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Seed predation is key to preventing population growth of the weed *Alopecurus myosuroides*

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Abstract

1. Seed predation can reduce the abundance and spread of unwanted vegetation in agricultural and other semi-natural ecosystems. However, knowledge of how variations in seed predation rates affect plant species population dynamics is needed for decision making and knowledge-based ecosystem management.

2. We developed a stage-classified stochastic matrix population model for *Alopecurus myosuroides* Huds. (blackgrass), an annual plant species thriving as a weed in temperate agroecosystems of Western and Northern Europe. The model was parameterised using empirical demographic data from long-term experiments in Swedish winter wheat fields, including information on post-dispersal seed losses by vertebrate and invertebrate seed predators.

3. For agroecosystems with highly effective weed control measures (e.g. chemical and mechanical weed control), model simulations showed that seed losses via seed predation need to reach at least 78% at peak seed shedding to suppress population growth of *A. myosuroides*.

4. The field experiment showed that vertebrates were most important for seed predation in July, at peak seed shedding. In August, after crop harvest, invertebrates were responsible for almost all seed predation. The model indicated that weed seed predation was much more important for weed regulation when it occurred before crop harvest in July. Vertebrates most strongly reduced population growth of *A. myosuroides*, although both vertebrates and invertebrates were needed to prevent it entirely.

5. *Synthesis and applications*. We showed that weed seed predation by vertebrate and invertebrate seed predators is key for reducing the population growth of winter annual weeds like *A. myosuroides* in intensively managed agroecosystems. Therefore, protection of weed seed predators is essential for making management of unwanted vegetation less dependent on chemical and mechanical measures.

KEYWORDS
agroecosystem, blackgrass, ecological weed management, ecosystem service, invertebrate seed predators, stochastic matrix population model, vertebrate seed predators, weed population dynamics

1 | INTRODUCTION

Seed predation can have immediate detrimental effects on plant population growth (Andersen, 1988; Crawley, 2000). Hence, seed predation is an ecosystem service that can reduce the abundance of unwanted vegetation (i.e. weeds) in agroecosystems or the spread of invasive alien species in semi-natural ecosystems (Garren & Strauss, 2009; Losey & Vaughan, 2006). Yet, the effects of seed predators on the seed bank depend on ecosystem context as well as on plant species and their seed input to the soil (Crawley, 2000; Davis et al., 2011; Diekötter et al., 2016). To date, we are lacking a quantification of how seed predation alters plant species population dynamics (Petit et al., 2018).

Weed seed predators in temperate agroecosystems can be divided into two functional groups, vertebrates (especially rodents and mice) and invertebrates (mainly carabid beetles; Honek et al., 2013; Janzen, 1971; Kulkarni et al., 2015). The relative importance of vertebrates and invertebrates for seed predation appears to be context dependent (Harrison et al., 2003; Menalled et al., 2000; Tschumi et al., 2018), with small vertebrates preferring larger seeds than invertebrates (Booman et al., 2009; Brust & House, 1988). In a previous study across wheat fields, vertebrate predation rates were variable (30%–88%), but accounted for a larger proportion of seed consumption than by invertebrates (Westerman et al., 2003). Yet, in other experiments invertebrates were responsible for the majority of agricultural weed seed predation (Brust & House, 1988; Gallandt et al., 2005).

Plant population modelling makes it possible to link seed predation with weed species-specific population growth. Weed population models are often used as tools in weed management decision making, to forecast weed species abundance and associated crop losses under different management strategies (Burns et al., 2018; Davis et al., 2004; Liebman & Nichols, 2020). However, predicting plant population dynamics is challenging, due to the unpredictability of environmental conditions, the natural variation in plant fitness, reproduction and mortality induced by genetic variability and epigenetics, and uncertainties associated with parameter estimates (Holst et al., 2007). Variation and unpredictability of environmental conditions are explicitly accounted for by stochastic models. They rely on parameters extracted from probability distributions and provide a frequency distribution of key model outputs (e.g. population growth rate λ), allowing the quantification of their variability (Davison et al., 2019). Despite their potential, stochastic population models have not been applied previously to forecast the effects of weed seed predation on weed population dynamics.

In this study, we developed a stage-classified stochastic matrix model, representing the life cycle of winter annual grass weeds in temperate agroecosystems. The model species was *Alopecurus myosuroides* Huds. (blackgrass), an autumn-germinating winter annual grass species of north-western Europe and a typical weed in temperate cereal cropping systems (Cavan et al., 2000; Lutman et al., 2013). In the absence of adequate control measures, *A. myosuroides* infestation can increase rapidly, causing significant crop yield loses (Lutman

et al., 2013). For example, in England alone, winter wheat losses due to insufficiently controlled blackgrass populations has been estimated to 0.8 million tonnes per year (Varah et al., 2020), which accounts for approximately 8% of the average wheat production of the entire United Kingdom (based on 5 year average 2015–2019 according to Farming Statistics 2020—United Kingdom).

The model was parameterised with empirical demographic data on *A. myosuroides* life stages, including post-dispersal seed losses caused by vertebrate and invertebrate seed predators. The objectives of the study were (a) to determine the sensitivity of the population growth rate λ of *A. myosuroides* to changes in life cycle events; (b) to quantify the effect of weed seed predation and its temporal variability on the population growth of *A. myosuroides*; and (c) to determine the relative importance of vertebrate and invertebrate weed seed predators.

