



Are fungal epizootics a sign of successful biological control of cereal aphids?

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Abstract

Pandora neoaphidis is a common entomopathogenic fungus on *Sitobion avenae*, which is an important aphid pest on cereals in Europe. *Pandora neoaphidis* is known to cause epizootics (i.e. an unusually high prevalence of infected hosts) and the rapid collapse of aphid populations. We developed a weather-driven mechanistic model of the winter wheat-*S. avenae*-*P. neoaphidis* system to simulate the dynamics from spring to harvest. Aphid immigration was fixed at a rate that would lead to a pest outbreak, if not controlled by the fungus. We estimated the biocontrol efficacy by running pair-wise simulations, one with and one without the fungus. Uncertainty in model parameters and variation in weather was included, resulting in a range of simulation outcomes, and a global sensitivity analysis was performed. We identified two key understudied parameters that require more extensive experimental data collection to better assess the fungus biocontrol, namely the fungus transmission efficiency and the decay of cadaver, which defines the time window for possible disease transmission. The parameters with the largest influence on the improvement in yield were the weather, the lethal time of exposed aphids, the fungus transmission efficiency, and the humidity threshold for fungus development, while the fungus inoculum in the chosen range (between 10 and 70% of immigrant aphids carrying the fungus) was less influential. The model suggests that epizootics occurring early, around Zadoks growth stage (GS) 61, would lead to successful biocontrol, while later epizootics (GS 73) were a necessary but insufficient condition for success. These model predictions were based on the prevalence of cadavers only, not of exposed (i.e. infected but yet non-symptomatic) aphids, which in practice would be costly to monitor. The model suggests that practical Integrated Pest Management could thus benefit from including the cadavers prevalence in a monitoring program. We argue for further research to experimentally estimate these cadaver thresholds.

Keywords Epizootiology · Host–pathogen interactions · Simulation model · Sobol · Indices · Economic threshold

Key Message

- *Pandora neoaphidis* is a common entomopathogenic fungus of the English grain aphid *Sitobion avenae*.

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- We developed a mechanistic model of the *P. neoaphidis*-*S. avenae*-winter wheat system.
- We identified key parameters for biocontrol which require further experimental research.
- Epizootics occurring around flowering were a sign of successful biocontrol.
- Cadaver prevalence helped predicting successful biocontrol level in the model.

Introduction

Insect epizootics provide convincing displays of Integrated Pest Management (IPM) at work. Defined as the occurrence of an ‘unusually high incidence of a disease’ (Fuxa and Tanada 1987), they can be provoked by inundative or inoculative biocontrol, or erupt spontaneously from a

naturally occurring inoculum. The use and enhancement of pest natural enemies is an important principle in the European Union's Directive on Sustainable Use of Pesticides (2009/128/EC (SUD)). However, just as mushroom hunters may get frustrated by the unpredictability of their quarry, practitioners of IPM cannot always rely on the assistance of entomopathogenic fungi. Moreover, their efficacy as control agents can be elusive, as natural epizootics may occur late in the season. Natural enemies may provide ecosystem services as biocontrol agents in fields (Barzman et al. 2015; Giles et al. 2017). However, most tri-trophic studies focus on the pest-natural enemy population dynamics alone (e.g. Bahlai et al. 2013; Olfert et al. 2020) and leave out the resultant effect on crop yield, even though an estimation of yield loss is necessary to assess the success of biological control (e.g. Hallett et al. 2014).

Aphids such as the English grain aphid *Sitobion avenae* are important pests in cereals (Blackman and Eastop 2007). They directly damage cereals by sap-sucking and indirectly by (1) transmitting viruses (e.g. Yellow Dwarf Virus) and (2) obscuring photosynthesis by the combined effect of honeydew and fungi growing on it (Rabbinge et al. 1981; Wratten 1975). In spring, *S. avenae* migrates from its winter host (Poaceae) to cereals (e.g. Hansen 2006), in which it reproduces to form dense colonies. Winged (alate) and unwinged (apterous) morphs are produced depending on aphid density and plant quality (e.g. Carter et al. 1982). Before harvest, *S. avenae* emigrates from the crop to its winter host, where it either produces sexual morphs and lays overwintering eggs or, under milder winter conditions, continues to reproduce parthenogenetically (Dedryver et al. 2010). The population density varies greatly between years and outbreaks are commonly seen (Dedryver et al. 2010; Hansen 2000; Larsson 2005).

Sitobion avenae has been thoroughly modelled previously to understand the interactions between the aphid and the crop, as modulated by weather conditions (e.g. Carter et al. 1982; Duffy et al. 2017). Thus, models have been developed (1) to predict outbreaks (Carter et al. 1982; Carter and Rabbinge 1980; Duffy et al. 2017; Hansen 2006; Honek et al. 2017, 2018), (2) to estimate aphid damage on yield quantity and quality (Entwistle and Dixon 1987; Lee et al. 1981; Rossing 1991), and (3) to define economic thresholds for pesticide spraying (George and Gair 1979; Kieckhefer et al. 1995; Oakley and Walters 1994; Larsson 2005).

Aphids have many natural enemies, including predators, parasitoids, and entomopathogens. Yet most models focus on predators or parasitoids (Plantegenest et al. 2001; Hoover and Newman 2004; Kindlmann and Dixon 2010; Leblanc and Brodeur 2018; Olfert et al. 2020). The degree of

biocontrol has been estimated, for example, by simulating the system with and without natural enemies and then comparing the resulting pest densities (Maisonhaute et al. 2017). Entomopathogenic fungi in the subphylum Entomophthoromycotina have been mostly overlooked in pest insect-natural enemy models, even though they are known to have the capacity to create epizootics that eliminate the pest (Hajek and Delalibera 2010). One of the main entomopathogenic fungal species attacking *S. avenae* is *Pandora neoaphidis* (= *Erynia neoaphidis*) (Entomophthoromycotina) (Barta and Cagán 2006; Eilenberg et al. 2019).

Fungi in the Entomophthoromycotina infect their host horizontally by spores (conidia) landing on a susceptible host cuticle. Under favourable environmental conditions, conidia germinate and penetrate the insect cuticle. The fungus then multiplies inside its host at a temperature-dependent rate (e.g. Nielsen et al. 2001) and kills the host insect. The period between infection and host death is called the lethal time. During infection development, the host continues feeding on the crop and reproducing. The fungal-killed, mummified insect ('cadaver') will then produce conidiophores. Cadavers sporulate only under favourable conditions, such as high humidity, when they actively project new conidia into the environment (Kalkar 2005). When fungal transmission and infection processes are successful, the prevalence can greatly increase, and an epizootic may occur (Fuxa and Tanada 1987). Fungi in the Entomophthoromycotina may produce resting spores under unfavourable conditions e.g. winter or drought (Klingen et al. 2008; Duarte et al. 2013). These can enter the pathogen reservoir and provide inoculum in the following years (Hajek and Meyling 2018).

Pandora neoaphidis may enter an aphid colony from several sources and by several routes (Eilenberg et al. 2019). In wheat fields, aphids are estimated to fall to the ground and climb a straw again at a rate of 20–35% per day (Winder et al. 2013). This promotes the spread of aphids in the field at the risk of picking up pathogens from the soil, where the overwintering stages of *P. neoaphidis* (e.g. resting spores; Scorsetti et al. 2012) can remain infective for several years (Baverstock et al. 2008; Nielsen et al. 2003). Thus, the field itself can be an inoculum source; however, the importance of this source relative to external ones is unknown. Conidia from Entomophthoromycotina are spread by wind and may be transported over variable distances depending on aerodynamic and climatic conditions (Hajek et al. 1999; Hemmati et al. 2001b; Steinkraus et al. 1996). Indeed, Hemmati et al. (2001a) found a conidial discharge of *P. neoaphidis* at distance of 6–9 mm from the cadaver, which might be far enough for conidia to leave the plant boundary layer and enter the airstream. Ekesi et al. (2005) showed that conidia

of *P. neoaphidis* can disperse passively in the airstream from sporulating aphid cadavers and initiate infections in aphids located within 1 m of the source. The importance of infection by airborne conidia under field conditions is unknown. Conidia can also be vectored by other natural enemies as they attack both infected and susceptible colonies (e.g. Roy et al. 2001). However, the best described route for inoculum is by infected aphid immigrants that colonise the cereal fields. Thus, Chen and Feng (2004a) found that up to 68% of immigrating *S. avenae* were infected by *P. neoaphidis*. Immigrant, infected *S. avenae* are able to disperse and initiate colonies and to transmit the pathogen to their progeny (Chen and Feng 2004b).

Only two models of fungi in the Entomophthoromycotina on cereal aphids have been published. Schmitz et al. (1993) modelled *P. neoaphidis* infecting *S. avenae*, including intermediate stages of host infection to account for delays in the infection cycle. They showed the importance of offspring production by infected hosts, which greatly modifies the disease dynamics. Ardisson et al. (1997) continued this work with a model differentiating non-infectious (non-sporulating) and infectious (sporulating) cadavers. They simplified their model by considering environmental conditions to be constant and optimal and by ignoring winged morph production and aphid dispersal.

We developed a mechanistic, weather-driven model of the winter wheat-*S. avenae*-*P. neoaphidis* system to simulate the

dynamics during the summer season. The aphid immigration rate was set high enough to initiate an outbreak, if not curtailed by the pathogen. Fungus inoculum was entering the model only through infected aphids colonizing the field, thus representing the external fungus pressure through all inoculum pathways in reality. An extended discussion of the chosen model boundaries and simplifications can be found in Supplementary Information. We applied global uncertainty and sensitivity analysis (Saltelli et al. 2008) to find out (1) under which conditions *P. neoaphidis* would control the pest; and (2) if epizootics are a sign of successful biological control.

Material and methods

Modelling paradigm

The model follows an object-oriented paradigm (Reynolds and Acock 1997) and was constructed using Universal Simulator software (Holst 2013, 2022). All source code is freely available, together with installation files that allow the user to replicate all simulations presented in this paper (see Supplementary Information).

