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# Agricultural management intensity determines the strength of weed seed predation

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ABSTRACT

Agricultural intensification both increases disturbances at the field level and reduces habitat heterogeneity at the landscape level and this can have detrimental effects on biodiversity-driven ecosystem services. A few studies have shown that agricultural intensification can diminish the ecosystem service of weed seed predation, but it is not known to what extent availability of crop and non-crop habitat can provide disturbance refugia for weed seed predators and how those effects cascade to ecosystem service provisioning. Using data from 13 fields in Southern Sweden, we first combined diet preference traits, activity density and metabolic theory, in order to develop a metric that approximates the community strength of seed predation. We then explored how the impact of field management intensity and habitat refugia on seed card predation rates mediated by weed seed availability and the metric of community strength of seed predation. We found that increasing field management intensity directly reduced seed card predation rates and weed seed availability and that reduced weed seed availability in turn impaired the community strength of seed predation. This suggests an indirect mechanism by which field management limits seed predator potential for weed seed predation. We found no evidence that either crop or non-crop refugia can increase seed card predation rates or community strength of seed predation during disturbances in the crop. Consequently, weed seed predation can be promoted by reducing disturbances at the field level, regardless of the availability of disturbance refugia in the landscape. Reduction of field management intensity can directly increase weed seed predation and indirectly seed predator communities' potential for weed seed predation by increasing weed seed availability. Future research is needed to explore if supporting a diversity of non-competitive weeds to enhance seed availability can improve the suppression of dominant and competitive weed species.

## 1. Introduction

Agricultural intensification both increases disturbances at the field level, e.g., through pesticide application and mineral fertilization, and reduces habitat heterogeneity at the landscape level, e.g., through loss of semi-natural habitats and reduction in crop diversity (Foley et al., 2005; Chaplin-Kramer et al., 2011). At both scales, agricultural intensification has been found to weaken biodiversity-driven ecosystem services such as pollination and biological control of invertebrate pests (Dainese et al., 2019). In recent years it has become evident that weed seed predation is another ecosystem service that can benefit agricultural production by reducing weeds (Carbonne et al., 2020; Daouti et al., 2022). To date, however, we lack a mechanistic understanding of how agricultural intensification affects weed seed predation.

In agricultural fields, predation by both invertebrate and vertebrate seed predators contributes to weed regulation (Daouti et al., 2022). In many instances, carabid beetles compromise the most important seed predator group (Cromar et al., 1999; Menalled et al., 2000) and recent work suggests that carabid beetles can regulate weed seed bank communities (Bohan et al., 2011; Carbonne et al., 2020). At the field level, a few studies have found that disturbances such as pesticide applications and tillage can decrease weed seed predation rates (Menalled et al., 2007; Trichard et al., 2013). At the landscape level, however, effects of agricultural intensity on weed seed predation are less straightforward. While many carabid predators use temporarily undisturbed habitats to shelter from disturbances and benefit from the presence of refugia close to the field, some species breed inside crop fields and are common in large-scale agricultural landscapes (Aguilera et al., 2020). As a result, the effect of landscape heterogeneity on weed seed predation is variable and context-dependent. For instance, Trichard et al. (2013) found weed

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seed predation to increase with landscape diversity in France, whereas Jonason et al. (2013) found higher predation rates in simplified landscapes with a higher proportion of annual crops in Sweden.

Seed availability may be a critical, but often ignored, driver of seed predation rates (Saska et al., 2008). Evidence shows that high weed seed availability can increase carabid seed predator abundance (Carbonne et al., 2022) which can lead to enhanced seedbank regulation (Bohan et al., 2011). Theoretically, if seed predators are able to regulate weed populations they should respond to seed availability in a density-dependent manner (Westerman et al., 2008; Baraibar et al., 2012). However, as a consequence of intense agricultural management and the increased use of herbicides in particular, weed abundance and thus seed availability today is only a fraction of what was found in many conventionally managed agricultural fields five decades ago (Andreasen et al., 1996; Sutcliffe and Kay, 2000). As a result, the reduction of weed seeds as a food source can potentially affect predator responses to seed availability and consequently weed seed predation rates. Davis and Raghu (2010) manipulated and measured seed rain for three weed species, and found that seed supply is an important driver of weed seed predation. However, we lack information on how natural seed availability affects the response of seed predators towards seeds and how this affects weed seed predation.