2 | MATERIALS AND METHODS

2.1 | Study system

Alopecurus myosuroides Huds., an annual grass species native to Eurasia, is one of the main weed species in temperate cereal-growing regions of Europe. This species prefers cultivated or disturbed heavy soils with poor structure and poor drainage (Barallis, 1968). Newly shed seeds have a variable level of primary dormancy and, if dry, an almost stationary metabolic activity (Finch-Savage & Footitt, 2017). The level of primary dormancy is largely regulated by maternal growing conditions during seed production (Menegat et al., 2018; Swain et al., 2006). The process of dormancy release is initiated by environmental signals indicating favourable conditions for germination: temperatures above 0°C, a light stimulus and sufficiently high soil moisture content (Andersson & Espeby, 2009). Seedlings have the ability to emerge from a maximum soil depth of about 5 cm (Koch, 1968). Juvenile plants overwinter in two-leaf to five-tiller stage, with vigorous resumption of growth in spring. A small proportion of plants emerge in spring, but due to the shortened vegetative growth phase they have much lower seed production than plants emerging in autumn. Mature plants have a shallow root system and can reach a height of 80 cm (Naylor, 1972). Autumn-germinated plants start flowering around mid-May, with anthesis beginning at the apex of the spike and continuing towards the base of the spike within 7–14 days (Holm et al., 1997). Seed shedding starts at the end of June and can last until mid-August (Menegat et al., 2018). The dispersal unit of *A. myosuroides* is a spikelet, although the term 'seed' is used here for consistency with other publications.

2.2 | Matrix population model

A stage-classified periodic matrix model representing the life cycle of *A. myosuroides* was developed and calibrated. Its life cycle

is divided into five periods, each characterised by agronomic and/or environmental events that are expected to have an impact on the life cycle (Figure 1). The key state variables are: (a) the fraction of non-dormant seeds in the soil seed bank ($\psi_{i,j}$), (b) the actual germination and emergence rate driven by environmental parameters ($\varepsilon_{i,j}$), (c) seed predation rate ($\sigma_{i,j}$), (d) plant mortality rate, including natural plant death and death due to agronomic measures ($\delta_{i,j}$); and (e) plant reproduction (number of seeds produced per plant) ($\varphi_{i,j}$). The subscripts i and j denote source and destination life cycle nodes (Figure 1). In the following, if i and/or j are not further specified, the respective parameter is valid for more than one life stage transition. For example, $\delta_{i,10}$ (with $i = 6$ or 7) describes the mortality of plants emerging after crop harvest due to seedbed preparation and sowing of the following crop (node 6 or 7 to node 10, Figure 1). The key output of the model is the population growth rate λ.

Starting from a newly produced seed, the description of the life cycle of *A. myosuroides* in the model begins in late summer.

The seasonal matrix LS (Late Summer) describes the fate of seeds in the soil seed bank between weed seed shedding in summer and sowing of the following crop in early autumn. $ls_{6,8}$ and $ls_{6,10}$ describe the fate of old seeds from the previous year, while $ls_{7,9}$ and $ls_{7,10}$ refer to newly produced seeds (Equation 1).

$$LS = \begin{bmatrix} ls_{6,8} & 0 \\ 0 & ls_{7,9} \\ ls_{6,10} & ls_{7,10} \end{bmatrix}$$

(1)

$$= \begin{bmatrix} 1 - (\psi_{6,j} * \varepsilon_{i,10}) & 0 \\ 0 & (1 - \sigma_{i,j}) * (1 - (\psi_{7,j} * \varepsilon_{i,10})) \\ (\psi_{6,j} * \varepsilon_{i,10}) * (1 - \delta_{i,10}) & (1 - \sigma_{i,j}) * (\psi_{7,j} * \varepsilon_{i,10}) * (1 - \delta_{i,10}) \end{bmatrix}.$$

Here, $1 - (\psi_{6,j} * \varepsilon_{i,10})$ is the fraction of old seeds from the previous year that do not germinate and remain in the soil seed bank. Accordingly, $1 - (\psi_{7,j} * \varepsilon_{i,10})$ is the fraction of newly produced seeds that do not germinate and enter the soil seed bank. $1 - \sigma_{i,j}$ describes the fraction of seeds that are not removed by predation and $1 - \delta_{i,10}$ the fraction of seedlings that survive seedbed preparation and crop sowing. Seedbed preparation and crop sowing takes place at the end of this period (affecting $ls_{6,10}$ and $ls_{7,10}$). Both agronomic measures terminate already emerged *A. myosuroides* plants with probability $\delta_{i,10}$.

The seasonal matrix EA (Early Autumn) describes the soil seed bank and plant population from crop sowing until after the first weed management measure in autumn. The matrix elements $ea_{8,11}$ and $ea_{9,11}$ represent the fate of old and newly produced, but dormant,
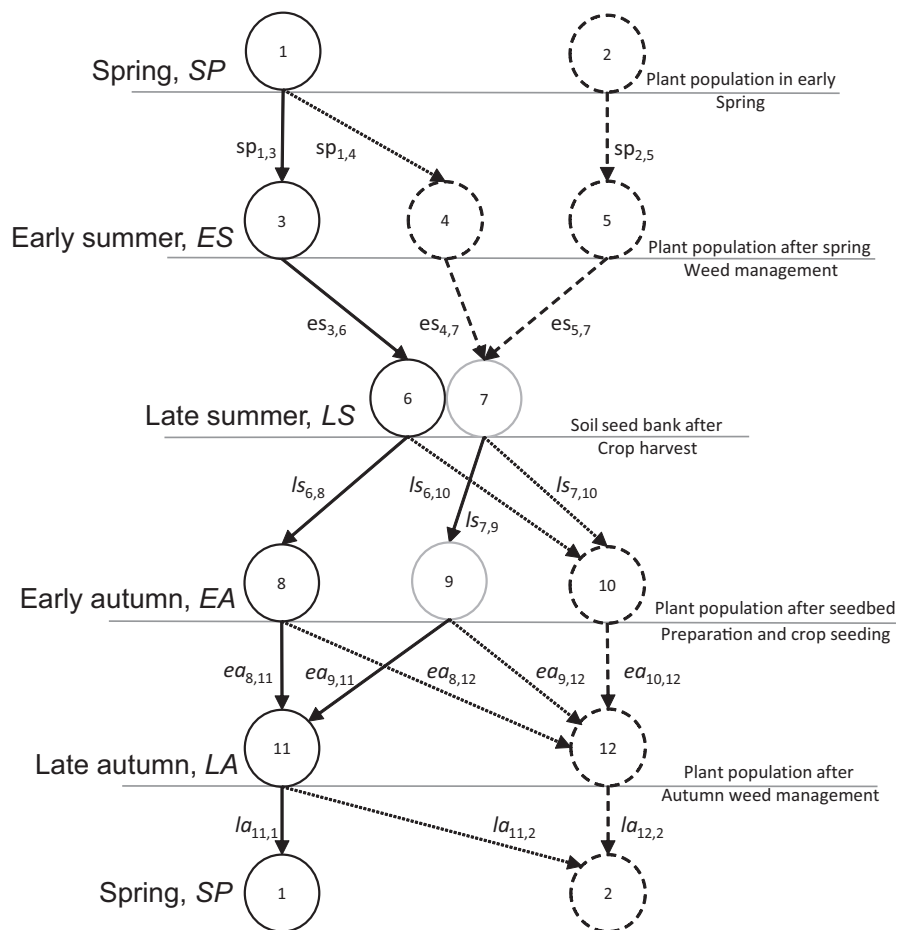