The model allows parameter uncertainty, which accounts for natural variation in biology and environment, statistical uncertainty in parameter estimates and mechanisms not

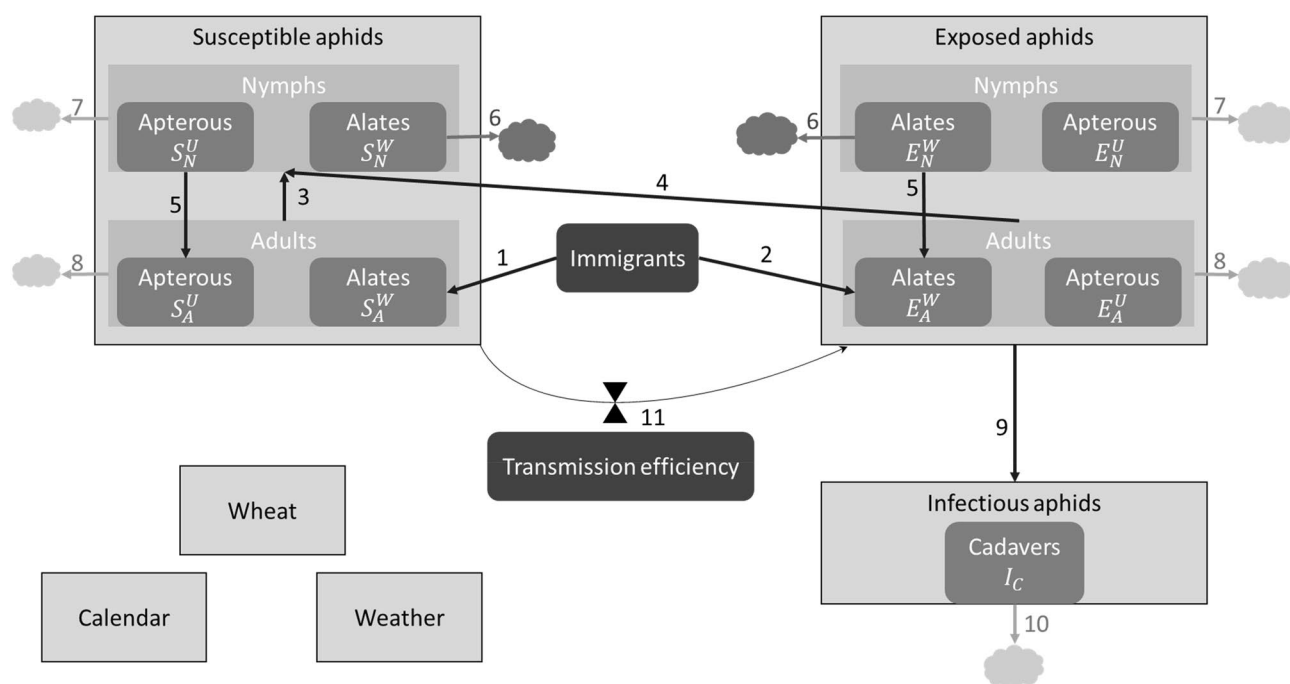


Fig. 1 Major objects of the model and their interactions. Sub-populations of susceptible (S_s^m) and exposed (E_s^m) aphids were further divided by morph (m), unwinged (U) or winged (W), and stage (s),

nymph (N) or adult (A). Cadavers were merged into one sub-population (I_C). Numbers refer to processes explained in text

included in the model. In general, parameter uncertainty was described by the distribution $F_\alpha(x_{\min}, x_{\max})$ to designate a normal distribution centred at $\mu = (x_{\min} + x_{\max})/2$ and truncated at $[x_{\min}; x_{\max}]$ to cover only the central $(1 - \alpha)$ part of the normal distribution. F_α will converge toward a uniform distribution as $\alpha \rightarrow 1$. We chose $\alpha = 0.05$ to achieve a central tendency in F_α that matches scientists' intuition about uncertainty. Alternatively, the uniform distribution $U(x_{\min}, x_{\max})$ was used to choose a random integer value in the interval $[x_{\min}; x_{\max}]$.

Model structure

The model building blocks are arranged into a hierarchy of boxes, the upper-most ones presented in Fig. 1. Lower-level boxes encapsulate functionalities, such as fecundity, mortality, morph determination, infection rate, etc. A *Calendar* object keeps track of time with a 1-day time step, while *Weather* supplies daily weather records of average temperature and maximum relative humidity, and *Wheat* simulates crop development on the Zadoks scale (Zadoks et al. 1974). Aphids were compartmentalised into sub-populations according to the SEI nomenclature of epidemiology (Keeling and Rohani 2008), designating Susceptible (uninfected), Exposed (infected) and Infectious (sporulating cadaver) pathological phases.

Daily fluxes (arrows in Fig. 1) between model objects are determined by calendar, ambient temperature and humidity, wheat growth stage and density-dependence. Aphid immigrants provide susceptible (1) and exposed (2) winged adults. Susceptible adults reproduce (3) and give rise to aphid nymphs both with (alitriform) and without (apteriform) wing-buds. Adult aphids that have been exposed to the fungi reproduce as well, but with a lower reproduction capacity due to the fungal infection (4); there is no vertical transmission of fungus to nymphs. Apteriform nymphs develop into unwinged adults for both susceptible and exposed aphids (5) whereas alitriform nymphs leave the system at adulthood (6). Nymphs may suffer from mortality (7) while adults die of old age (8). Exposed aphids may turn into cadavers (9), which decay at some rate (10). Susceptible aphids may become exposed, depending on the transmission rate (11). They are removed from the susceptible sub-populations to the corresponding life stage and morph among the exposed sub-populations.

Aphid development and reproduction

The four sub-populations holding susceptible aphids (apteriform and alitriform nymphs: S_N^U and S_N^W ; and unwinged and winged adults: S_A^U and S_A^W) and the cadaver sub-population (I_C) (Fig. 1) were implemented as distributed delays

(Manetsch 1976), which, given an average longevity and a shape parameter (k), produce maturation times following an Erlang distribution. The distributed delay has been used extensively to model physiological development (Gutierrez 1996); it is a deterministic procedure that produces a fixed distribution of maturation times. Maturation time varies among individuals due to differences in genetics and experienced microclimate. Earlier modellers have set k to 20 or 30 (Carruthers et al. 1986; Graf et al. 1990; Gutierrez et al. 1993). For all distributed delays, we chose one common $k = U(15, 30)$, except for aphid fecundity.

The attrition parameter was added to the distributed delay model by Vansickle (1977). We set attrition < 1 to account for mortality pertinent to the whole aphid maturation process, such as juvenile development. With attrition > 1 we modelled fecundity, in which case 'attrition' is a misnomer as it stands for net reproduction (R_0). For fecundity we set $k = 1$ to obtain a realistic age-dependent fecundity (commonly denoted m_x in life tables).

The four aphid sub-populations (E_j^i ; Fig. 1) holding exposed aphids were implemented as two-dimensional distributed delays, a technique for modelling insect-pathogenic fungi pioneered by Carruthers et al. (1986), which includes two orthogonal development processes each following a distributed delay (Larkin et al. 2000).

Model inputs

The model was driven by daily average air temperature (T , °C) and maximum relative humidity (H_{\max} , %) obtained from Agrometeorology Norway (2018). We selected four locations in the cereal production area of south-eastern Norway, namely Rygge (59° 22' N 10° 45' E), Ramnes (59° 25' N 10° 16' E), Aarnes (60° 07' N 11° 28' E) and Ilseng (60° 46' N 11° 13' E). We collated 10 years of weather data for each location (2004–2006, 2012–2018). Missing data were interpolated, if there were less than 5 consecutive days without measurements, or else replaced by corresponding data from the closest weather station. The complete set of weather data enabled us to run model simulations for 40 different scenarios defined by location and year, picked randomly by file number $U(1, 40)$.

Winter wheat sub-model

We developed a sub-model to predict phenological growth stages (G , Zadoks scale) for winter wheat based on Norwegian data. The model assumes that the crop starts developing in spring after five consecutive days with average air

temperature above 5 °C (Korsæth and Rafoss 2009). Crop development then follows a sigmoid log-logistic function,

$$G = G_0 + \frac{G_{\max} - G_0}{1 + \exp \{g(\ln(\tau) - \ln(\tau_{50}))\}} \quad (1)$$

where G_0 is the crop growth stage reached at the end of winter; $G_{\max} = 99$; τ is degree-days (°D) above a base temperature of 0 °C; τ_{50} is the inflection point of the sigmoid curve (°D) at $(G_{\max} - G_0)/2$; and g is the crop development rate. We fitted this equation to three years' data (different wheat varieties and locations) by non-linear regression (details not shown) and estimated $g = 2.8 \text{ °D}^{-1}$, $\tau_{50} = F_{\alpha}(750, 850) \text{ °D}$ and $G_0 = F_{\alpha}(10, 30)$.

Aphid sub-model

The model simulates the dynamics on an average tiller in the field. Thus, aphid density is in individuals per tiller.

Development

Sitobion avenae development was described by a standard degree-day model with a lower temperature threshold for development (T_{\min} , °C), only extended with a downward trend between optimum (T_{opt} , °C) and maximum (T_{\max} , °C) temperatures,

$$\Delta\tau = \begin{cases} 0 & T < T_{\min} \\ (T - T_{\min})\Delta t & T_{\min} \leq T < T_{\text{opt}} \\ (T_{\text{opt}} - T_{\min})(T_{\max} - T)/(T_{\max} - T_{\text{opt}})\Delta t & T_{\text{opt}} \leq T < T_{\max} \\ 0 & T \geq T_{\max} \end{cases} \quad (2)$$

where $\Delta\tau$ (°D) is the daily ageing increment and $\Delta t = 1 \text{ d}$ is the integration time step. We assumed that under Scandinavian conditions, *S. avenae* does not develop when $T_{\min} < 3 \text{ °C}$ and $T_{\max} > 30 \text{ °C}$ (Dean 1974; Hansen 2006). The estimated optimal temperature ranges from 16 to 20 °C (Dean 1974; Schmitz et al. 1993). We chose $T_{\text{opt}} = 18 \text{ °C}$.

Based on data from Dean (1974), we estimated that apteriform nymphs required $L_N^U = 172 \text{ °D}$ to reach adulthood, while alate nymphs required $L_N^W = 195 \text{ °D}$. Unwinged adults live on average for 20 days when reared at 10–25 °C (Duffy et al. 2017). Based on the optimum temperature, we get a longevity of $L_A^U = 20 \text{ d} \cdot (18 - 3 \text{ °C}) = 300 \text{ °D}$ for unwinged adults.

Aphid immigration

Sitobion avenae immigration is a major factor driving aphid population dynamics during a large part of the season (Jonsson and Sigvald 2016). In Norway, *S. avenae* has not been found in winter wheat before stem elongation at growth stage

GS 31 (unpublished data). Rabbinge et al. (1979) found that immigration stops at the end of flowering (GS 69). Consequently, we modelled *S. avenae* immigration as a constant rate of influx (ΔA_{im} , tiller⁻¹ d⁻¹) between GS 31 and GS 69.

The rate of *S. avenae* immigration into cereal fields varies between years and locations. In France, Vialatte et al. (2007) measured it with a vacuum sampler and found a maximum rate of 15 aphids m⁻² d⁻¹; the typical tiller density in Norway is 750 m⁻² (Einar Strand, pers. comm.). In our analysis, we aimed for an immigration pressure that would cause an outbreak, if not controlled by the fungus. Hence, we set $\Delta A_{\text{im}} = 15/750 = 0.02 \text{ tiller}^{-1} \text{ d}^{-1}$. For simplicity, we considered immigrants as new-born and allocated them the same longevity as unwinged adults $L_A^W = L_A^U = 300 \text{ °D}$. Since the model simulates an average tiller, immigration includes within-field dispersion.

Aphid reproduction, survival, and morph determination

Sitobion avenae reproduction, survival and morph determination have all been modelled extensively over the years. Our model combines the equations developed by Duffy et al. (2017), Plantegenest et al. (2001) and Carter et al. (1982) with parameters estimated on data from Dean (1974) and Schmitz et al. (1993). See Supplementary Information.