We know that a wide variety of carabid species contribute to weed seed predation (Honek et al., 2013), yet identifying community determinants of the strength of service provision remains a key challenge. Usually, taxonomic measures such as abundance or species richness have been used to infer relationships with seed predation rates (Jonason et al., 2013; Petit et al., 2017). However, it has become evident that levels of ecosystem services are often better predicted by the distribution of functional traits such as trophic guild differentiation (Petit et al., 2014) and body mass (Honek et al., 2007) rather than taxonomic diversity (Gagic et al., 2015). Here, we developed a metric that approximates carabid community strength of seed predation, by combining predator activity density with species-specific seed preferences, likelihood of granivory, and body-mass related feeding rates. To test if this metric can predict measured seed predation rates in the field we related it to seed removal rates on seed cards.

We used structural equation modelling to investigate how disturbances through agricultural management and the availability of crop and non-crop habitat expected to function as disturbance refugia for carabid beetles in the landscape, affected weed seed predation in thirteen wheat fields in southern Sweden (Fig. 1). Based on prior knowledge of the negative effects of field management on weed seed predation rates (Trichard et al., 2013), above ground seed availability (Petit et al., 2011), and carabid communities (Navntoft et al., 2006; Shearin et al., 2007; Thorbek and Bilde, 2004), we predicted field management intensity to reduce the community strength of seed predation, the above ground seed availability and seed card predation rates. Additionally, we expected negative effects of management intensity on seed card predation rates to be mediated indirectly by above ground seed availability and the community strength of seed predation. Since habitat refugia are expected to provide continuous access to food resources and shelter from disturbance for the carabid predators (Gaba et al., 2010; Landis et al., 2000; Tscharntke et al., 2012), we predicted a direct positive effect of habitat refugia on seed card predation rates and the community strength of seed predation. Additionally, we expected the positive effect of habitat refugia on seed card predation rates to be mediated indirectly by the community strength of seed predation. By providing continuous access to resources and shelter from disturbances, crop and non-crop habitat refugia are likely to enhance both, predator abundance and richness (Carbonne et al., 2022) and thus increase community strength of seed predation and therefore weed seed predation.

## 2. Methods

### 2.1. Study area and experimental design

Fieldwork was conducted across the predominantly agricultural province of Scania, Southern Sweden (Fig. 2a), an area characterized by high input cropping systems dominated by cereals with oilseed rape as the most common break crop. We selected 15 conventionally managed winter wheat fields to represent a landscape gradient ranging from 5 % to 95 % of arable land in the surrounding 1 $km^2$. Field sampling took place on two occasions in the summer of 2018. The first sampling session was conducted during milk and dough development of wheat in mid-June (June 17, 2018 until June 28, 2018) and the second during wheat ripening in mid-July (July 7, 2018 until July 18, 2018). The sampling sessions were timed to coincide with activity periods of both spring and autumn breeding carabid beetles (Thiele, 1977) and weed species seed shed (Lundkvist and Fogelfors, 2004). In each field, the