FIGURE 1 Life cycle diagram for *Alopecurus myosuroides* Huds. In a reduced tillage system without deep burial of seeds. Consecutively numbered nodes depict life stages considered in the model. Solid circles represent the soil seed bank of old seeds (black) and of newly produced seeds (grey). Solid arrows represent soil seed bank dynamics. Dotted arrows represent seed germination processes. Dashed circles denote life stages of plants emerging in autumn (first cohort) and plants emerging in spring (second cohort, node 4). Dashed arrows correspond to the transition probability between two life stages

seeds in the soil seed bank. The size of the plant population at this stage is determined by the number of non-dormant and emerged plants ($ea_{8,12}$ and $ea_{9,12}$) and by the plant mortality rate caused by autumn weed management ($\delta_{i,12}$).

$$
\mathbf{EA} = \begin{bmatrix} ea_{8,11} & ea_{9,11} & - \\ ea_{8,12} & ea_{9,12} & ea_{10,12} \end{bmatrix}
$$

$$
= \begin{bmatrix} 1-(\psi_{8,j}*\varepsilon_{i,12}) & 1-(\psi_{9,j}*\varepsilon_{i,12}) & 0 \\ (\psi_{8,j}*\varepsilon_{i,12})*(1-\delta_{i,12}) & (\psi_{9,j}*\varepsilon_{i,12})*(1-\delta_{i,12}) & 1-\delta_{i,12} \end{bmatrix},
$$

(2)

where $1-(\psi_{i,j}*\varepsilon_{i,j})$ is the fraction of old or new seeds that do not germinate and emerge. $1-\delta_{i,j}$ is the fraction of emerged plants that survive autumn weed management measures.

The seasonal matrix LA (Late Autumn) describes the fate of dormant seeds in the soil seed bank and the fate of the plant population after autumn weed management, from late autumn until the beginning of the vegetation period in early spring. Plants emerging from the soil seed bank ($la_{11,2}$) between late autumn and the end of the vegetation period bypass autumn weed control. After the end of the vegetation period, no newly emerged plants are expected. Plants that have survived autumn weed control ($la_{12,2}$) and plants emerging before the end of the vegetation period undergo overwintering losses ($\delta_{i,2}$). LA is thus

$$
\mathbf{LA} = \begin{bmatrix} la_{11,1} & 0 \\ la_{11,2} & la_{12,2} \end{bmatrix} = \begin{bmatrix} 1-(\psi_{11,j}*\varepsilon_{11,2}) & 0 \\ (\psi_{11,j}*\varepsilon_{11,2})*(1-\delta_{i,2}) & 1-\delta_{i,2} \end{bmatrix}.
$$

(3)

The seasonal matrix *SP* (SPring) describes the fate of seeds in the soil seed bank from early spring until after spring weed management. The number of seeds remaining in the soil seed bank ($s_{1,3}$) is determined by the proportion of dormant seeds. A proportion of seeds from the soil seed bank germinate after spring weed management and form a second cohort of plants ($s_{1,4}$) in addition to those germinated already in autumn that survived the spring weed management ($s_{2,5}$). Field observations suggest that germination and emergence after spring weed management is rather low due to secondary seed dormancy ($\psi_{1,j}$; Andersson & Espeby, 2009). It was assumed in the model that no further seed germination takes place after crop canopy closure in late spring, due to resulting low red (R):far-red (FR) light ratios (Batlla & Benech-Arnold, 2014; Batlla et al., 2000).

$$
\mathbf{SP} = \begin{bmatrix} sp_{1,3} & 0 \\ sp_{1,4} & 0 \\ 0 & sp_{2,5} \end{bmatrix} = \begin{bmatrix} (1-\sigma_{1,j})*(1-(\psi_{1,j}*\varepsilon_{1,4})) & 0 \\ (1-\sigma_{1,j})*(\psi_{1,j}*\varepsilon_{1,4}) & 0 \\ 0 & 1-\delta_{2,5} \end{bmatrix}.
$$

(4)

The seasonal matrix ES (Early Summer) describes the number of seeds produced per plant depending on the number of reproductive spikes per plant and the number of viable seeds produced per spike. The average number of seeds produced by plants from the

second cohort is lower than for plants from the first cohort ($\varphi_{5,7}$, $\varphi_{4,7}$), because of the considerably shorter growing period, which reduces competitiveness due to greater plant size differences compared with the crop and autumn-germinated plants of the first cohort (Naylor, 1972).

$$
\mathbf{ES} = \begin{bmatrix} es_{3,6} & 0 & 0 \\ 0 & es_{4,7} & es_{5,7} \end{bmatrix} = \begin{bmatrix} (1-\sigma_{3,6}) & 0 & 0 \\ 0 & \varphi_{4,7}*(1-\sigma_{3,6}) & \varphi_{5,7}*(1-\sigma_{3,6}) \end{bmatrix}.
$$

(5)

2.3 | Model assumptions

The model is density independent and assumes that weed control measures effectively reduce weed population densities (e.g. no herbicide resistance). Under such conditions, densities of *A. myosuroides* remain below densities where intraspecific competition becomes apparent (Chauvel et al., 2005). Interspecific competition with the crop is implicit, since all parameters are estimated from field data measured under standard winter wheat densities. While the model is general, it was used to simulate an intensive agroecosystem for winter wheat production typical for southern Sweden and other regions in Europe with temperate climate. We are assuming shallow soil tillage before crop sowing with a maximum burial depth of newly shed weed seeds of 5 cm, as this is representative for the common farmers practice in the study region. In case of inversion tillage systems, the model can be extended by a vertical seed distribution model as in, for example, Grundy et al. (1999). The model was parameterised based on empirical data, as described in Section 2.4.

