Dynamic role of grasslands as sources of soil-dwelling insect pests: New insights from in silico experiments for pest management strategies

Sylvain Poggi, Mike Sergent, Youcef Mammeri, Manuel Plantegenest, Ronan Le Cointe, Yoann Bourhis

▶ To cite this version:

Sylvain Poggi, Mike Sergent, Youcef Mammeri, Manuel Plantegenest, Ronan Le Cointe, et al.. Dynamic role of grasslands as sources of soil-dwelling insect pests: New insights from in silico experiments for pest management strategies. Ecological Modelling, 2021, 440, 10.1016/j.ecolmodel.2020.109378 . hal-03344605

Dynamic role of grasslands as sources of soil-dwelling insect pests: new insights from *in silico* experiments for pest management strategies

Sylvain Poggi*[a], Mike Sergent[a], Youcef Mammeri[b], Manuel Plantegenest[a], Ronan Le Cointe[a], Yoann Bourhis[c]

[a] INRAE, Agrocampus Ouest, Université de Rennes, IGEPP, F-35650 Le Rheu, France
[b] LAMFA, Université de Picardie Jules Verne, CNRS UMR 7352, F-80000 Amiens, France
[c] Rothamsted Research, Department of Biointeraction and Crop Protection, Harpenden, Herts. AL5 2JQ, UK

Keywords: pest control, population dynamics, landscape dynamics, reservoir, sink, connectivity, reaction-diffusion-advection model, land-use change, wireworm, click beetle

Highlights:

- The role of grassland in field colonisation by insect pests is investigated in silico
- Population dynamics of wireworms is modelled, accounting for life cycle and dispersion
- Spatiotemporal effects of grassland in field history, field neighbourhood or their interaction, depend on the pest life cycle and its dispersal capacity
- Grassy areas can act either as pseudo-sinks or as sources on neighbouring crops
- Control strategies based on grassland arrangements appear trait-specific

Abstract:

Sustainable pest control strategies hinge on the knowledge of movement ecology within the agricultural landscape where contrasted habitat qualities intermingle, thereby influencing arthropod dispersal. Hence, habitat manipulation in space and time can be a lever for action to control pests with regard to landscape compositional constraints. In this study, we examined the role of grassland arrangements in field colonisation by soil-dwelling pests within a dynamic agricultural landscape, and discussed the implications for pest management with a focus on wireworms. For this purpose, we proposed a framework combining (i) a spatially explicit and mechanistic model describing the pest population dynamics in both aerial and soil compartments involved along its life cycle, and (ii) spatiotemporal representations of various landscape contexts. We addressed the role of grassland in plot history, in plot neighbourhood, or in both history and neighbourhood. Our results show that species with a short life cycle are more responsive to changes in land use, and that the neighbourhood effect strongly relies on dispersal mechanisms (random vs directed movements). We also highlight how the arrangement of grassy landscape elements in space and time can mitigate crop infestation by soil-dwelling pests, thereby emphasizing the relevance of managing grassland regimes. Once informed by critical pest life traits, our approach opens avenue for the exploration of the spatiotemporal land use manipulation meant for pest

management. Future research consists in the exploration of suppressive patterns in simplified but realistic agricultural landscapes, generated under agronomic constraints at the farm or landscape scales.

1. Introduction

Targeting a sustainable crop protection, freed from its reliance on pesticides, requires a better understanding of field colonisation processes driving pest population dynamics. Looking for environmental-friendly strategies for pest control reemphasizes the importance of movement ecology. Indeed, insect pest habitats are fragmented rendering dispersal a key process determining pest population dynamics at the agricultural landscape scale. This suggests that agricultural landscape is a relevant scale for designing pest resilient agroecosystems that minimise the use of pesticides (Bourhis et al., 2017, 2015; Tscharntke and Brandl, 2004).

Such a pest control approach should account for processes operating at different spatial and temporal scales, thereby requiring an extensive knowledge about pest ecology. The survival of species hinge on their ability to detect and reach suitable resources when necessary in their life cycle (Dunning et al., 1992; Vasseur et al., 2013). Interestingly, a few studies have suggested that some insects effectively move between asynchronous land uses depending on resource availability (Aviron et al., 2018; Bressan et al., 2010; Men et al., 2004). Habitat connectivity in space and time (Martensen et al., 2017; Moilanen and Hanski, 2001; Taylor et al., 1993) is thus a pivotal driver of pest dispersal success in dynamic agricultural landscapes. Consequently, the spatial and temporal arrangement of land uses can be a lever for action to control species abundances with regard to landscape compositional constraints (Fischer and Lindenmayer, 2007; Jonsson et al., 2010; Parisey et al., 2016; Polasky et al., 2008; Roques and Hamel, 2007; With and King, 2001)

In that, Elateridae can be considered as relevant model organisms (Blackshaw et al., 2017). Wireworms, the larvae of click beetles (Coleoptera: Elateridae) of which there are more than 10,000 species in about 400 genera known worldwide, are among the most notorious soil-dwelling pests (Balachowsky and Mesnil, 1935; Miles, 1942; Traugott et al., 2015). Elaterid pest species are capable of exploiting both cultivated and uncultivated areas in the agricultural mosaic (Milosavljević et al., 2016). Consequently, understanding their movement from sources that sustain important populations, i.e. uncultivated areas, to vulnerable crops is central in the development of pest management strategies. The larvae undergo a number of instars and the complete elaterid life cycle varies between two to five years (Balachowsky and Mesnil, 1935; Furlan, 1998; Miles, 1942; Sufyan et al., 2013). In Europe, *Agriotes* spp. are the most harmful species. They attack the roots and tubers of a wide range of crops, thereby inflicting severe economic damage in potatoes, maize and vegetable production, and may even threaten perennial crops such as soft fruits or orchards (Traugott et al., 2015).