Fungus

The fungal inoculum

In our model, fungal inoculum arrives via infected immigrants only, assuming that a fixed proportion of all immigrants is infected (δ). We chose a wide span for this parameter, $\delta = F_{\alpha}(0.1, 0.7)$, which functionally covers all inoculum pathways. Thus δ in the model is a surrogate parameter that represents the total inoculum pressure, not just the inoculum pathway via exposed immigrants. This choice of a single, uncertain parameter reflects our current lack of detailed knowledge about the sources of fungal inoculum in this system (see extended discussion in Supplementary Information).

Aphids exposed to *P. neoaphidis*

Aphids exposed to *P. neoaphidis* were taken from the four sub-populations of susceptible aphids (S_j^i) and transferred to the corresponding four sub-populations of exposed aphids (E_j^i) (Fig. 1), each represented by a two-dimensional distributed delay. In one dimension, development runs in day-degrees defined for the aphid (Eq. 2) since infected aphids

have the same longevity as susceptible aphids. The other dimension describes infection development. It runs on a day-degree scale of the fungus with its own set of cardinal temperatures (T_{\min} , T_{\max} and T_{opt}) (Eq. 2). The fungus does not germinate, grow or sporulate for $T_{\min} < 2$ °C or $T_{\max} > 30$ °C (Nielsen et al. 2001). *Pandora neoaphidis* is a mesophilic species with an optimal temperature (T_{opt}) for growth, lethal time and host mortality between 15 and 25 °C (Barta and Cagan 2006; Morgan et al. 1995; Nielsen et al. 2001; Schmitz et al. 1993; Stacey et al. 2003). For Entomophthoraceae species in general, T_{opt} depends on the climatic origin of the isolate. Klingen and Nilsen (2009) found that for a Norwegian strain of *Neozygites floridana*, sporulation was higher at 13 and 18 °C compared to 23 °C. On this basis, we set $T_{\text{opt}} = 18$ °C for *P. neoaphidis*.

The time *P. neoaphidis* needs to kill its host, i.e. the lethal time (L_{lethal} , °D), is highly variable. The median lethal time ranges from 73 to 115 °D (calculated from Nielsen et al. 2001; Saussure et al. 2019; Schmitz et al. 1993). The lethal time differs between *S. avenae* stages (Schmitz et al. 1993) but is similar for unwinged and winged morphs (Dromph et al. 2002). We chose a range of lethal times to reflect this variability $L_{\text{lethal}} = F_{\alpha}(50, 115)$ °D and applied this across all host life stages and morphs. For the exposed immigrants (Fig. 1), we assumed that their infection was quite recent. Thus, they survived the entire lethal time on the wheat. Exposed nymphs may turn into either cadavers or exposed adults. Schmitz et al. (1993) showed that *S. avenae* nymphs infected with *P. neoaphidis* do not reproduce if they reach adulthood. This detail was included in the model.

Reproduction capacity of exposed aphids

Infected *S. avenae* adults can reproduce, but most likely at a reduced rate. Infection with *P. neoaphidis* has been shown to reduce fecundity from 0 to 35% depending on fungal isolate and aphid species (Baverstock et al. 2006; Parker et al. 2017; Saussure et al. 2019). We included this immunity cost ($\nu \in [0; 1]$), defined by Parker et al. (2017) as a reduction in lifetime fecundity of infected compared to susceptible adults. We chose $\nu = F_{\alpha}(0, 0.4)$.

The cadaver unit

When exposed aphids succumb to the infection, they turn into cadavers. Cadavers of winged *S. avenae* produce fewer conidia than those of the unwinged morph (Hemmati et al. 2001a). We expect nymphs to produce fewer conidia than adults due to the size difference. Hence, we enumerated the cadaver sub-population in standardised ‘cadaver units’, counting cadavers as 1 (unwinged adults), 0.66 (winged adults) and 0.5 (nymphs). Cadavers were kept in the one-dimensional distributed delay I_c (Fig. 1).

Sporulating cadavers

Cadavers decay at a rate that depends on temperature and moisture. We expressed temperature-dependency on the same day-degree scale as for fungus development in exposed aphids (2.7.2), i.e. using Eq. (3) with $(T_{\min}, T_{\text{opt}}, T_{\max}) = (2, 18, 30)$ °C. Yet, we do not know the ‘longevity’ of aphid cadavers (L_c). Grasshopper cadavers infected with *Entomophaga grylli* have a median longevity in the field of 2.8 days while 5% last 12.3 days (Sawyer et al. 1997). We chose a longevity of 3–7 days at 18 °C giving $L_c = F_{\alpha}(48, 112)$ °D.

Grasshopper cadavers can go through cycles of dehydration and rehydration according to moisture conditions and sporulate whenever hydrated (Sawyer et al. 1997). This is also the case for *P. neoaphidis*-killed aphids (pers. obs.). At 20 °C, *S. avenae* cadavers may sporulate for a total period of 2 days (Ardisson et al. 1997) and *Acyrtosiphon pisum* cadavers for 3 days (Bonner et al. 2003). When a cadaver has exhausted its capacity for spore production, it disappears. This means that under high moisture conditions it will last a shorter time than expressed by L_c , which only depends on temperature. We accommodated this effect by accelerating the development time step ($\Delta\tau$, Eq. 3) by a factor (h) under high moisture. We chose $h = F_{\alpha}(1, 3)$.

To trigger sporulation (and germination, see 2.7.6), Entomophthoraceae need a high-moisture environment, corresponding to a relative humidity $H > 80\%$ or even $H = 100\%$, depending on the species (e.g. Sawyer et al. 1997). The model works with a daily time step but H can vary dramatically during a day, and *P. neoaphidis* needs only 3 h at 18 °C with $H = 95\%$ to sporulate (Ardisson et al. 1997). Therefore, we chose to compare the daily maximum relative humidity (H_{\max} , %) against a threshold value (H_{\max}^* , %). For any 24 h day with $H_{\max} > H_{\max}^*$, sporulation was assumed to be ongoing and the acceleration factor h applied on $\Delta\tau$. To reflect uncertainty in the relation between ambient relative humidity and the humidity experienced by the fungus we set $H_{\max}^* = F_{\alpha}(80, 99)\%$.

Transmission efficiency

Conidial transmission from cadavers to susceptible aphids within and between colonies drives the spread of the disease in the host population (Sawyer et al. 1994; Steinkraus et al. 1993; Steinkraus 2006). It depends on a complex of parameters (McCallum et al. 2017). Like Ardisson et al. (1997) we describe the whole process of disease transmission by one parameter: the transmission efficiency (ϵ , d⁻¹). Under laboratory conditions with one cadaver per 10 *S. avenae*, they estimated $\epsilon = 0.0072 \text{ h}^{-1} = 0.17 \text{ d}^{-1}$. The aphids used were a mix of life stages kept at a high density (20 per tiller).

We used the classical functional response model of Nicholson and Bailey (1935) to model disease transmission,

$$\Delta E_i^j = \Delta S_i^j (1 - \exp(-\epsilon I_c \Delta t)) \quad (3)$$

It computes the density of newly exposed hosts (ΔE_i^j) from the transmission efficiency and the densities of cadavers (I_c) and susceptible aphids (S_i^j) over a time period (Δt) for stage i and morph j (Fig. 1). This equation, traditionally used to describe the attack rate of parasitoids (Nicholson and Bailey 1935), sets a necessary limit to the number of newly infected hosts ($\Delta E_i^j \leq \Delta S_i^j$). Sporulation and spore germination happen only under high humidity. Thus for $H_{\max} \leq H_{\max}^*$, we set $\epsilon = 0 \text{ d}^{-1}$, otherwise $\epsilon = F_\alpha(0.1, 4.0) \text{ d}^{-1}$. This interval includes the estimate of Ardisson et al. (1997) and was widened to account for the many biological processes distilled into just one parameter (McCallum et al. 2017). Trials runs with the model (see Supplementary Information) revealed that values up to $\epsilon = 4.0 \text{ d}^{-1}$ were needed to match the fungal dynamics observed in the field.

Model outcomes

The model gives daily values for the density of all aphid stages and morphs, susceptible or exposed, cadavers and yield loss. To assess the dynamic impact of the fungus, every simulation constituted two scenarios run in tandem—identical except for the proportion of exposed immigrant aphids (δ). In one scenario, it was set to $\delta = F_\alpha(0.1, 0.7)$ in the other $\delta = 0$, *i.e.* one scenario was with and one without fungus inoculum (Fig. 2a). Simulations ran from 1 April to 31 August to ensure that the whole growing season was included.

To detect the occurrence of epizootics, we used two alternative measures: peak prevalence of exposed aphids (P_E ; %) and peak prevalence of cadavers (P_C ; %), both calculated as the maximum percentage occurring before dough development (GS 80), when the system dynamics change abruptly as the wheat becomes an unsuitable host and causes an exodus of aphids (Fig. 2b). P_E was calculated as the percentage of live aphids and P_C , as the percentage of live aphids + cadavers.

As a measure of the degree of biological control success, the percentage yield loss caused by the aphids was calculated according to Entwistle and Dixon (1987). For each simulation, the biocontrol exerted by the fungus was computed as the difference in final yield losses (ΔY ; %-points), with and without fungus inoculum (all parameters being equal). We did not consider the “yield improvement” offered by the fungus ΔY as an accurate estimate of the actual value of biocontrol but used it to divide the model outcomes into two groups: the first one was called ‘more successful biocontrol’

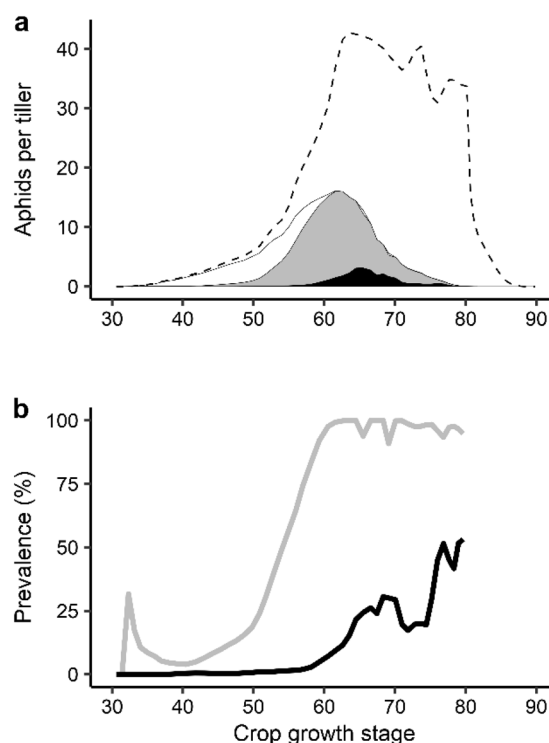


Fig. 2 A typical example of model population dynamics. **a** Aphid density without fungus present (dashed line), and aphid density with fungus present (solid line) distributed among susceptible (white), exposed (grey) and cadavers (black). **b** Prevalence of exposed aphids (grey) and cadavers (black); only considered until crop growth stage 80. The improvement in yield by the fungus was $\Delta Y = 4.8\%$ -points in this example

constituting the upper 10% percentile of all ΔY values, the remaining 90% regarded as ‘less successful biocontrol’.