2.4 | Empirical data collection and analysis

Plant survival between life stages ($\delta_{i,j}$) and fecundity ($\varphi_{i,j}$) were measured in two long-term field experiments in southern Sweden (56°24′N, 12°26′E) cropped with winter wheat. Measurements were made in experimental plots with and without weed management and repeated over three to six winter wheat cropping seasons. Five quadrats of 0.25 m² each were randomly positioned within the experimental plots. Plant survival was determined by visiting the quadrats once per life stage to count the number of *A. myosuroides* plants, divided into newly emerged plants and plants that were already present at previous life stages. The number of dead plants was calculated through comparison with plant numbers of the previous life stage. In the same quadrats, fecundity ($\varphi_{i,j}$) was measured by counting and harvesting *A. myosuroides* spikes from plants emerging in autumn and spring. Samples were cleaned and spikelets without caryopsis were removed. Number of spikes per plant and number of seeds per spike were counted.

Seed dormancy release was determined as in Menegat et al. (2018). Seeds were collected over the course of 5 years from 40 *A. myosuroides* populations in the study region. For modelling seed dormancy release and germination dynamics in dependency of

accumulated growing degree days, several assumptions have been made as described in the following. Post-harvest crop residue management incorporates newly produced seeds into shallow soil layers, while causing short light exposure of old seeds in the soil seed bank. Assuming that dormancy of old seeds ($\psi_{6,j}$) is low and that old seeds in the soil seed bank are hydrated, a short light exposure stimulates their germination (Andersson & Espeby, 2009). Incorporation of newly produced seeds into shallow soil layers allows their hydration, while minimising the risk of dehydration. Under these conditions, the release of primary dormancy of newly produced seeds, and hence germination and emergence dynamics, can be considered a function of accumulated growing degree days (GDDs) from seedbed preparation to crop seeding described by a three-parameter type 1 Weibull function (Bonner & Dell, 1976; Gonzalez-Andujar et al., 2016).

$$\psi_{i,j} = 1 - \exp(-\exp(b(\log(GDD) - \log(c)))), \qquad (6)$$

where c is the inflection point of the curve and b is the slope of the curve around the inflection point. The described Weibull function was fitted for each of the 40 *A. myosuroides* populations and parameters c and b were determined.

In summer 2019, post-dispersal seed predation rates ($\sigma_{i,j}$) were measured as in Davis et al. (2011). In each of the two field experiments, sampling was performed along 12 24-m long transects every 4 weeks from mid-May to August (i.e. post-harvest). For this, 30 seeds of *A. myosuroides* were attached to non-woven waterproof sanding pads ($115 \times 42 \times 8$ mm; Davis et al., 2003; Menalled et al., 2000), representing a density of 6,000 seeds/m^2—within the range previously documented at the field site (unpubl. data). The pads were sprayed with repository glue, and covered with potting soil, to create a surface similar to field conditions. Finally some more glue was added and seeds were added to the soil covered pads. Two seed pads were installed at each of two sampling points located at 8 m and 16 m from the field edge along the transect. One of the seed pads was covered by a metal net cage to exclude vertebrates (dimensions: $115 \times 180 \times 90$ mm; mesh size: 12 mm), whereas the other pad was exposed to both vertebrate and invertebrate seed predators. Each pad was placed flush to the soil surface. Seeds were counted every day and, after four consecutive days of exposure, the pads were collected and the number of remaining seeds recorded. Seed survival was quantified as the ratio of the number of remaining seeds to the number initially offered.

2.5 | Model parameterisation

To account for environmental stochasticity, all matrix elements were extracted randomly from their probability distribution for each modelled full weed life cycle. For rate variables, for example, plant mortality ($\delta_{i,j}$) or predation ($\sigma_{i,j}$), a beta distribution was assumed, extending over the interval 0 to 1. A log-normal distribution was used for plant reproduction parameters (Caswell, 2001). Parameter estimates and their probabilistic distributions were derived from the

empirical study described in Section 2.4 and, when not available, from literature data in similar cropping systems in the same region. Their distributions, values and sources are summarised in Table 1.

Harvest and crop residue management were set to August 15 and crop sowing was set to September 1. For each simulated year, the number of accumulated GDD between these two dates was chosen randomly among 45 years of observed accumulated GDD values for south-west Sweden (SMHI climate station number 53430, latitude 55°41′N 13°13′E). Parameters b and c for the dormancy release function were randomly selected from one of the 40 dormancy release curves described above. The end of the vegetation period was set to December 1. After the end of the vegetation period, no newly emerged plants are expected until the beginning of the following vegetation period in spring.

Parameter estimates for the proportion of non-dormant seeds in the soil seed bank are taken from Andersson and Espeby (2009). These estimates were derived from germination experiments with *A. myosuroides* seeds originating from winter wheat fields in the same study region as the long-term experiments. Therefore, it can be assumed that the same ecotype of the plant was studied. Parameter estimates for plant mortality due to autumn and spring weed management rely on Menegat and Nilsson (2019). In order to account for the interaction of agronomic practice and herbicide efficacy, we have used average efficacy values across the tested agronomic variables in Menegat and Nilsson (2019).

2.6 | Simulations and model output

Key output of our model is the population growth rate λ after a 1-year-long cycle. For ensuring a reduction of the future population density of a weed, the aim of any weed management decision is to achieve a $\lambda \leq 1$ within the respective cropping season. Here we focus on the implications of weed seed predation on the population growth rate λ as well as on the perturbation analysis of the presented life cycle of *A. myosuroides*, independent of the initial weed density.