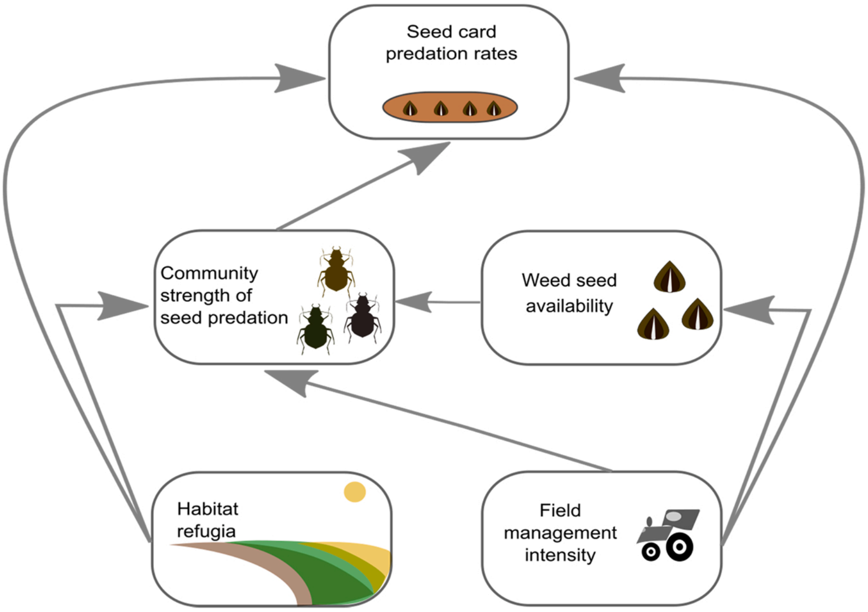

**Fig. 1.** A priori piecewise structural equation model (pSEM) describing direct and indirect effects of field management intensity and habitat refugia on the community strength of seed predation, weed seed availability and seed card predation rates.

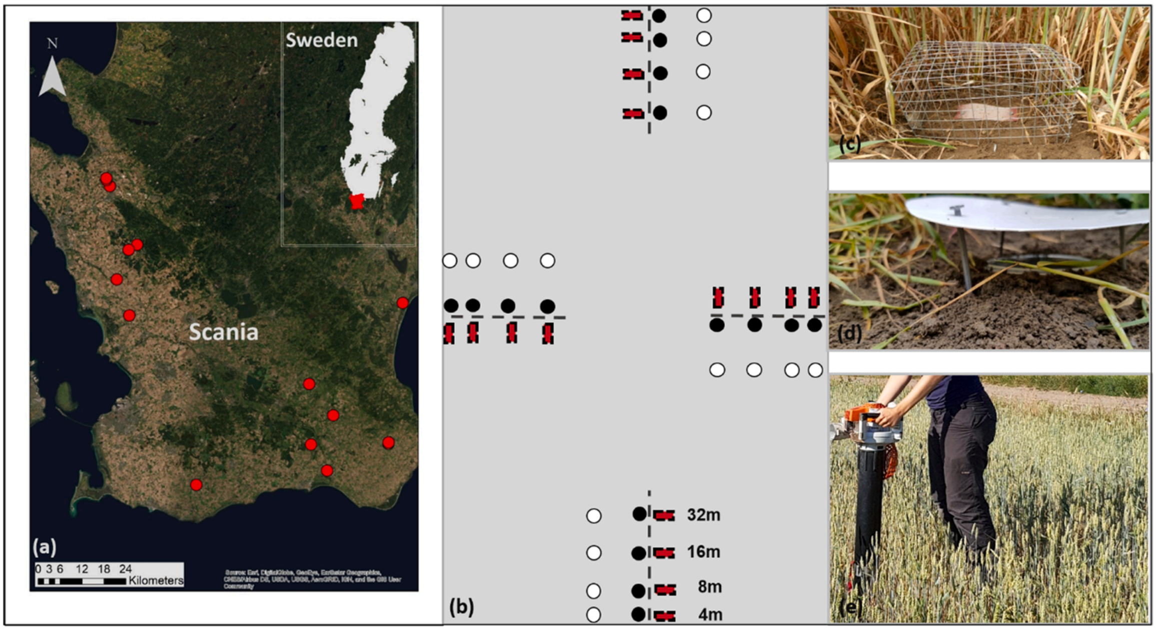

**Fig. 2.** Experimental design of the weed seed predation experiment. (a) Fifteen fields (of which two were excluded from the analysis due to lack of management information), were selected across Scania, the most southern province of Sweden. (b) In each field, four transects (dashed lines) were placed starting from the field edge with sampling points at 4 m, 8 m, 16 m and 32 m into the field, respectively. At each distance, we estimated weed seed predation (dashed red rectangles), carabid predator activity density (black circles) and above ground seed availability (white circles). (c) We estimated weed seed predation for invertebrate predators using seed cards with fifty *Poa annua* seeds which were covered with a metal net cage (mesh size: 11 mm) to prevent predation from vertebrates. (d) One meter to the side of each pair of seed cards, we placed one pitfall trap to estimate carabid activity density. (e) Two meters to the side of the pitfall traps, we estimated above ground seed availability using a suction sampler. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sampling design included four transects extending into the crop from different field edges (for details see Fig. 2).