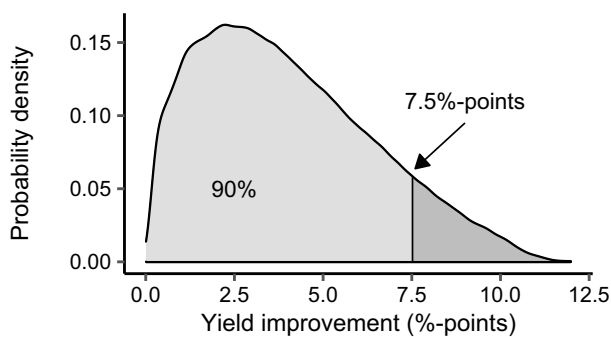
Oakley and Walters (1994) recognised three different timings of insecticide sprays against *S. avenae* in England: at early booting (GS 41–45), early flowering (GS 61) and early milk development (GS 73). This concurs with the practice in Norway, where spraying is rarely later than the milky stage (Andersen 2003). Accordingly, we noted the prevalence of cadavers at GS 43, 61 and 73 and related that to the ultimate success in fungus biocontrol, to find out if successful biocontrol could be anticipated at the time of chemical aphid control.

Uncertainty and sensitivity analysis

During model development we identified 11 parameters likely to contribute to uncertainty in model outcomes (Table 1). The model was run repeatedly with values sampled from the 11-dimensional parameter space by way of Sobol’ quasi-random numbers (Maurer 2021; Sobol’ 1976), which secure an optimal dispersion of sample points in n

Table 1 The 11 model parameters considered uncertain following either a uniform (U) or a normal distribution truncated to the central α proportion (F_α , $\alpha = 0.95$). Distribution parameters specify the min–max limits

Parameter	Section	Distribution	References
Shape of distributed delay for development (k)	2.3	$U(15, 30)$	Carruthers et al. (1986) Graf et al. (1990) Gutierrez et al. (1993)
Weather file number	2.4	$U(1, 40)$	Agrometeorology Norway (2018)
Initial plant growth stage (G_0)	2.5	$F_\alpha(10, 30)$	Unpubl. data
Time to 50% plant development (τ_{50})	2.5	$F_\alpha(750, 850)^\circ\text{D}$	Unpubl. data
Proportion of exposed immigrants (δ)	2.7.1	$F_\alpha(0.1, 0.7)$	Chen and Feng (2004a)
Lethal time (L_{lethal})	2.7.2	$F_\alpha(50, 115)^\circ\text{D}$	Nielsen et al. (2001) Saussure et al. (2019) Schmitz et al. (1993)
Immunity cost (v)	2.7.3	$F_\alpha(0, 0.4)$	Baverstock et al. (2006) Parker et al. (2017) Saussure et al. (2019)
Humidity threshold for sporulation (H_{max}^*)	2.7.5	$F_\alpha(80, 99)\%$	Sawyer et al. (1997)
Cadaver duration (L_c)	2.7.5	$F_\alpha(48, 112)^\circ\text{D}$	Sawyer et al. (1997)
High humidity time acceleration of? (h)	2.7.5	$F_\alpha(1, 3)$	Ardisson et al. (1993) Bonner et al. (2003) Brobyn et al. (1985)
Transmission efficiency (ϵ)	2.7.6	$F_\alpha(0.1, 4.0)d^{-1}$	Ardisson et al. (1997)

**Fig. 3** Probability density distribution of yield improvement (ΔY) caused by the fungus, showing the 90% (light grey) and 10% (dark grey) fractile of all simulations

dimensions (Saltelli et al. 2010). The uncertainty in model outcomes was explored visually and statistically.

In addition to the uncertainty analysis (UA), we carried out a sensitivity analysis (SA), which aims at identifying the parameters most influential on the uncertainty in model outcomes (Saltelli et al. 2008). Note that both UA and SA were global, *i.e.* parameters were allowed to vary simultaneously—not just one at a time, which is incorrect though quite prevalent in the literature (Saltelli et al. 2019).

Two Sobol' sensitivity indices (Saltelli et al. 2008; Sobol' 1990,) were computed for each parameter and for each model outcome (2.9): the S_i index indicates how much the

variance of a model outcome would be reduced if parameter X_i were fixed anywhere inside its distribution. S_i can be considered the main effect of X_i , while the total index S_{T_i} includes both the X_i main effect and all its effects in interaction with the other parameters ($S_i \leq S_{T_i}$). The indices are scaled such that $\sum_i S_i \leq 1$. If the effects of all X_i are purely additive, then $\sum_i S_{T_i} = 1$. If $S_{T_i} = 0$ then X_i is non-influential (Saltelli et al. 2008).

The number of simulations needed to compute Sobol' indices is $N(p + 2)$ where N is the so-called sample size and p is the number of parameters. Sobol' quasi-random number sequences are of length 2^n ; hence we are bound by $N = 2^n$. We chose $n = 17$ resulting in 1,703,936 simulations (used for both UA and SA), which took 43 h on a standard computer. The sample size was determined by increasing n until the resulting S_i and S_{T_i} values stabilised (see Supplementary Information). Confidence limits on S_i and S_{T_i} were estimated by the 2.5% and 97.5% fractiles of 10,000 bootstrap samples (Saltelli et al. 2008).

For parameters identified as important by the SA, their individual (*i.e.* first-order) effects were visualised by a general additive regression model (*gam* function of R *mgcv* package) (Wood 2021) showing their impact on the model outcomes.

Finally, model predictions were compared to observed aphid population dynamics (see Supplementary Information).

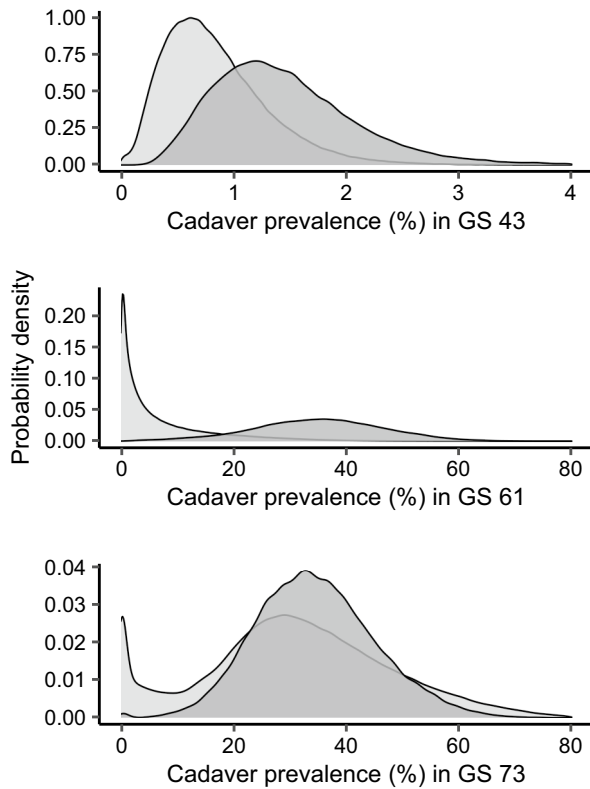


Fig. 4 The prevalence of cadavers at progressive crop growth stages (GS). Simulations are divided according to the ultimate fate of biocontrol, either more ($\geq 10\%$ yield improvement, dark grey) or less ($< 10\%$ yield improvement, light grey) successful. Note the different scales

Table 2 Sums of first-order (ΣS_i) and total sensitivity indices (ΣS_{Ti}) for the model outcomes: Peak prevalence of exposed aphids (P_E) and cadavers (P_C), and yield improvement by biocontrol (ΔY). Uncertainties are bootstrapped 95% confidence limits, which were all symmetric

Outcome	ΣS_i	ΣS_{Ti}
P_E	0.49 ± 0.06	1.58 ± 0.06
P_C	0.67 ± 0.05	1.48 ± 0.05
ΔY	0.86 ± 0.05	1.15 ± 0.05

Results

Epizootics versus successful biocontrol

The 10% of the 1,703,936 simulations resulting in the highest yield improvement ($\Delta Y > 7.5\%$ – points) were considered the successful cases of biocontrol (Fig. 3).

During stem elongation (GS 43), the outcome of biocontrol was unpredictable based on cadaver prevalence and epizootics did not yet occur (Fig. 4). However, at the beginning

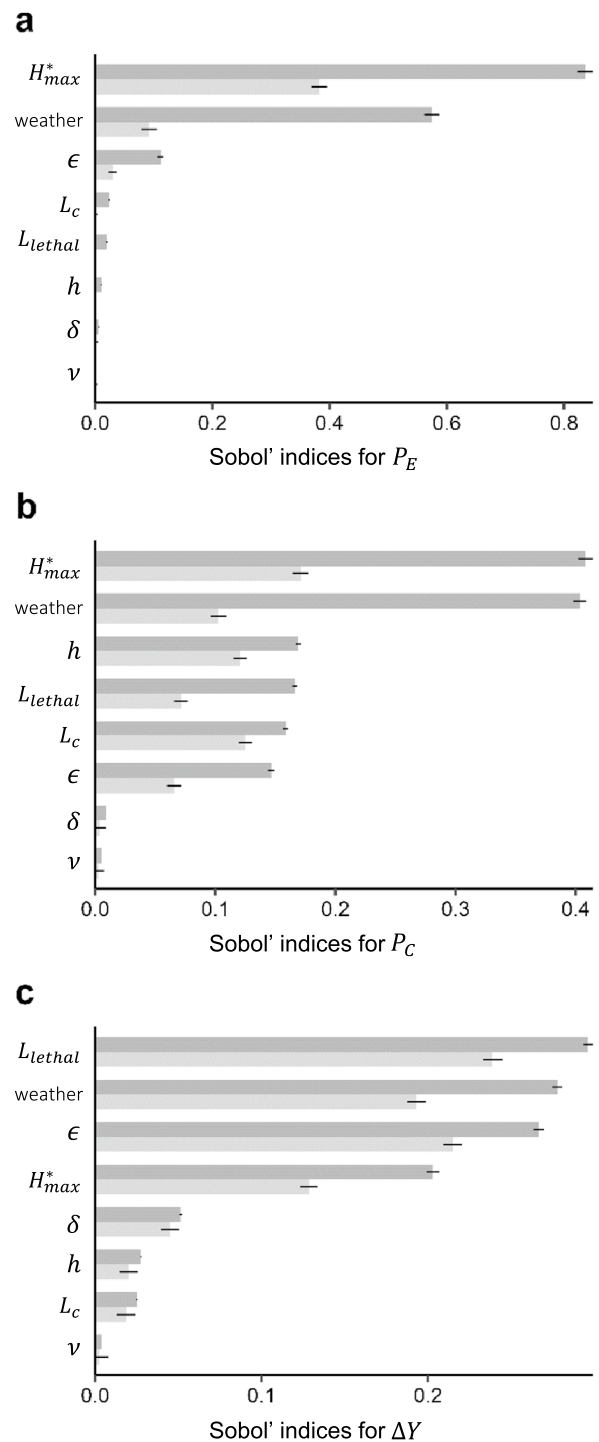


Fig. 5 Sobol' indices (S_{Ti} : dark grey; S_i : light grey) showing model sensitivity to eight parameters (cf. Table 1) in terms of three model outcomes: **a** peak prevalence of exposed aphids (P_E), **b** peak prevalence of cadavers (P_C), and **c** yield improvement due to biocontrol (ΔY). The model parameters are listed in order of importance for each outcome according to S_{Ti} . Error bars show 95% confidence limits

of flowering (GS 61), cadaver prevalence could reach an epizootic level (20–50%) but only in cases when biocontrol was ultimately successful. At milk development (GS 73), an epizootic was nearly always evident. Thus, an early epizootic was a sign of successful control, but a late epizootic was not.