To investigate the implications of seed predation for population growth rate of *A. myosuroides*, seed predation rate before ($\sigma_{3,6}$) or after ($\sigma_{i,j}$) crop harvest was varied stepwise from 0 to 1, with 0.01 increments. The full life cycle of the weed was simulated with 10^4 iterations, each time with all other parameters sampled according to their distribution (Table 1). The 10^4 model outputs were used to determine the stochastic growth rate, and its sensitivity and elasticity. The logarithm of the stochastic growth rate was calculated using Tuljapurkar's approximation (Caswell, 2001; Tuljapurkar, 1990). Sensitivities and elasticities of the stochastic growth rate were calculated according to Caswell (2001, section 14.4.1). The sensitivity of λ to changes in matrix entries ($a_{i,j}$) estimates the impact of an absolute change in the different vital rates on λ, whereas the elasticity of λ to changes in matrix entries estimates the effect of a proportional change in the different vital rates on λ (Caswell, 2001). All simulations and analyses were carried out with R (version 4.03 to 4.1, R Core Team, 2020).

TABLE 1 Parameter estimates used for the matrix modelling of *Alopecurus myosuroides* and their sources

Seasonal matrix	Period	Parameter		Min	Mean	Max	Sampling distribution	Shape parameter		Data source
					of observed data			α (log mean)	β (log SD)	
SP	Plant population after spring weed management	$\psi_{1,j}$	Proportion of non-dormant seeds in the soil seed bank	0.31	0.79	0.99	beta	4.92	1.33	Andersson and Espeby (2009)
		$\varepsilon_{1,4}$	Actual plant germination and emergence rate	0.24	0.68	0.96	beta	6.10	2.90	Menegat (2021)
		$\delta_{2,5}$	Plant mortality due to spring weed control measures	0.00	0.90	0.99	beta	1.82	0.26	Menegat and Nilsson (2019)
ES	Soil seed bank after crop harvest	$\sigma_{3,6}$	Seed predation rate invertebrates (caged seed cards)	0.00	0.16	0.99	beta	0.34	1.14	Daouti and Jonsson (2021)
		$\sigma_{3,6}$	Seed predation rate invertebrates + vertebrates (open seed cards)	0.00	0.89	0.99	beta	1.98	0.41	
		$\phi_{i,7}$	Number of ears per plant	0.20	3.90	8.50	Log-normal	(1.02)	(1.03)	Menegat (2021)
		$\phi_{4,7}$	Number of viable seeds per ear, first cohort	34	97	303	Log-normal	(4.48)	(0.42)	
		$\phi_{5,7}$	Number of viable seeds per ear, second cohort	25	57	136	Log-normal	(4.06)	(0.34)	
LS	Soil seed bank after seedbed preparation and crop seeding, early autumn	$\sigma_{i,j}$	Seed predation rate invertebrates (caged seed cards)	0.00	0.60	0.99	beta	1.47	1.03	Daouti and Jonsson (2021)
		$\sigma_{i,j}$	Seed predation rate invertebrates + vertebrates (open seed cards)	0.00	0.64	0.99	beta	1.30	0.76	
		$\psi_{6,j}$	Proportion of non-dormant seeds from previous year	0.72	0.91	0.99	beta	13.28	1.33	Andersson and Espeby (2009)
		$\psi_{7,j}$	Proportion of non-dormant seeds from present year	Weibull function						Menegat et al. (2018)
		$\varepsilon_{i,10}$	Germination and emergence rate	0.24	0.68	0.96	beta	6.10	2.90	Menegat (2021)
		$\delta_{i,10}$	Plant mortality due to seedbed preparation and crop seeding	0.39	0.82	0.99	beta	5.20	1.10	
EA	Plant population after autumn weed management	$\psi_{8,j}$	Proportion of non-dormant seeds (old seeds)	0.74	0.93	0.99	beta	21.44	1.50	Andersson and Espeby (2009)
		$\psi_{9,j}$	Proportion of non-dormant seeds (new seeds)	Weibull function						Menegat et al. (2018)
		$\varepsilon_{i,12}$	Germination and emergence rate	0.24	0.68	0.96	beta	6.10	2.90	Menegat (2021)
		$\delta_{i,12}$	Plant mortality rate due to autumn weed management	0.00	0.74	0.99	beta	0.67	0.25	Menegat and Nilsson (2019)
LA	Plant population in early spring	$\psi_{11,j}$	Proportion of non-dormant seeds in the soil seed bank	Weibull function						Menegat et al. (2018)
		$\varepsilon_{11,2}$	Germination and emergence rate	0.02	0.23	0.73	beta	1.60	5.20	Menegat (2021)
		$\delta_{i,2}$	Plant overwintering losses	0.00	0.14	0.48	beta	0.96	6.03	

3 | RESULTS

The population growth rate λ of *A. myosuroides* was most sensitive to changes in (a) the probability that newly shed seeds accumulate in the soil seed bank ($s_{7,9}^{LS}$, $s_{9,11}^{EA}$); and (b) the proportion of seeds that remain in the soil seed bank and germinate after the spring weed control measure ($s_{11,1}^{LA}$, $s_{1,4}^{SP}$; Table 2). The elasticity of λ followed the same pattern, with the highest elasticities of λ to changes in soil seed bank dynamics ($e_{7,9}^{LS}$, $e_{9,11}^{EA}$ and $e_{11,1}^{LA}$; Table 2). Furthermore, the population growth rate was more sensitive to the amount of viable seeds produced by spring-germinating plants than by autumn-germinating plants (compare $e_{4,7}^{es}$ and $e_{5,7}^{es}$).