### 2.2. *Weed seed predation*

We estimated levels of weed seed predation using seed cards (Westerman et al., 2003), manufactured from 95 × 40 mm sandpaper (grain size 60; Bosch, Stuttgart, Germany; Fig. 2c). On each card's surface, we attached 50 seeds of the common weed *Poa annua* using sprayed repositionable glue (3 M Spray Mount, Minnesota, United States) (Westerman et al., 2003; Daedlow et al., 2014). We covered the remaining glue with fine sand to resemble the soil surface. We selected *P. annua* due to its (i) widespread geographical distribution, (ii) reproduction strategy which includes early maturation and seed shed (Hallgren et al., 1999) and (iii) level of attractiveness to carabid beetles (Saska et al., 2008). The density of seeds on the seed cards corresponded to 13 157 seeds per m$^2$ which is within the natural range of weed seed densities (1 150–58 980 per m$^2$) that have been documented in arable fields (Leguizamón and Roberts, 1982). At each sampling point, we anchored a seed card to the soil surface using metal nails (Fig. 2b & 2c). The seed cards were enclosed by a wire cage (dimensions: 115 × 180 × 90 mm and mesh size: 11 mm) to exclude vertebrate predators (Fig. 2c). After seven consecutive days of exposure, we collected the seed cards and recorded the number of remaining seeds. For each sampling session, we quantified seed card predation as the proportion of the number of removed seeds to the number initially offered. We assumed that all seeds that disappeared had been consumed and thereby seed removal was treated as a measure of seed card predation rate (Westerman et al., 2003; Jonason et al., 2013).

### 2.3. *Above ground seed availability*

For each field and sampling session, we estimated above ground seed availability on the soil surface using suction sampling (Fig. 2e). At each sampling point, we took two subsamples located 0.5 m apart. We conducted the sampling on days with low wind speed and no rain. Samples were stored and preserved in 70% ethanol. For each sample, we counted the total number of seeds to estimate above ground seed availability at each sampling point.

### 2.4. *Carabid predator activity density*

We monitored the activity density of carabid seed predators using pitfall traps (Fig. 2d). We installed each trap using a polypropylene pipe (dimensions: 70 mm diameter, 150 mm depth) buried flush to the soil surface. Inside each pipe, we placed a plastic cup (dimensions: 270 ml, 75 mm diameter, 108 mm height) filled with 100 ml of a preservative solution of saltwater and odourless detergent to reduce surface tension. To minimize the risk of flooding, we installed a plastic cover 10 cm above each trap using metal nails (Fig. 2d). At each sampling session, we opened the traps at the same time as we exposed the seed cards to predation and we emptied them after seven consecutive days. We collected the content of each trap and preserved it in 70% ethanol until species identification. We counted and identified carabid beetles to species level following Lindroth (1985).

### 2.5. *Community strength of seed predation*

We developed a metric that approximates the strength of seed predation for the given seeds (here: *Poa annua*) by a carabid community. The metric depends on the potential predation strength exerted by each individual predator within the community and is a function of species-specific seed preference, likelihood of granivory, metabolic rate and activity density. Since cafeteria experiments have shown that different carabid species prefer different weed seed taxa (Honek et al., 2007; Saska et al., 2008; Petit et al., 2014), we created a preference index for *P. annua* seeds $P_i$. The metric was based on data available from feeding experiments investigating seed preferences for individual carabid species (Saska et al., 2008). We estimated preference values of each species based on the proportion of seeds eaten in those experiments. For species that we were unable to retrieve preference data for, we used averaged preference values, of the existing data, based on each species respective trophic position (Table A1). Since in the cafeteria experiments only seeds were offered and no animal prey, feeding rates on seeds might have been overestimated for many carabid species that in the field would also consume animal prey. To account for this, we corrected the preference index by adding another variable in the metric, the likelihood of granivory $L_i$ which describes how likely is a seed to be eaten based on the trophic level of each predator. Following Lindroth (1985), we thus divided carabids into carnivorous, omnivorous, and granivorous species. Assigned probabilities were arbitrarily set to 0.1 for carnivorous, 0.5 for omnivorous and 0.9 for granivorous carabid beetles (Table A1). Next, we estimated feeding rates, utilizing a similar methodology as Feit et al. (2019) where feeding rate was approximated as a function of species-specific metabolic rates that scales as a function of body mass. Following Jarošík (1989), we estimated dry body mass $M_i$ (mg) of individual predator species as a function of body length:

$$M_i = 0.03969 \times {BL_i}^{2.64}$$

where $BL_i$ is the species-specific average body length retrieved from Lindroth (1985). We then estimated the metabolic rate $I_i$ of individual carabid species as a proxy for their feeding rate:

$$I_i = 0.544 \times {M_i}^{3/4}$$

where 0.544 is a normalization constant for carabids (Ehnes et al., 2011) and $M_i$ is the average dry body mass of species $i$. We then estimated the risk of predation $R_i$ on *P. annua* seeds by a given carabid species within a community based on its preference strength for *P. annua* $P_i$, likelihood of granivory $L_i$, activity density $A_i$ and metabolic rate $I_i$:

$$R_i = P_i \times L_i \times A_i \times I_i$$

Finally, we calculated the community strength of seed predation $W$, as the sum of risk of predation on *P. annua* by $n$ number of predators at each sampling point during each sampling session:

$$W = \sum_{i=1}^{n} R_i$$

### 2.6. Field management intensity and habitat refugia

For each field, we calculated an index of field management intensity based on the total number of field visits by the farmer to conduct operations during the cropping season. This index was a proxy for each field's disturbance level and it has been shown to reduce carabid species abundance (Carbonne et al., 2022). Field visits encompassed tillage, sowing, and harvest as well as the application of fertilizers, pesticides and growth regulators. When several operations were carried out during the same visit, this was counted as one visit. We collected the data, by sending individual questionnaires to the farmers managing the respective fields (Table A2). We were unable to retrieve field management data from two out of 15 originally selected fields and therefore were excluded from the analysis. The remaining 13 fields covered a gradient of field management intensity ranging from 5 to 13 field visits (mean ± SD = 9 ± 2; Table A3) and it was correlated with the number of pesticide applications ($r = 0.93$. $p < 0.001$) which were predominantly made up of herbicide and fungicide applications.

To quantify crop and non-crop habitat as potential habitat refugia, we obtained landscape data from the Integrated Administration and Control System (IACS), a database maintained by the Swedish Board of Agriculture (Jordbruksverket). We mapped land use at 200 m radius around each transect, using the 'buffer' tool in ArcMap (ESRI, v. 10.4.1). We selected this scale because it is relevant for short-term movements of carabid beetles (Firle et al., 1998) and because it lies within the range of scales that has been identified to have an impact on carabid predator assemblages in similar systems (Rusch et al., 2016). Land cover classes were merged into six larger habitat categories: annual crops, semi-natural habitat (SNH), forest, rural settlements, and water. Included SNH types were grassed strips, meadows, pastures, field edges, and hedgerows. Carabid species have preferred microclimatic ranges that are affected by soil and vegetation (Thiele, 1977; Diehl et al., 2012), and since semi-natural habitat (SNH) and unharvested annual crops provide vegetation cover and favourable microclimatic conditions for the carabid species (Thiele, 1977), they were considered as potential refugia that carabid species could shelter in after a disturbance event during the crop season. Since forests may be of a greater importance as overwintering habitats (Thiele, 1977), we did not consider them as potential refugia during the crop season.

The percentage area of unharvested annual crops (crop refugia) was negatively correlated with percentage cover of semi-natural habitat (SNH refugia) (Spearman's correlation $= -0.76$, $p = 0.001$). Consequently, their effects on response variables were explored in separate analyses. Crop and SNH refugia covered a broad range of values. Crop refugia covered a range of 0–75 % of habitats within 200 m while SNH coverage ranged from 0 % to 43 % (Table A3).