Conditions conducive to biocontrol

The confidence intervals for the two indices from the sensitivity analysis, ΣS_i and ΣS_{Ti} , did not overlap (Table 2). Hence, there were significant interactions among the model parameters determining model outcomes, which means that the model cannot be reduced to a simple sum of non-interacting components.

The sensitivity analysis (Fig. 5) showed that the three model outcomes (P_E , P_C , ΔY) were in general highly sensitive to weather (temperature and relative humidity), fungus humidity threshold (H_{max}^*) and transmission efficiency (ϵ). The two parameters with a direct impact on cadavers, cadaver duration (L_c) and the acceleration of cadaver degradation at high humidity (h), had their largest impact on peak cadaver prevalence (Fig. 5b). Aphid lethal time (L_{lethal}) had an increasing importance through Figs. 5a (P_E), b (P_C) and c (ΔY). The proportion of exposed immigrants (δ) had a minor influence on yield (ΔY) only, while the influence of immunity cost (ν) was hardly detectable. In general, the influential parameters were all involved in interactions ($S_{Ti} > S_i$). The crop parameters (G_0 , τ_{50}) and the distributed delay parameter (k) were not influential at all ($S_{Ti} = 0$; not shown).

The first-order effects of the influential parameters identified in Fig. 5 are shown in Fig. 6, ranked horizontally

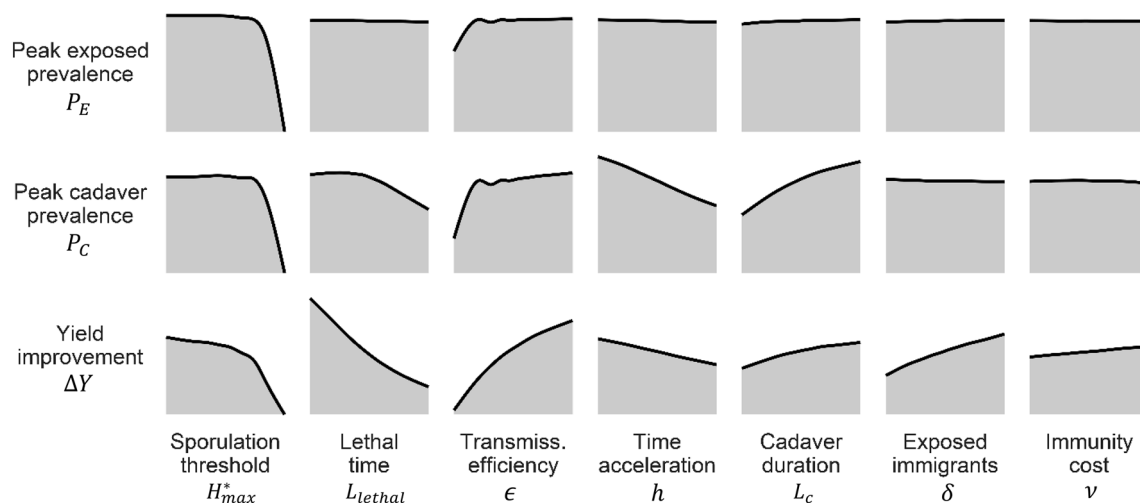


Fig. 6 The response of three model outcomes (P_E : peak density of exposed aphids; P_C : peak density of cadavers; ΔY : yield improvement by biocontrol) to variation in the seven most influential model parameters (excluding weather). y-scales for model outcomes are

2018	0	0	1	1
2017	9	8	6	12
2016	16	19	8	3
2015	20	15	16	15
2014	2	0	9	10
2013	13	14	16	13
2012	18	14	29	23
2006	4	0	7	7
2005	2	0	5	9
2004	20	14	9	13
	Aarnes	Ilseng	Ramnes	Rygge

Fig. 7 The 10% of the simulations resulting in the most successful biocontrol (cf. Figure 3) are shown distributed among the four weather stations and ten years (2004–2006, 2012–2018). Numbers show percentage successful simulations (rounded) for each combination. Grey scale shows increasing biocontrol (increasing with darkness)

according to their overall influence, except for the effect of weather which is shown in Fig. 7. Note that the pair-wise correlations in Fig. 6 only show the marginal effects of the model parameters, even though interaction effects were also important (Fig. 5).

P_E [14; 100]%, P_C [3; 86]%, and ΔY_L [0.3; 7.1]%. The x-scale for each model parameter is the interval explored in the sensitivity analysis (see Table 1). Areas under curves are filled for accentuation

A high humidity requirement (H_{\max}^*) precluded epizootics and hindered a successful control (Fig. 6). A short lethal time (L_{lethal}) would speed up fungus development, while a high transmission efficiency (ϵ) would speed up its spread. Both effects were seen, especially in terms of yield improvement. The prevalence of cadavers reached a higher peak (P_C) if cadaver duration (L_C) was long and if there was no shortening of cadaver duration at high humidity (h). An increasing proportion of exposed immigrants (δ) would lead to a higher yield improvement but not to higher peak prevalences. Hence, a high proportion of exposed immigrants lowered aphid density (an absolute measure with direct effect on yield) without affecting fungus prevalence (a relative measure with indirect effect on yield).

The model was highly sensitive to the choice of weather file (Fig. 7). With no systematic effect of location and year, this table would show 10% for all location year \times combinations. Due to the huge sample size (10% of $n = 1,703,936$), the percentages shown are accurate. Some years were more conducive to biocontrol (2012, 2015), others less (2018). There were no obvious patterns in the differences among locations. No prior hypotheses, as to how weather patterns would influence biocontrol, had been formulated and hence no statistical analysis was carried out.

Discussion

Cereal aphid population dynamics is typically exponential (Carter et al. 1982; Watt 1979). This leads to a race against natural enemies, such as fungi, which must catch up with the pest in time to be successful. We set the aphid immigration rate high enough to reach outbreak densities if not controlled. This caused most simulations, whether biocontrol turned out to be successful or not, to conclude with an epizootic late in the season. However, if an epizootic occurred earlier (around the onset of flowering) it was a sign of successful biocontrol. It is noteworthy that cadaver prevalence, which in practice would be easier to assess than the prevalence of exposed aphids, was a sufficient indicator of successful biocontrol.

Fungal epizootics are caused by many interplaying factors (Hajek and Delalibera 2010), but Hajek et al. (1993) hypothesized that epizootics can only occur if the host density exceeds a threshold allowing sufficient disease transmission to susceptible individuals. If such a threshold exists, it was evidently reached in our model setting. Model outcomes were highly dependent on parameters related to the spread of the disease: humidity threshold (H_{\max}^*), lethal time (L_{lethal}) and transmission efficiency (ϵ) (Figs. 5–6). Lethal time (L_{lethal}) is generally of importance for the development of insect epizootics (Bonsall 2004). In our model it was influential on the prevalence of cadavers

(P_C) and yield improvement (ΔY) but not on the prevalence of exposed aphids (P_E) (Figs. 5, 6). Our interpretation is that an increased lethal time (L_{lethal}) would delay the production of cadavers, thus leading directly to a lower prevalence of cadavers (P_C) and ultimately to a lower improvement of yield (ΔY).

Transmission is defined as the process by which a pathogen is passed from a source of infection to a new host (Fuxa and Tanada 1987). Transmission efficiency is a key process in host–pathogen interactions (McCallum et al. 2001, 2017; Steinkraus 2006). However, it is challenging to measure directly (Antonovics 2017; Lello and Fenton 2017) and few studies have been conducted with Entomophthoromycotina (e.g. Ardisson et al. 1997; Ekesi et al. 2005). How to model transmission efficiency correctly has been debated (Ardisson et al. 1997; McCallum et al. 2001). It is a composite parameter subsuming many processes, such as the probability of the host to encounter the pathogen and the probability of this contact to initiate a disease (McCallum et al. 2017; Reeson et al. 2000). Moreover, it does not discern between intra- and intercolonial transmission, nor between differences in susceptibility between alate and apterous morphs as found for *A. pisum* (Parker et al. 2017). We modelled it (Eq. 3) as a constant rate in effect only under high humidity conditions, as suggested by Brown and Hasibuan (1995). This simplification might not be appropriate for all host-entomopathogen systems (Elder et al. 2008; Reeson et al. 2000).

The monitoring of disease prevalence as an IPM tool was suggested for the control of cotton aphids by *Neozygites fresenii* (Entomophthoromycotina) in USA (Hollingsworth et al. 1995; Steinkraus 2007). Their approach demanded organized sampling of aphids, which were sent to a central laboratory for diagnosis by microscopy of squashed aphids. A threshold prevalence of exposed aphids and cadavers $P_E + P_C > 15\%$ was estimated, above which insecticide spraying could safely be withheld. As an IPM case, this was successful but the costs for monitoring prevalence should be considered. Our model suggests that for the IPM control of cereal aphids, it would be necessary to scout only for the cadavers (P_C) in the field (Fig. 4), which would be less costly.

The process of cadaver degradation in the environment has been mostly overlooked (but see Sawyer et al. 1997). In our model, the duration of cadavers is determined by two parameters (L_C and h ; Fig. 6), which mediate the effects of temperature and humidity on cadaver degradation rate. The uncertainty ascribed to these parameters does not consider other factors such as heavy rainfall. Thus, the model's indication of cadaver prevalence as a valid indicator of biocontrol is weakened by the lack of knowledge on the fate of cadavers.

The consideration of natural enemies in the definition of economic thresholds could be valuable for IPM in several

systems (reviewed by Giles et al. 2017). However, as argued by Leather and Atanasova (2017), economic pest thresholds used nowadays rely on studies undertaken several decades ago with another genetic base of crops and pests. The damage model (Entwistle and Dixon 1987) incorporated in our model is an example.