In the empirical study, the average seed removal rate in July, that is, at peak seed shedding, was 89% for seed cards exposed to both invertebrate and vertebrate predators and 16% for cards accessible only to invertebrates (Figure 2a; Figure S1; Table 1, seasonal matrix ES). After crop harvest, the seed removal rate decreased to 62% for cards accessible to both vertebrates and invertebrates and increased to 61% for cards accessible only to invertebrates (Figure 2b; Figures S1; Table 1, seasonal matrix LS). Thus seed predation before crop harvest was dominated by vertebrates, whereas seed predation after crop harvest was almost entirely attributable to invertebrates. The empirical data were used to determine the corresponding beta distributions for weed seed predation by invertebrates (black lines in Figure 2) and vertebrates and invertebrates together (grey lines), before and after crop harvest (panels a and b in Figure 2). The derived beta distributions were used for the subsequent modelling step.

The stepwise variation of the seed predation rates in the model shows that a minimum seed predation rate of 78% at peak seed shedding (July) was needed to keep $\lambda \leq 1$ and hence to prevent weed population growth (Figure 3a). In contrast, even complete absence of seed predation in the post-harvest seed predation rate in August did not lead to $\lambda \geq 1$ (Figure 3b). The variation in λ, and in model

output uncertainty, increased with decreasing seed predation rate. Assuming as high seed predation rates as observed in our field experiments, the proportion of non-dormant seeds in the soil seed bank ($\psi_{7,j}$) before crop sowing in late summer (LS) and the actual germination and emergence rate ($\epsilon_{i,10}$) had marginal effects on the population growth rate, with λ not exceeding 0.4 (results not shown).

4 | DISCUSSION

A stage-classified stochastic matrix model was developed using the winter annual weed species *Alopecurus myosuroides* as a model system. The model was parameterised using empirical demographic data, including field measurements of seed losses via weed seed predation. Seed predation emerged as a key regulator of the population growth rate of *A. myosuroides*. The model sensitivity analysis showed that the population growth rate of *A. myosuroides* depends on continuous recruitment of new seedlings from the soil seed bank, and seed predation has a direct impact on the amount of seeds entering the soil seed bank ($es_{4,7}$, $es_{5,7}$, $ls_{7,9}$ cascading into $ea_{9,11}$).

We could show that, during crop growth in July at peak seed shedding of *A. myosuroides*, a minimum seed predation rate of 78% was needed to keep the weed population growth rate $\lambda \leq 1$ and hence to prevent *A. myosuroides* population growth (Figure 3a). In contrast, even complete absence of seed predation post-harvest appeared not to increase the weed population growth rate. The increase in variability of λ with decreasing seed predation rate points to the need for stochastic models to capture the variability in growth rate, when the impact of biotic and abiotic stressors on weed population dynamics are studied.

In our field experiments, predation by vertebrates and invertebrates reached 89% ± 2% (mean ± *SE*) in July, and thus well exceeded the 78% required to prevent population growth of *A. myosuroides*. It is possible that the observed high predation rates

TABLE 2 Summary of the sensitivity and elasticity matrices of population growth rate λ to changes in the respective matrix entries. The sensitivity of λ to changes in matrix entries estimates the impact of an absolute change in the different vital rates on λ, whereas elasticity of λ to changes in matrix entries estimates the effect of a proportional change in the different vital rates on λ (Caswell, 2001). The highest values (marked in bold) in each seasonal matrix denote the matrix entry to which λ has the highest sensitivity/elasticity