### 2.7. Statistical analysis

We developed a structural equation model (SEM) to investigate the direct and indirect effects of field management intensity and habitat refugia on weed seed predation (Fig. 1). We used piecewise SEMs (pSEMs) that allow for modelling data that does not meet the assumptions of classical SEM such as nested non-normally distributed data (Lefcheck, 2015).

To test the hypothesized direct and indirect effects within each pSEM we performed individual generalized mixed-effect models (GLMM; for seed card predation and above ground seed availability) and a linear mixed-effects model (LMM; for the community strength of seed predation) (Lefcheck, 2015). We included the interactions between habitat refugia (crop or SNH refugia) and field management intensity as additional predictors. We included a random effect term of sampling session and to account for the nested structure of our experimental design, we also included a nested random effects term (field /transect) (Zuur et al., 2007). To account for overdispersion, we included an observation level random effect (Bolker et al., 2009). For the LMM, we log-transformed the community strength of seed predation to ensure normality of model residuals. We tested normality by visually checking the Q-Q plots of component model residuals. Since crop and SNH refugia were highly correlated (Fig. A1) and their effects on response variables were explored in separate analyses. Collinearity was low in all individual models, as indicated by variance inflation factors (VIF) below 2.0. The overall fit of our path model was assessed using Fischer's C statistic (Shipley, 2016) and AIC values. We improved our model fit and the replication per variable, by dropping non-significant predictors and random effects. All analyses were conducted in R version 4.1.0 (R Core Team, 2021). The R packages "lme4" (Bates et al., 2015) and "piecewiseSEM" (Lefcheck, 2015) were used for SEM development and analyses.

## 3. Results

### 3.1. Community strength of seed predation, weed seed availability and seed card predation rates

We collected a total of 14 507 carabid beetles which comprised 10 granivorous, 5 omnivorous and 32 carnivorous species (Table A1). Omnivorous species accounted of 72 % of all captured species while carnivorous comprised 26 % and granivorous 2 % (Table A4). *Pterostichus melanarius* (an omnivore) was by far the most abundant species, accounting for 56.6% of the total activity density of carabid beetles while the second most abundant, *Anchomenus dorsalis* (a carnivore), accounted for 9.20 % of the total activity density (Table A1). The calculated community strength of seed predation *W* per sampling point ranged from 0.02 to 2 504 (mean ± SD = 596 ± 490). Using suction sampling, we collected a total of 4 927 seeds (12.6 ± 32.7 per sampling point) which corresponds to 31.5 ± 81.7 seeds per $m^2$, belonging to 46 weed species. On each sampling point, an average of 13 ± 18 % out of 50 *Poa annua* seeds on the seed cards were predated.

### 3.2. Weed seed predation pSEM

Our SEM model showed good fit (Fisher's C = 1.82 with p = 0.4023; Fig. 3 and Table A5) and the D-separation test did not reveal missing paths with significant path coefficients. Including the interaction term between habitat refugia and management intensity did not increase the fit of the model and had no significant effect on the hypothesized pathways (for results with interactions see Table A6).

Field management intensity had direct negative effects on the availability of weed seeds and on seed card predation rates (Fig. 3 and Table A5). Furthermore, by reducing seed availability, field management intensity had an indirect negative effect on community strength of seed predation (Fig. 3 and Table A5). Directly, however, field management intensity had no effect on community strength of seed predation (Fig. 3 and Table A5). There was no significant link between community strength of seed predation and seed card predation rates (Fig. 3 and Table A5).

Proportion cover of SNH as a descriptor of habitat refugia had no effect either on the community strength of seed predation or on seed card predation rates (Fig. 3 and Table A7). Similarly the model with crop refugia had no effect on neither on the community strength of seed predation nor on seed card predation rates (Table A8) and had a lower fit compared to SNH refugia (Fisher's C = 5.434 with p = 0.246 and on 4 degrees of freedom; Table A8).