The pressure of fungus inoculum, as represented in the model by the proportion of exposed immigrants (δ), only influenced ΔY (Fig. 5); a high δ led to a generally lower aphid density, thus improving ΔY , but without affecting the peaks P_C and P_E (Fig. 6). This alone would explain why an epizootic is not a sufficient condition for success; and are relative measures that do not directly express aphid density, which is the variable that determines yield loss. In our model, we used a constant δ , whereas in nature it is likely to vary during the season (Chen and Feng 2004a). Moreover δ is a surrogate parameter covering all sources of inoculum (airborne conidia, resting spores in soil and crop residues, immigrating exposed aphids). Thus δ in the model represents the total inoculum pressure, not just the inoculum pathway via exposed immigrants. If a high δ is needed to secure successful biocontrol, it is problematic because Entomophthoromycotina, such as *P. neoaphidis*, are difficult to produce industrially (e.g. Hua and Feng 2003). Environmental management to secure a high natural prevalence of the fungus (conservation biocontrol) does not seem straightforward either.

Despite the known cost of fungus immunity on the reproductive rate of aphids (Baverstock et al. 2006; Saussure et al. 2019), it was not influential on the population dynamics of this system (Fig. 5). The effect was limited to $v \in [0, 0.4]$ in our model; a higher immunity cost would be needed for a systems effect.

The distributed delay commonly appears in the literature to model development (e.g. Carruthers et al. 1986; Graf et al. 1990; Gutierrez et al. 1993) with k set arbitrarily. Our model was insensitive within a broad range, $k \in [15, 30]$. Since models are sensitive to k in terms of execution time (increasing with k), our results indicate that computationally intensive models should be tested for sensitivity to k with the aim to cut down execution time.

Our model reflects several choices, which were made to match model details with the details of current knowledge in light of the questions asked. Thus, the model is not spatially explicit, horizontally, or vertically. This belies the facts that microclimate differs down through the canopy, and that aphids are spatially distributed in colonies (e.g. Winder et al. 2013). The spatial dynamics are moreover played out on a scene set by the landscape. The time step was set at 1 day, a commonly chosen time resolution for agro-ecological models (e.g. Gutierrez 1996), even though most biological processes work in a diurnal rhythm (e.g. photosynthesis). In our model, it is noteworthy that some fungal processes

run on a nocturnal schedule. Sporulation, spore germination and host infection all depend on a high humidity and tend to occur in the early morning at dewfall (Hemmati et al. 2001a; Steinkraus 2007). To avoid the complexity of a microclimate model, we used daily maximum relative humidity (H_{\max}^*) as a surrogate variable. The assumption is not that the fungal processes are directly governed by H_{\max}^* but that they are governed by hidden, microclimatic variables which are correlated with H_{\max}^* . This rationale is akin to using daily average temperature at 2 m height as a surrogate for the variable microclimatic temperatures experienced by aphids and fungus round the clock. An extended discussion of model boundaries and simplifications can be found in Supplementary Information.

The model was designed as a generic crop-pest-entomopathogenic fungus model. It enabled us to collate existing knowledge into a consistent structure that captures the governing mechanisms of the real system. The model can simulate the dynamics of similar systems in other geographical regions by adjusting the parameters describing crop development and the biology of pest and fungus. For an economic analysis of the benefits of aphid control (biological or otherwise), the crop damage model needs to be calibrated to obtain estimates accurate enough for IPM purposes.

Model parameters could be adjusted to simulate the system with alternative aphid species, such as *Rhopalosiphum padi* or *Metopolophium dirhodum*, but currently validation data are not available to evaluate such models. *Pandora neoaphidis* is the most common cause of disease in cereal aphids. Other important pathogens include *Entomophthora planchoniana* and *Conidiobolus obscurus* (Barta and Cagán, 2006; Chen and Feng 2004a; Hatting et al. 2000). All three species belong to the same subphylum and are thus well described by our model. However, data for parameter estimation are lacking for the other two fungal species.

We used the model to explore the possibility of including a natural enemy threshold in the IPM of cereal aphids. Our finding, that an early epizootic is a promise of successful control, must be substantiated by experiments that establish the relation between the timing of epizootics and the degree of aphid control.

Transmission efficiency was identified as a key parameter in the model, but this is a parameter that, due to a knowledge gap, combines and thereby confuses many underlying processes. More experimental data is needed on the whole transmission process, along with a critical conceptualization of this multi-layered process (cf. McCallum et al. 2017). A mostly neglected process brought to light by our study is the decay of cadavers. Cadavers define the time window for possible disease transmission, as well as for immediate detection by the human eye.

Weather caused much uncertainty on the outcome of aphid-fungus dynamics. In reality the effect of weather is

modulated by the microclimate at the site of aphid-fungus interaction. Hence, no straightforward relation can be expected between weather and successful control and, most likely, the success of *P. neoaphidis* cannot be predicted from the weather. In an IPM perspective, this stresses the need to scout for aphid cadavers to assess the status of any ongoing fungal biocontrol.

According to the model, a higher intensity and especially an earlier occurrence of the pathogen would improve biocontrol. Unfortunately, Entomophthoromycotina are difficult to produce industrially (Lacey et al. 2015; Pell et al. 2010). Hence, a biopesticide based on these species is not expected soon. The inoculum could possibly be furthered through conservation biocontrol, but this necessitates more studies on the year-round life cycle of the fungi, both inside and outside the field. In a cost-benefit analysis, the effect of fungi must be compared to the benefits of other natural enemies and, indeed, other IPM options (e.g. host plant resistance). Interactions, such as ladybirds consuming infected aphids and thereby reducing the fungus biocontrol (e.g. Roy et al. 1998) complicates the analysis. These complications are best approached by modelling as presented in this paper to identify the most important system components and processes.

In conclusion, fungal epizootics are a sign of successful biological control but only if they occur early enough. We reached this conclusion through simulation modelling, which we used as a tool to improve our understanding of the system and to clarify the limits of our knowledge. To make the detection of epizootics a practical IPM tool, further field work and statistical models that relate the timing of epizootics to the biocontrol outcome are needed.

Author contributions

IK acquired the main funding. RM and SS acquired secondary funding. SS, NH conceptualized the research questions. SS, NH and AGRH developed the model while RM and IK brought expertise on biology and ecology when necessary. SS and NH analysed and interpreted the results. SS and NH wrote the manuscript. AGRH, RM and IK reviewed and edited it.

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Code availability Model software and source code is available at www.ecolmod.org

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication All authors read and approved the manuscript.

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References

- Agrometeorology Norway, 2000–2016. <http://lmt.nibio.no>. Accessed Mar 2018
- Andersen A (2003) *Bladlus På Korn*. Grønn Kundskap 7:1–3
- Antonovics J (2017) Transmission dynamics: critical questions and challenges. *Philos Trans R Soc b: Biol Sci* 372:20160087. <https://doi.org/10.1098/rstb.2016.0087>
- Ardisson CN, Pierre JS, Plantegenest M, Dedryver C-A (1997) Parameter estimation for a descriptive epizootiological model of the infection of a cereal aphid population by a fungal pathogen (entomophthorale). *Entomophaga* 42:575–591. <https://doi.org/10.1007/BF02769817>
- Bahlai CA, Weiss RM, Hallett RH (2013) A mechanistic model for a tritrophic interaction involving soybean aphid, its host plants, and multiple natural enemies. *Ecol Model* 254:54–70. <https://doi.org/10.1016/j.ecolmodel.2013.01.014>
- Barta M, Cagán L (2006) Aphid-pathogenic Entomophthorales (their taxonomy, biology and ecology). *Biologia* 61:S543–616. <https://doi.org/10.2478/s11756-007-0100-x>
- Barzman M, Bärberi P, Birch ANE, Boonekamp P, Dachbrodt-Saaydeh S, Graf B, Hommel B, Jensen JE, Kiss J, Kudsk P, Lamichhane JR (2015) Eight principles of integrated pest management. *Agron Sustain Dev* 35:1199–1215. <https://doi.org/10.1007/s13593-015-0327-9>
- Baverstock J, Roy HE, Clark SJ, Alderson PG, Pell JK (2006) Effect of fungal infection on the reproductive potential of aphids and their progeny. *J Invertebr Pathol* 91:136–139. <https://doi.org/10.1016/j.jip.2005.11.005>
- Baverstock J, Clark SJ, Pell JK (2008) Effect of seasonal abiotic conditions and field margin habitat on the activity of *Pandora neoaphidis* inoculum on soil. *J Invertebr Pathol* 97:282–290. <https://doi.org/10.1016/j.jip.2007.09.004>