| Seasonal matrix	Life stage parameter		Sensitivity	Elasticity
SP	Plant population after spring weed management	$\begin{bmatrix} sp_{1,3} & - \\ sp_{1,4} & - \\ - & s_{2,5} \end{bmatrix}$	$\begin{bmatrix} 0.02 & - \\ \mathbf{3.24} & - \\ - & 1.54 \end{bmatrix}$	$\begin{bmatrix} 0.04 & 0 \\ \mathbf{0.86} & 0 \\ 0 & 0.09 \end{bmatrix}$
ES	Soil seed bank after crop harvest	$\begin{bmatrix} es_{3,6} & - & - \\ - & es_{4,7} & es_{5,7} \end{bmatrix}$	$\begin{bmatrix} 0.06 & - & - \\ - & 0.03 & <0.01 \end{bmatrix}$	$\begin{bmatrix} 0.04 & 0 & 0 \\ 0 & \mathbf{0.86} & 0.09 \end{bmatrix}$
LS	Soil seed bank after seedbed preparation and crop seeding	$\begin{bmatrix} ls_{6,8} & - \\ - & ls_{7,9} \\ ls_{6,10} & ls_{7,10} \end{bmatrix}$	$\begin{bmatrix} 0.02 & - \\ - & \mathbf{9.36} \\ 0.01 & 0.85 \end{bmatrix}$	$\begin{bmatrix} 0.04 & 0 \\ 0 & \mathbf{0.95} \\ <0.01 & 0.01 \end{bmatrix}$
EA	Plant population after autumn weed management	$\begin{bmatrix} ea_{8,11} & ea_{9,11} & - \\ ea_{8,12} & ea_{9,12} & ea_{10,12} \end{bmatrix}$	$\begin{bmatrix} 0.04 & \mathbf{4.46} & - \\ <0.01 & 0.66 & 0.09 \end{bmatrix}$	$\begin{bmatrix} 0.04 & \mathbf{0.90} & 0 \\ <0.01 & 0.04 & 0.01 \end{bmatrix}$
LA	Plant population in early spring	$\begin{bmatrix} la_{11,1} & - \\ la_{11,2} & la_{12,2} \end{bmatrix}$	$\begin{bmatrix} \mathbf{2.21} & - \\ 0.31 & 0.16 \end{bmatrix}$	$\begin{bmatrix} \mathbf{0.90} & 0 \\ 0.03 & 0.06 \end{bmatrix}$
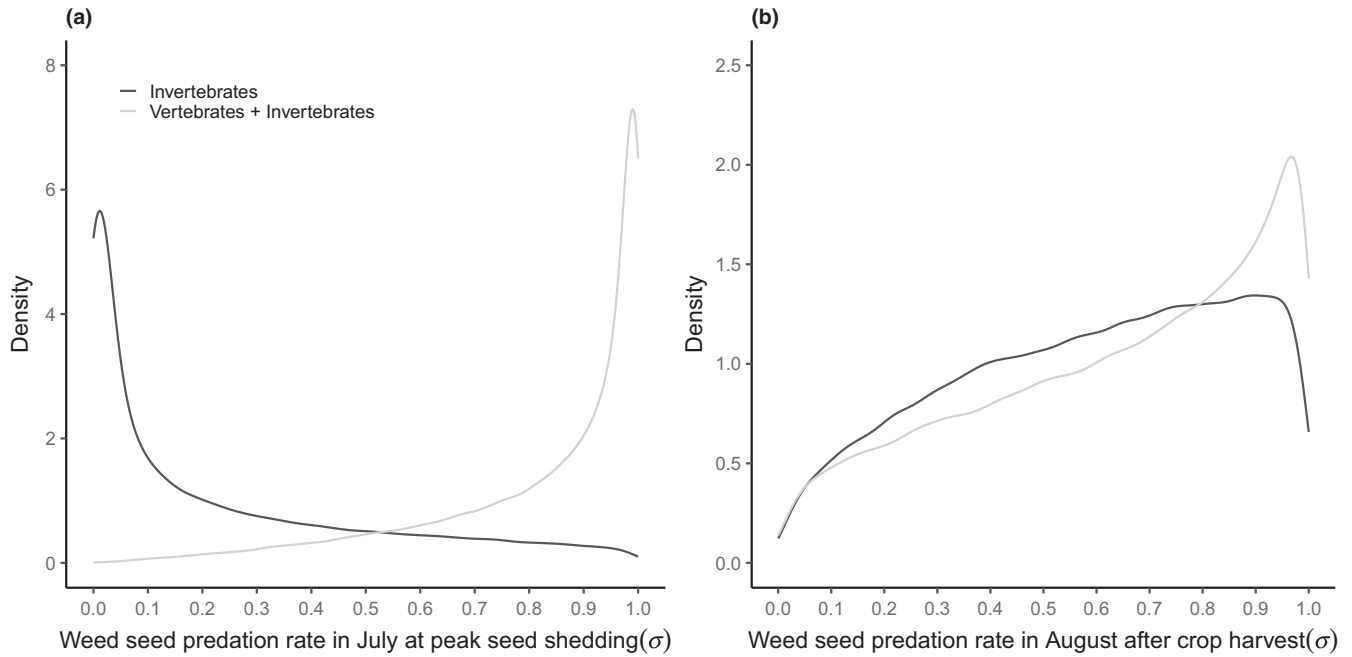
FIGURE 2 Beta distribution of weed seed predation rate σ for invertebrates (black lines) and invertebrates + vertebrates (grey lines) (a) in July, at peak seed shedding and (b) in August, after crop harvest. The distributions are fitted to the empirical data. The respective α and β shape parameters are presented in Table 1 and the predation rates for all sampling sessions in Figure S1
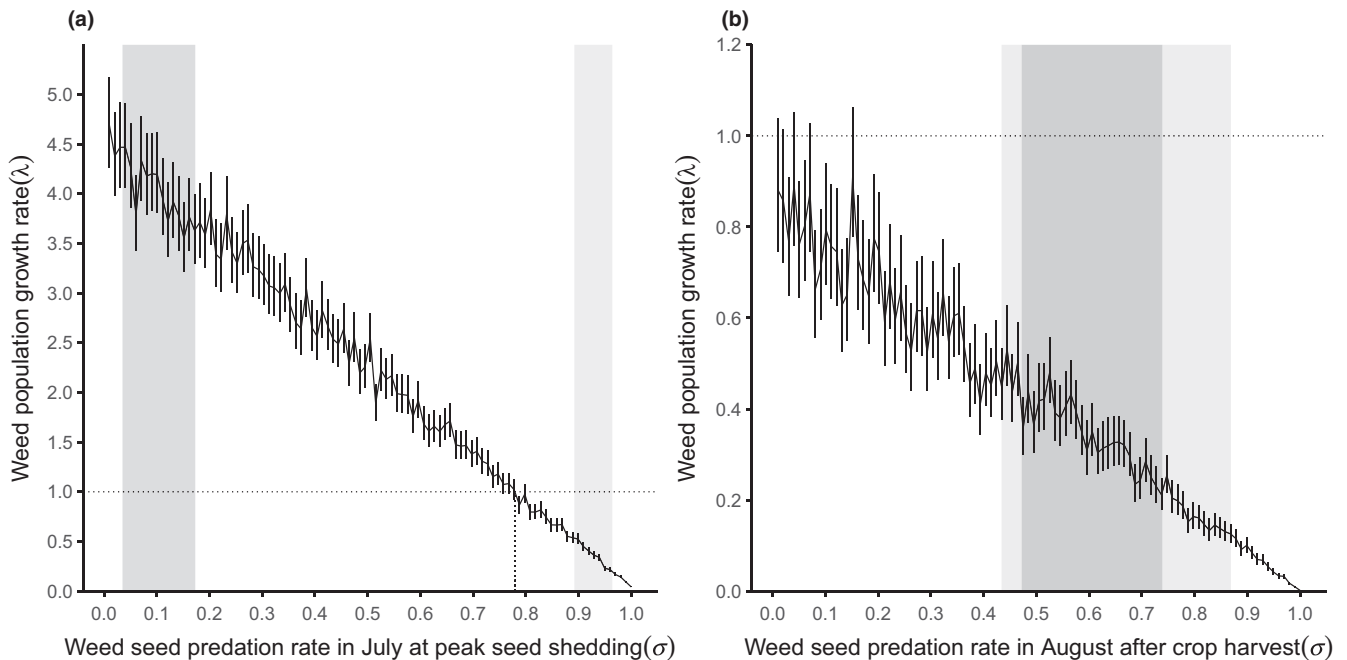