## 4. Discussion

We demonstrated that field management intensity impairs the ecosystem service of weed seed predation. Field management intensity reduced seed card predation rates directly and our metric of community strength of seed predation indirectly. The indirect negative effect of field management intensity on community strength of seed predation, was mediated by the positive effect of seed availability on this metric. This positive link, indicates a positive density-dependent effect of seed availability on predator seed demand. Our results are in line with similar findings indicating that weed seed predation levels are reduced in intensively managed agricultural environments (Menalled et al., 2007; Trichard et al., 2013). In contrast to our expectations, crop and non-crop refugia, had no effect on either the strength of weed seed predation or seed card predation rates. We also found no link between community strength of seed predation and seed card predation rates.

We developed a metric that approximates community strength of seed predation by combining seed predator abundance with species-specific seed preference, likelihood of granivory, and body-mass related feeding rate. Our metric was positively influenced by weed seed availability. However, we detected no relationship with seed card predation rates, in contrast to our expectations. We can provide two possible explanations for the absence of a link between these two variables. Firstly, we cannot rule out that other invertebrates such as ants (Baraibar et al., 2011) and carabid larvae (Saska and Jarosik, 2001) might act as additional seed predators in our system, and they were not included in our metric of community strength of seed predation. Secondly, it is likely that a low weed seed density in our fields led to lower seed demand from the carabids which weakened the link between seed card predation rates and the community strength of seed predation. Seed card predation rates and weed seed availability in our fields, were lower compared to several other studies (Daedlow et al., 2014; Saska et al., 2008). Similarly, Saska et al. (2008) found that activity density of carabid predators did not explain weed seed predation estimates on seed cards. To improve the metric's predictability, molecular gut content analysis could be employed to evaluate realised feeding interactions between different carabid species and *P. annua*. Such analysis, can assist us to correctly predict likelihood of granivory for each carabid species as well as *P. annua* preference. Developing a functional metric of community strength of seed predation has several potential benefits. Firstly, compared to seed card predation rates that are snapshots in time, it can provide a more long term estimate of the ability of seed predator communities to provide weed seed predation at a specific location. Secondly, the index can easily be adjusted to encompass all relevant weeds present