- Blackman RL, Eastop VF (2007) Taxonomic issues. In: van Emden HF, Harrington R (eds) Aphids as crop pests. CABI, Wallingford, pp 1–29
- Bonner T, Gray SN, Pell JK (2003) Survival of *Erynia neoaphidis* in aphid cadavers in a simulated winter environment. IOBC WPRS Bulletin 26:73–76
- Bonsall MB (2004) The impact of diseases and pathogens on insect population dynamics. *Physiol Entomol* 29:223–236. <https://doi.org/10.1111/j.0307-6962.2004.00389.x>
- Brobyn PJ, Wilding N, Clark SJ (1985) The persistence of infectivity of conidia of the aphid pathogen *Erynia neoaphidis* on leaves in the field. *Ann Appl Biol* 107:365–376. <https://doi.org/10.1111/j.1744-7348.1985.tb03153.x>
- Brown GC, Hasibuan R (1995) Conidial discharge and transmission efficiency of *Neozygites floridana*, an entomopathogenic fungus infecting two-spotted spider mites under laboratory conditions. *J Invertebr Pathol* 65:10–16. <https://doi.org/10.1006/jjpa.1995.1002>
- Carruthers RI, Whitfield GH, Tummala RL, Haynes DLA (1986) systems-approach to research and simulation of insect pest dynamics in the onion agroecosystem. *Ecol Model* 33:101–121. [https://doi.org/10.1016/0304-3800\(86\)90035-9](https://doi.org/10.1016/0304-3800(86)90035-9)
- Carter N, Dixon AFG, Rabbinge R (1982) Cereal Aphid Populations: biology, simulation and prediction; Simulation Monographs; Centre for Agricultural Publ. and Doc: Wageningen; ISBN 978-90-220-0804-1. ISBN 90-220-0804-5
- Carter N, Rabbinge R (1980) Simulation models of the population development of *Sitobion avenae*. IOBC/WPRS Bull 3:93–98
- Chen C, Feng M (2004a) Observation on the initial inoculum source and dissemination of Entomophthorales-caused epizootics in populations of cereal aphids. *Sci China, Ser C Life Sci* 47:38–43. <https://doi.org/10.1360/02yc0261>
- Chen C, Feng M-G (2004b) *Sitobion avenae* alatae infected by *Pandora neoaphidis*: their flight ability, post-flight colonization, and mycosis transmission to progeny colonies. *J Invertebr Pathol* 86:117–123. <https://doi.org/10.1016/j.jip.2004.05.006>
- Dean GJ (1974) Effect of temperature on the cereal aphids *Metopolophium dirhodum* (Wlk.), *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (F.) (Hem., Aphididae). *Bull Entomol Res* 63:401–409. <https://doi.org/10.1017/S000748530040888>
- Dedryver C-A, Le Ralec A, Fabre F (2010) The conflicting relationships between aphids and men: a review of aphid damage and control strategies. *CR Biol* 333:539–553. <https://doi.org/10.1016/j.crvi.2010.03.009>
- Dromph KM, Pell JK, Eilenberg J (2002) Influence of Flight and Colour Morph on Susceptibility of *Sitobion avenae* to infection by *Erynia neoaphidis*. *Biocontrol Sci Tech* 12:753–756. <https://doi.org/10.1080/0958315021000039932>
- Duarte VS, Westrum K, Ribeiro AEL, Gondim MGC Jr, Klingen I, Delalibera I Jr (2013) Abiotic and biotic factors affecting resting spore formation in the mite pathogen *Neozygites floridana*. *Int J Microbiol*. <https://doi.org/10.1155/2013/276168>
- Duffy C, Fealy R, Fealy RM (2017) An improved simulation model to describe the temperature-dependent population dynamics of the grain aphid, *Sitobion avenae*. *Ecol Model* 354:140–171. <https://doi.org/10.1016/j.ecolmodel.2017.03.011>
- Eilenberg J, Saussure S, Fekih IB, Jensen AB, Klingen I (2019) Factors driving susceptibility and resistance in aphids that share specialist fungal pathogens. *Curr Opi Insect Sci* 33:91–98. <https://doi.org/10.1016/j.cois.2019.05.002>
- Ekesi S, Shah PA, Clark SJ, Pell JK (2005) Conservation biological control with the fungal pathogen *Pandora neoaphidis*: implications of aphid species, host plant and predator foraging. *Agric for Entomol* 7:21–30. <https://doi.org/10.1111/j.1461-9555.2005.00239.x>
- Elder BD, Dushoff J, Dwyer G (2008) Host-pathogen interactions, insect outbreaks, and natural selection for disease resistance. *Am Nat* 172:829–842. <https://doi.org/10.1086/592403>
- Entwistle JC, Dixon AFG (1987) Short-term forecasting of wheat yield loss caused by the grain aphid (*Sitobion avenae*) in summer. *Ann Appl Biol* 111:489–508. <https://doi.org/10.1111/j.1744-7348.1987.tb02007.x>
- Fuxa JR, Tanada Y (1987) Epidemiological concepts applied to insect epizootiology. In: Fuxa JR, Tanada Y (eds) Epizootiology of insect diseases. Wiley, New York, pp 3–21
- George KS, Gair R (1979) Crop loss assessment on winter wheat attacked by the grain aphid, *Sitobion avenae* (F.), 1974–77. *Plant Pathol* 28:143–149. <https://doi.org/10.1111/j.1365-3059.1979.tb02630.x>
- Giles KL, McCornack BP, Royer TA, Elliott NC (2017) Incorporating biological control into IPM decision making. *Curr Opi Insect Sci* 20:84–89. <https://doi.org/10.1016/j.cois.2017.03.009>
- Graf B, Rakotobe O, Zahner P, Delucchi V, Gutierrez AP (1990) A simulation model for the dynamics of rice growth and development: Part I—the carbon balance. *Agric Syst* 32:341–365. [https://doi.org/10.1016/0308-521X\(90\)90099-C](https://doi.org/10.1016/0308-521X(90)90099-C)
- Gutierrez AP (1996) Applied population ecology. Wiley, New York
- Gutierrez AP, Neuenschwander P, Vanalphen JJM (1993) Factors affecting biological-control of cassava mealybug by exotic parasitoids - a ratio-dependent supply-demand driven model. *J Appl Ecol* 30:706–721. <https://doi.org/10.2307/2404249>
- Hajek AE, Delalibera I (2010) Fungal pathogens as classical biological control agents against arthropods. *Biocontrol* 55:147–158. <https://doi.org/10.1007/s10526-009-9253-6>
- Hajek AE, Meyling NV (2018) Fungi. In: Hajek AE, Shapiro-Ilan DI (eds) Ecology of invertebrate diseases. Wiley, London, pp 327–377
- Hajek AE, Larkin TS, Carruthers RI, Soper RS (1993) Modeling the dynamics of *Entomophaga maimaiga* (Zygomycetes: Entomophthorales) epizootics in gypsy moth (Lepidoptera: Lymantriidae) populations. *Environ Entomol* 22:1172–1187. <https://doi.org/10.1093/ee/22.5.1172>
- Hajek AE, Olsen CH, Elkinton JS (1999) Dynamics of airborne conidia of the gypsy Moth (Lepidoptera: Lymantriidae) Fungal pathogen *Entomophaga maimaiga* (Zygomycetes: Entomophthorales). *Biol Control* 16:111–117. <https://doi.org/10.1006/bcon.1999.0740>
- Hallett RH, Bahlai CA, Xue Y, Schaafsma AW (2014) Incorporating natural enemy units into a dynamic action threshold for the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Pest Manag Sci* 70:879–888. <https://doi.org/10.1002/ps.3674>
- Hansen LM (2000) Establishing control threshold for bird cherry-oat aphid (*Rhopalosiphum padi* L.) in spring barley (*Hordeum vulgare* L.) by aphid-days. *Crop Prot* 19:191–194. [https://doi.org/10.1016/S0261-2194\(99\)00094-0](https://doi.org/10.1016/S0261-2194(99)00094-0)
- Hansen LM (2006) Models for spring migration of two aphid species *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.) infesting cereals in areas where they are entirely holocyclic. *Agric for Entomol* 8:83–88. <https://doi.org/10.1111/j.1461-9563.2006.00289.x>
- Hatting JL, Poprawski TJ, Miller RM (2000) Prevalences of fungal pathogens and other natural enemies of cereal aphids (Homoptera: Aphididae) in wheat under dryland and irrigated conditions in South Africa. *Biocontrol* 45:179–199. <https://doi.org/10.1023/A:1009981718582>
- Hemmati F, Pell JK, McCartney HA, Clark SJ, Deadman ML (2001a) Conidial discharge in the aphid pathogen *Erynia neoaphidis*. *Mycol Res* 105:715–722. <https://doi.org/10.1017/S0953756201004014>
- Hemmati F, Pell JK, McCartney HA, Deadman ML (2001b) Airborne concentrations of conidia of *Erynia neoaphidis* above cereal fields. *Mycol Res* 105:485–489. <https://doi.org/10.1017/S0953756201003537>

- Hollingsworth RG, Steinkraus DG, McNewz RW (1995) Sampling to predict fungal epizootics in cotton aphids (Homoptera: Aphididae). *Environ Entomol* 24:1414–1421. <https://doi.org/10.1093/ee/24.6.1414>
- Holst N (2013) A universal simulator for ecological models. *Eco Inform* 13:70–76. <https://doi.org/10.1016/j.ecoinf.2012.11.001>
- Holst N (2022) Universal Simulator. Version 3.0.5 or later. Ecological Modelling Laboratory, Aarhus University, Denmark. www.ecolmod.org. Accessed 6 Oct 2022
- Honek A, Martinkova Z, Dixon AFG, Saska P (2017) Annual predictions of the peak numbers of *Sitobion avenae* infesting winter wheat. *J Appl Entomol* 141:352–362. <https://doi.org/10.1111/jen.12344>
- Honek A, Martinkova Z, Saska P, Dixon AF (2018) Aphids (Homoptera: Aphididae) on winter wheat: predicting maximum abundance of *Metopolophium dirhodum*. *J Econ Entomol* 111:1751–1759. <https://doi.org/10.1093/jee/toy157>
- Hoover JK, Newman JA (2004) Tritrophic interactions in the context of climate change: a model of grasses, cereal aphids and their parasitoids. *Glob Change Biol* 10:1197–1208. <https://doi.org/10.1111/j.1529-8817.2003.00796.x>
- Hua L, Feng MG (2003) New use of broomcorn millets for production of granular cultures of aphid-pathogenic fungus *Pandora neoaphidis* for high sporulation potential and infectivity to *Myzus persicae*. *FEMS Microbiol Lett* 227:311–317. [https://doi.org/10.1016/S0378-1097\(03\)00711-0](https://doi.org/10.1016/S0378-1097(03)00711-0)
- Jonsson M, Sigvald R (2016) Suction-trap catches partially predict infestations of the grain aphid *Sitobion avenae* in winter wheat fields. *J Appl Entomol* 140:553–557. <https://doi.org/10.1111/jen.12290>
- Kalkar Ö (2005) An SEM study of the sporulation process of *Pandora neoaphidis* and *Neozygites fresenii*. *Turk J Biol* 29:137–147
- Keeling MJ, Rohani P (2008) Modeling infectious diseases in humans and animals. Princeton University Press, Princeton. <https://doi.org/10.1515/9781400841035>
- Kieckhefer RW, Gellner JL, Riedell WE (1995) Evaluation of the aphid-day standard as a predictor of yield loss caused by cereal aphids. *Agron J* 87:785–788. <https://doi.org/10.2134/agronj1995.00021962008700050001x>
- Kindlmann P, Dixon AF (2010) Modelling population dynamics of aphids and their natural enemies. *Aphid Biodiv Under Environ Change*. https://doi.org/10.1007/978-90-481-8601-3_1
- Klingen I, Nilsen SS (2009) Mechanisms important for the epidemic development of *Neozygites floridana* in *Tetranychus urticae*. *IOBC WPRS Bull* 45:287–289
- Klingen I, Wærsted G, Westrum K (2008) Overwintering and prevalence of *Neozygites floridana* (Zygomycetes: Entomophthorales) in hibernating females of *Tetranychus urticae* (Acari: Tetranychidae) under cold climatic conditions in strawberries. *Exp Appl Acarol* 46:231–245. <https://doi.org/10.1007/s10493-008-9178-2>
- Korsæth A, Rafoss T (2009) Tidlige prognoser for kornavlingene ved bruk av værdata. *Bioforsk Report* 4:13
- Lacey LA, Grzywacz D, Shapiro-Ilan DI, Frutos R, Brownbridge M, Goettel MS (2015) Insect pathogens as biological control agents: back to the future. *J Invertebr Pathol* 132:1–41. <https://doi.org/10.1016/j.jip.2015.07.009>
- Larkin TS, Carruthers RI, Legaspi BC (2000) Two-dimensional distributed delays for simulating two competing biological processes. *Trans Soc Comput Simul Int* 17:25–33
- Larsson H (2005) A crop loss model and economic thresholds for the grain aphid, *Sitobion avenae* (F.), in winter wheat in southern Sweden. *Crop Prot* 24:397–405. <https://doi.org/10.1016/j.cropro.2004.08.011>
- Leather SR, Atanasova D (2017) Without up-to-date pest thresholds sustainable agriculture is nothing but a pipe-dream. *Agric Entomol* 19:341–343. <https://doi.org/10.1111/afe.12244>
- Leblanc A, Brodeur J (2018) Estimating parasitoid impact on aphid populations in the field. *Biol Control* 119:33–42. <https://doi.org/10.1016/j.biocontrol.2018.01.002>
- Lee G, Stevens DJ, Stokes S, Wratten SD (1981) Duration of cereal aphid populations and the effects on wheat yield and breadmaking quality. *Ann Appl Biol* 98:169–178. <https://doi.org/10.1111/j.1744-7348.1981.tb00750.x>
- Lello J, Fenton A (2017) Lost in transmission...? *Philos Trans R Soc b: Biol Sci* 372:20160082. <https://doi.org/10.1098/rstb.2016.0082>
- Maisonhaute J-É, Labrie G, Lucas E (2017) Direct and indirect effects of the spatial context on the natural biocontrol of an invasive crop pest. *Biol Control* 106:64–76. <https://doi.org/10.1016/j.biocontrol.2016.12.010>
- Manetsch TJ (1976) Time-varying distributed delays and their use in aggregate models of large systems. *IEEE Trans Syst Man Cybern SMC* 6:547–553. <https://doi.org/10.1109/TSMC.1976.4309549>
- Maurer J (2021) Boost C++ libraries. Random library
- McCallum H, Barlow N, Hone J (2001) How should pathogen transmission be modelled? *Trends Ecol Evol* 16:295–300. [https://doi.org/10.1016/S0169-5347\(01\)02144-9](https://doi.org/10.1016/S0169-5347(01)02144-9)
- McCallum H, Fenton A, Hudson PJ, Lee B, Levick B, Norman R, Perkins SE, Viney M, Wilson AJ, Lello J (2017) Breaking beta: reconstructing the parasite transmission function. *Philos Trans R Soc b Biol Sci* 372:20160084. <https://doi.org/10.1098/rstb.2016.0084>
- Morgan LW, Boddy L, Clark SJ, Wilding N (1995) Influence of temperature on germination of primary and secondary conidia of *Erynia neoaphidis* (Zygomycetes: Entomophthorales). *J Invertebr Pathol* 65:132–138. <https://doi.org/10.1006/jipa.1995.1020>
- Nicholson AJ, Bailey VA (1935) The Balance of animal populations.—Part I. *Proc Zool Soc Lond* 105:551–598
- Nielsen C, Hajek AE, Humber RA, Bresciani J, Eilenberg J (2003) Soil as an environment for winter survival of aphid-pathogenic Entomophthorales. *Biol Control* 28:92–100. [https://doi.org/10.1016/S1049-9644\(03\)00033-1](https://doi.org/10.1016/S1049-9644(03)00033-1)
- Nielsen C, Eilenberg J, Dromph K (2001) Entomophthorales on cereal aphids: Characterization, growth, virulence, epizootiology and potential for microbial control. *Pesticides Res.* 53. The Danish Environmental Protection Agency, Copenhagen
- Oakley JN, Walters KFA (1994) A field evaluation of different criteria for determining the need to treat winter wheat against the grain aphid *Sitobion avenae* and the rose-grain aphid *Metopolophium dirhodum*. *Ann Appl Biol* 124:195–211. <https://doi.org/10.1111/j.1744-7348.1994.tb04128.x>
- Olfert O, Weiss RM, Vankosky M, Hartley S, Doane JF (2020) Modelling the tri-trophic population dynamics of a host crop (*Triticum aestivum*; Poaceae), a major pest insect (*Sitodiplosis mosellana*; Diptera: Cecidomyiidae), and a parasitoid of the pest species (*Macroglenes penetrans*; Hymenoptera: Pteromalidae): a cohort-based approach incorporating the effects of weather. *Can Entomol* 152:311–329. <https://doi.org/10.4039/tce.2020.17>
- Parker BJ, Barribeau SM, Laughton AM, Griffin LH, Gerardo NM (2017) Life-history strategy determines constraints on immune function. *J Anim Ecol* 86:473–483. <https://doi.org/10.1111/1365-2656.12657>
- Pell JK, Hannam JJ, Steinkraus DC (2010) Conservation biological control using fungal entomopathogens. *Biocontrol* 55(1):187–198. <https://doi.org/10.1007/s10526-009-9245-6>
- Plantegenest M, Pierre JS, Dedryver C-A, Kindlmann P (2001) Assessment of the relative impact of different natural enemies on population dynamics of the grain aphid *Sitobion avenae* in the field.