FIGURE 3 Stochastic population growth rate λ of *Alopecurus myosuroides* as a function of the weed seed predation rate (a) before crop harvest in July and (b) after crop harvest in August. For the modelling approach, predation rates ranged from 0 to 1, with 0.01 increments. For each predation rate, 10^4 iterations were considered with all other model parameters than the predation rate extracted from their respective distributions (see Table 1). Vertical bars extend over the 95% confidence interval. The horizontal dotted line corresponds to $\lambda = 1$. Dark-grey shaded areas are the first and third quartile of the empirical invertebrate predation rates measured in the field experiments (caged seed cards). Light-grey areas extend over the first and third quartile of the empirical invertebrate + vertebrates predation rates measured in the field experiments (open seed cards). In (a), the vertical dotted line denotes the minimum weed seed predation rate in order to keep the population growth rate ≤1

stem from the well-established *A. myosuroides* population at the field experiment sites, making *A. myosuroides* seeds a familiar prey item for both invertebrate and vertebrate seed predators (Greenwood, 1985; Partridge, 1981). The model results and empirical observations both indicated that seed predation can regulate weed population, assuming that other weed control measures are as effective as simulated and predator seed demand is relatively high.

The relative importance of invertebrate and vertebrate seed predators varied strongly over time. Vertebrates were most important in July, at peak seed shedding, whereas in August, after crop harvest, the relative importance of the two groups was reversed. We have two potential explanations for these patterns. First, before crop harvest, the crop canopy might minimise the predation risk for vertebrates species (Tew & Macdonald, 1993) whereas after crop harvest the absence of a crop canopy reduces their protection and therefore lowers their seed predation level (Tschumi et al., 2018). Second, predation differences might attributed to different foraging behaviours between groups in relation to seed availability. Westerman et al. (2008) observed that invertebrate seed predators respond slower to changes in seed availability compared to vertebrate species. Since the model showed that weed seed predation was much more important for weed regulation in July, it can be concluded that vertebrates contributed most to weed regulation, although the contribution of both groups was needed to reduce the growth rate below 1 (regulation threshold of 78%). Previous results regarding the contribution of each functional group during the crop year are inconclusive, with invertebrates being identified as most important during crop growth in some studies (Harrison et al., 2003; Mauchline et al., 2005) and with vertebrates being most important in others (Tschumi et al., 2018; Westerman et al., 2003). Thus, we do not yet know under which conditions vertebrates and invertebrates contribute most to weed seed predation. The present study demonstrated, in field studies and by modelling, that both groups are service providers for weed regulation. It also revealed that their relative importance is defined not only by high predation rates, but also by the overlap between high seed predation and peak seed availability. In situations where an overlap occurs, weed seed predation can have great potential in helping to reduce the abundance of weeds in agroecosystems or the spread of invasive alien species.

Although we have used a stochastic modelling approach and estimation of vital rates was based on long-term datasets, we have identified four sources for potential uncertainties in our model: (a) Estimation of vital rates are based on data covering up to 10 years, that is, a wide range of potential weather conditions. However, these estimates rely on experiments in close proximity why the range of, for example, soil types is limited. Using long-term experiments for model parametrisation is a robust approach but also makes the result uncertain considering other edaphic and climatic conditions. (b) The predictive accuracy of the model has not been tested, for example, by using a subset of the empirical data for validation purposes. In case the model is used in a predictive way, for example, for projecting future population sizes, a thorough validation of the model is recommendable (Morris & Doak, 2002). (c) A single seed density was used in empirical seed predation assessments, assuming that seed predators respond in a linear manner to increasing seed availabilities with increasing seed predation rates (Baraibar et al., 2012; Pannwitt et al., 2017). This was motivated by the typically episodic character of seed predation in relation to pulses in seed availability (Davis et al., 2011). In reality, however, weeds often differ in weed patch distribution and density (Cardina et al., 1997; Metcalfe et al., 2018) and this may influence predation rates in a nonlinear manner (Westerman et al., 2008). (d) The population model presented here is density independent. In contexts with high weed densities, for example, due to reduced weed control efficacy during spring control measures, density dependence needs to be considered in order to account for intraspecific competition.

5 | MANAGEMENT IMPLICATIONS

Currently available measures for direct weed control cannot achieve 100% control efficacy. This even applies when direct weed control measures are used in integrated weed management approaches, where chemical, mechanical, cultural and biological means of weed control are combined (Menegat & Nilsson, 2019). The rapid spread of herbicide-resistant weed populations and the rationalisation of today's cropping systems in terms of crop and crop management diversity further underlines this issue and calls for alternative solutions for weed management based on ecological principles (MacLaren et al., 2020). However, from a practitioner's perspective, the unpredictability of the abundance of seed predators and other biological means for weed control might hamper their acceptability and targeted use in weed management strategies.

Based on empirical data and model results, we showed how dependent today's intensified cropping systems are on ecosystem services like weed seed predation. Despite the high efficiency of the applied weed control measures, seed predation was essential for the reduction of *A. myosuroides* population growth. Hence, protection of vertebrate and invertebrate seed predators in agroecosystems is necessary for management of unwanted vegetation, in particular when aiming at reducing the dependence on chemical measures. Increased input farming and intensive soil cultivation such as inversion tillage can undermine populations of seed predators (Navntoft et al., 2006; Thorbek & Bilde, 2004; Witmer et al., 2007). As such, maintaining a sufficient population of weed seed predators can support crop yield stability and the ecological, social and economic sustainability of modern agricultural practices. To this end, it is necessary to extend existing environmental stewardship programmes for protection of vertebrates and invertebrates in agroecosystems, and to design joint initiatives by farmers, researchers and policymakers to gain a better understanding

of the effect of agricultural practices on the abundance of seed-predating organisms.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS
A.M., E.D., M.J. and G.V. conceived the ideas and designed methodology; A.M. and E.D. collected the data; A.M. analysed and visualised the data; A.M. developed and programmed the matrix model; A.M. and E.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data available via Zenodo https://doi.org/10.5281/zenodo.5569527 (Daouti & Jonsson, 2021) and https://doi.org/10.5281/zenodo.5554798 (Menegat, 2021).

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