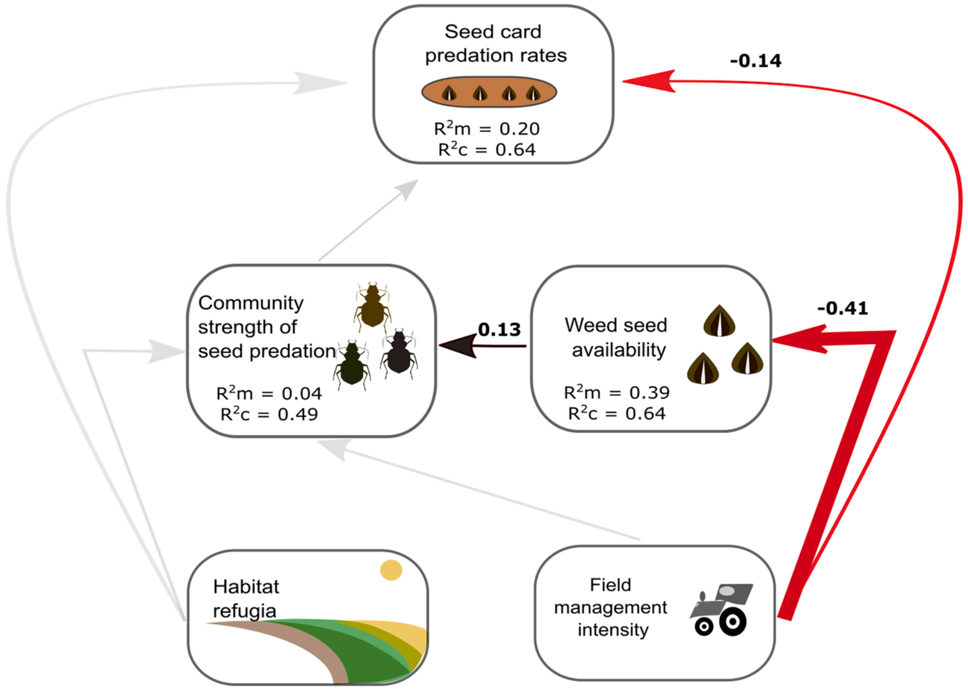

**Fig. 3.** Piecewise structural equation model (pSEM) describing direct and indirect effects of field management intensity and habitat refugia on the community strength of seed predation, weed seed availability, and seed card predation rates. Marginal ($R^2m$) and conditional ($R^2c$) values are given for all component models as estimates of variation explained by fixed and both fixed and random effects respectively. Thickness of the paths is proportional to standardised path coefficients. Black arrows indicate positive, red negative effect. Light grey arrows indicate a non-significant effect (for details see Table A5 and A7).(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in a field whereas seed card predation estimates are limited to one or a few preselected species. Finally, the index can be applied to datasets where seed card predation rates have not been estimated and this can provide novel insights into how agricultural management, landscape composition and other variables impacts the potential for weed seed predation.

Field management intensity reduced the availability of weed seeds, which in turn reduced the community strength of seed predation. This finding, demonstrates that the frequently found negative effects of field management intensity on carabid communities (Navntoft et al., 2006; Shearin et al., 2007) can be mediated by reduced seed availability. Weed seeds are an important food source for carabid beetles (Gaba et al., 2019; Saska, 2008) and intensively managed fields with frequent herbicide applications and intensive soil cultivation can limit seed availability and this may cascade to lower community strength of seed predation. The positive link between seed availability and the community strength of seed predation also suggests a positive density-dependent mechanism between the carabid predators and their food source (Westerman et al., 2008; Baraibar et al., 2012). For seed predators to be able to regulate weed populations it is a prerequisite that seeds are consumed in a density-dependent manner (Holling, 1959). Our finding, thus provides further evidence that carabid beetles can regulate weed populations (Bohan et al., 2011; Carbonne et al., 2020).

In contrast to our expectations, availability of habitat refugia including unharvested crops and semi-natural habitat, neither affected the community strength of seed predation nor seed card predation rates. Thus, changes in seed card predation rates were mediated entirely by increased field management, rather than by changes in the surrounding landscape. Theoretical predictions (Tscharntke et al., 2016) and empirical findings (Ricci et al., 2019) suggest that in some cases landscape effects on ecosystem services can be offset by field management intensity. Specifically, natural habitat can fail to enhance an ecosystem service when intense agricultural practises hinder the establishment of natural enemies (Tscharntke et al., 2016). In our case, it is possible that by removing weed seeds as an important food source, agricultural management impeded the establishment of carabid communities that would otherwise provide biological weed control. Additionally, the dominance of *Pterostichus melanarius* among the captured carabid species could potentially explain the absence of effect of SNH refugia on community strength of seed predation. *Pterostichus melanarious* is well adapted to intensified agroecosystems (Holland, 2002), it has a low dispersal ability compared to other carabid species (Firle et al., 1998) and it is potentially indifferent to the presence of SNH refugia.

## 5. Conclusions

We have taken the first steps into developing a metric of community strength of seed predation that can be used to estimate seed predation potential of carabid communities in different settings. Even though the metric was not able to predict seed card predation rates in the field, it provided important insights into how agricultural management affects the seed predator communities by reducing seed availability. Our work furthermore showed that increased levels of weed seed predation can be achieved by reducing management-related disturbances in the field. It thus appears that, conventional, input-driven farming with frequent disturbances that aims to completely eradicate weeds, likely jeopardises the potential for biological weed control by failing to maintain enough weed seeds to sustain seed predator communities. From the farmers perspective maintaining weed seed availability might seem like a risky practice that may threaten crop yield. Approaches such as cover crops (Blubaugh et al., 2016) or introducing rare (and non-destructive) weed species (Lang et al., 2021), might be useful tools to increase predation by sustaining seed availability. Future research should assess if enhancing seed availability of a diversity of non-destructive weeds can be used to improve the suppression of dominant and competitive weed species. We also encourage further work to improve the metric of seed predation, e.g. by parameterising it with molecular gut content data.

## 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.

## Data Availability

The data that support the findings of this study are openly available from the Swedish National Data Service: https://doi.org/10.5878/7w75-8764.

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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.2022.108132.

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