- Ecol Entomol 26:404–410. <https://doi.org/10.1046/j.1365-2311.2001.00330.x>
- Rabbinge R, Ankersmit GW, Pak GA (1979) Epidemiology and simulation of population development of *Sitobion avenae* in winter wheat. Neth J Plant Pathol 85:197–220. <https://doi.org/10.1007/BF01976821>
- Rabbinge R, Drees EM, Van der Graaf M, Verberne FCM, Wesselo A (1981) Damage effects of cereal aphids in wheat. Neth J Plant Pathol 87:217–232. <https://doi.org/10.1007/BF02084437>
- Reeson AF, Wilson K, Cory JS, Hankard P, Weeks JM, Goulson D, Hails RS (2000) Effects of phenotypic plasticity on pathogen transmission in the field in a Lepidoptera-NPV system. Oecologia 124:373–380. <https://doi.org/10.1007/s004420000397>
- Reynolds JF, Acock B (1997) Modularity and genericness in plant and ecosystem models. Ecol Model 94:7–16. [https://doi.org/10.1016/S0304-3800\(96\)01924-2](https://doi.org/10.1016/S0304-3800(96)01924-2)
- Rossing WAH (1991) Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae*. 3. Calculation of damage at various attainable yield levels. Neth J Plant Pathol 97:87–103
- Roy HE, Pell JK, Clark SJ, Alderson PG (1998) Implications of predator foraging on aphid pathogen dynamics. J Invertebr Pathol 71(3):236–247. <https://doi.org/10.1006/jjipa.1997.4736>
- Roy HE, Pell JK, Alderson PG (2001) Targeted dispersal of the aphid pathogenic fungus *Erynia neoaphidis* by the aphid predator *Coccinella septempunctata*. Biocontrol Sci Tech 11:99–110. <https://doi.org/10.1080/09583150020029781>
- Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M, Tarantola S (2008) Global sensitivity analysis. Wiley, London
- Saltelli A, Annoni P, Azzini I, Campolongo F, Ratto M, Tarantola S (2010) Variance based sensitivity analysis of model output. design and estimator for the total sensitivity index. Comput Phys Commun 181:259–270. <https://doi.org/10.1016/j.cpc.2009.09.018>
- Saltelli A, Aleksankina K, Becker W, Fennell P, Ferretti F, Holst N, Li S, Wu Q (2019) Why so many published sensitivity analyses are false: a systematic review of sensitivity analysis practices. Environ Model Softw 114:29–39. <https://doi.org/10.1016/j.envsoft.2019.01.012>
- Saussure S, Westrum K, Roer Hjelkrem A-G, Klingen I (2019) Effect of three isolates of *Pandora neoaphidis* from a single population of *Sitobion avenae* on mortality, speed of kill and fecundity of *S. avenae* and *Rhopalosiphum padi* at different temperatures. Fungal Ecol 41:1–12. <https://doi.org/10.1016/j.funeco.2019.03.004>
- Sawyer AJ, Griggs MH, Wayne R (1994) Dimensions, density, and settling velocity of Entomophthoralean conidia: implications for aerial dissemination of spores. J Invertebr Pathol 63:43–55. <https://doi.org/10.1006/jjipa.1994.1008>
- Sawyer AJ, Ramos ME, Poprawski TJ, Soper RS, Carruthers RI (1997) Seasonal patterns of cadaver persistence and sporulation by the fungal pathogen *Entomophaga grylli* (Fresenius) Batko (Entomophthorales: Entomophthoraceae) infecting *Camnula pellucida* (Scudder) (Orthoptera: Acrididae). Memoirs Entomol Soc Can 129:355–374. <https://doi.org/10.4039/entm129171355-1>
- Schmitz V, Dedryver C-A, Pierre J-S (1993) Influence of an *Erynia neoaphidis* infection on the relative rate of increase of the cereal aphid *Sitobion avenae*. J Invertebr Pathol 61:62–68. <https://doi.org/10.1006/jjipa.1993.1011>
- Scorsetti AC, Jensen AB, Lastra CL, Humber RA (2012) First report of *Pandora neoaphidis* resting spore formation in vivo in aphid hosts. Fungal Biol 116:196–203. <https://doi.org/10.1016/j.funbio.2011.11.002>
- Sobol' IM (1976) Uniformly distributed sequences with an additional uniform property. USSR Comput Math Math Phys 16:236–242. [https://doi.org/10.1016/0041-5553\(76\)90154-3](https://doi.org/10.1016/0041-5553(76)90154-3)
- Sobol' IM (1990) Sensitivity estimates for nonlinear mathematical models (in Russian). Matematicheskoe Modelirovanie 2:112–118
- Stacey DA, Thomas MB, Blanford S, Pell JK, Pugh C, Fellowes MDE (2003) Genotype and temperature influence pea aphid resistance to a fungal entomopathogen. Physiol Entomol 28:75–81. <https://doi.org/10.1046/j.1365-3032.2003.00309.x>
- Steinkraus DC (2006) Factors affecting transmission of fungal pathogens of aphids. J Invertebr Pathol 92:125–131. <https://doi.org/10.1016/j.jip.2006.03.009>
- Steinkraus D (2007) Management of aphid populations in cotton through conservation: delaying insecticide spraying has its benefits. In: Vincent C, Goettel MS, Lazarovits G (eds) Biological control: a global perspective. CABI, Wallingford
- Steinkraus DC, Boys GO, Slaymaker PH (1993) Culture, storage, and incubation period of *Neozygites fresenii* (Entomophthorales: Neozygiteaceae), a pathogen of the cotton aphid. Southwest Entomol 18:197–202
- Steinkraus DC, Hollingsworth RG, Boys JGO (1996) Aerial spores of *Neozygites fresenii* (Entomophthorales: Neozygiteaceae): density, periodicity, and potential role in Cotton aphid (Homoptera: Aphididae) epizootics. Environ Entomol 25:48–57. <https://doi.org/10.1093/ee/25.1.48>
- Vansickle J (1977) Attrition in distributed delay models. IEEE Trans Syst Man Cybern 7:635–638. <https://doi.org/10.1109/TSMC.1977.4309800>
- Vialatte A, Plantegenest M, Simon J-C, Dedryver C-A (2007) Farm-scale assessment of movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows. Agric for Entomol 9:337–346. <https://doi.org/10.1111/j.1461-9563.2007.00347.x>
- Watt AD (1979) The effect of cereal growth stages on the reproductive activity of *Sitobion avenae* and *Metopolophium dirhodum*. Ann Appl Biol 91:147–157. <https://doi.org/10.1111/j.1744-7348.1979.tb06485.x>
- Winder L, Alexander CJ, Woolley C, Perry JN, Holland JM (2013) The spatial distribution of canopy-resident and ground-resident cereal aphids (*Sitobion avenae* and *Metopolophium dirhodum*) in winter wheat. Arthropod-Plant Interact 7:21–32. <https://doi.org/10.1007/s11829-012-9216-1>
- Wood S (2021) mgcv: Mixed GAM computation vehicle with automatic smoothness estimation.
- Wratten SD (1975) The nature of the effects of the aphids *Sitobion avenae* and *Metopolophium dirhodum* on the growth of wheat. Ann Appl Biol 79:27–34. <https://doi.org/10.1111/j.1744-7348.1975.tb01518.x>
- Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Res 14:415–421. <https://doi.org/10.1111/j.1365-3180.1974.tb01084.x>

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