{NS} NpredSeeds_{di}$	$corrCoeff_d$ (seeds/seeds): coefficient for readjusting the number of predated seeds to fit the total seed predation rate
[20]	Actually predated seeds per species	$NpredSeeds'_{ds} = corrCoeff_d \cdot NpredSeeds_{ds}$	$NpredSeeds'_{ds}$ (seeds/m²): final number of predated seeds of species s
[21]	Return to weed seed bank	$NSB_{ds\ l=0} = NSB_{d-1\ s\ l=0} + Nseeds_{ds} - NpredSeeds'_{ds}$	NSB_{dsl} (seeds/m²): number of seeds of species s in soil layer l of weed seed bank

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77 Table A.2. Valeur des paramètres du modèle. Ces paramètres ont été estimés à partir de tests statistiques ou de la littérature (source)

Parameter	Meaning	Unit	Value	Source
e^A	Increase in predation rate due to daily temperature	$°C^{-1}$	2.39	Fitting a linear mixed model to data from Petit *et al.* (2014)
B	Increase in predation rate due to shading by canopy	no unit	0.293	
C	Reduction in predation rate due to incident light	no unit	-0.175	
D	Recovery of predation rate with time after harvest disturbance	$days^{-1}$	0.0358	
E	Recovery of predation rate with time after carabid emergence as well as drop in predation with time until carabid emergence	no unit	0.0751	
CP_s	Relative carabid preference for species s	no unit	Section *B.5* in supplementary material online (PCA, clustering, linear regressions, data from Trichard (2014))
$d_{emergence}$	Emergence date in spring of autumn-reproducing carabids	Julian day	144 (24 May)	(Petit *et al.*, 2014)
$impact_{Insecticide}$	Maximum impact of insecticide spraying on predation rate	seeds · seeds^{-1}	-0.43	(Cutler *et al.*, 2016)
$impact_{InvTill}$	Maximum impact of inverting tillage on predation rate	seeds · seeds^{-1}	-0.50	(Thorbek and Bilde, 2004; Shearin *et al.*, 2014)
$impact_{OthTill}$	Maximum impact of non-inverting tillage on predation rate	seeds · seeds^{-1}	-0.39	
$impact_{NoTill}$	Maximum impact of continuous no-till on predation rate	seeds · seeds^{-1}	+0.60	(Cromar *et al.*, 1999b; Menalled *et al.*, 2007; Trichard *et al.*, 2013)
$maxDistInf$	Distance to field edge over which seed predation is influenced by an adjacent field margin	m	39.8	Figure 3
$maxEffect_{FM}$	Maximum additional seed predation in field adjacent to field margin FM — Grass / Flower / Woody	seeds · seeds^{-1}	1.691 / 0.763 / 0.182	Section *B.4* in supplementary material online
$recoveryTime_{Emerge}$	Time before and after carabid emergence during which predation is reduced	days	15	Fitting a linear mixed model to data from Petit *et al.* (2014)
$recoveryTime_{Harvest}$	Time after harvest during which predation is reduced	days	18	
$recoveryTime_{Insecticide}$	Time after insecticide spraying during which predation is reduced	days	30	(Holland and Luff, 2000; Kulkarni *et al.*, 2015)
$recoveryTime_{InvTill}$	Time after inverting tillage during which predation is reduced	days	30	(Thorbek and Bilde, 2004)
$recoveryTime_{OthTill}$	Time after non-inverting tillage during which predation is reduced	days	18	
$upgradeTime_{NoTill}$	Time needed to reach to maximum beneficial impact of continuous no till on weed seed predation	years	4	(Petit *et al.*, 2017)

Parameter	Meaning	Unit	Value	Source
T_{max}	Maximum temperature for predation	°C	35	(Saska *et al.*, 2013; Noroozi *et al.*, 2016)
T_{min}	Minimum temperature for predation	°C	5	(Saska *et al.*, 2013)

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