Though scarce and fragmented, knowledge regarding the biology and the ecology of *Agriotes* spp. indicates that uncropped field margins and areas are the most favourable habitat for wireworms, and act as reservoirs from which they disperse into adjacent crops (Blackshaw et al., 2017). Based on correlative approaches, some studies have attempted to unravel relationships between larvae or adult abundances or densities and landscape features (Benefer et al., 2012; Blackshaw and Vernon, 2006; L. Furlan et al., 2017; Hermann et al., 2013; Kozina et al., 2015; Poggi et al., 2018a; Saussure et al., 2015). Altogether, these studies shed light on the potential for a dynamic landscape to shape wireworm populations. However, while providing insights of the main factors responsible for wireworm or click beetle density levels, such approaches fail in describing the mechanisms driving pest colonisation, and subsequently in elucidating the source/sink ecological processes that operate at the landscape scale.

The main objective of our study was to examine the role of grasslands in field colonisation by soil-dwelling pests within a dynamic agricultural landscape, and discuss its implications for pest management with a focus on wireworms. For this purpose, we first developed a spatially explicit and mechanistic model describing the pest population dynamics in both aerial and soil compartments involved along its life cycle. Larvae and adult mortality, larval development, oviposition, and adult movements (diffusion and advection) were the main processes considered. Model parameterisation stems from an extensive review of the literature dealing with the biology and ecology of wireworms. Then, landscape elements comprising grasslands and vulnerable habitats (cropped fields) were characterised by their carrying capacity. Combining these two framework components, we investigated the interplay of landscape spatiotemporal dynamics, considering grasslands as pest sources, and of species-specific traits (e.g. life cycle duration) on field infestation levels, as illustrated by the conceptual diagram (Fig. 1). We also highlighted how the balance between diffusion and advection movements drives the population flows on both sides of the boundaries between grassland and field crops. Finally, we demonstrated that spatiotemporal connectivity between grasslands significantly affects the pest infestation levels within crops.

Providing new insights into the role of grasslands in pest infestation in a dynamic agricultural mosaic, our findings bring an original contribution to the search for innovative landscape-scale strategies for pest management.

2. Material and methods

2.1. Population dynamics model

Insect pests considered in this study cause crop damage during larval development in soil but disperse as adults by walk and flight. Both the aboveground and the belowground compartments were explicitly considered. The population dynamics was derived along two spatial dimensions $\mathbf{x}=(x,y)$ through a set of reaction-advection-diffusion equations modelling the following biological and ecological mechanisms:

- the emergence of adults from mature larvae,
- the adult random and directed motions,
- the oviposition,

- the adult mortality,
- the larval development,
- and the larval density-dependent mortality.

Briefly, adults oviposit at a constant rate π, thereby increasing the belowground population that ages at a constant velocity c, undergoing a density-dependent mortality. Wireworms reaching the critical age m_c emerge as adults that disperse across the landscape to find resources and suitable habitat. The model can be formalised as a system of partial differential equations: for $t > 0$ and $0 < m < m_c$

$$\begin{cases} \partial_t A(\boldsymbol{x},t) = \tau(t)B(\boldsymbol{x},t,m_c) + D\Delta_{\boldsymbol{x}} A(\boldsymbol{x},t) - \vec{u}(\boldsymbol{x},t)\cdot\nabla_{\boldsymbol{x}} A(\boldsymbol{x},t) - \mu_A A(\boldsymbol{x},t) & (1) \\ \partial_t B(\boldsymbol{x},t,m) = -c\partial_m B(\boldsymbol{x},t,m) - \mu_B \left(\dfrac{\bar{B}(\boldsymbol{x},t)}{K(\boldsymbol{x},t)}\right)^{\beta} B(\boldsymbol{x},t,m) & (2) \end{cases}$$

with the dynamical boundary conditions w.r.t the maturation variable

$$\begin{cases} \partial_t B(\boldsymbol{x},t,0) = \pi A(\boldsymbol{x},t) - \mu_B \left(\dfrac{\bar{B}(\boldsymbol{x},t)}{K(\boldsymbol{x},t)}\right)^{\beta} B(\boldsymbol{x},t,0) & (3) \\ \partial_t B(\boldsymbol{x},t,m_c) = -c\partial_m B(\boldsymbol{x},t,m_c) - \tau(t)B(\boldsymbol{x},t,m_c) - \mu_B \left(\dfrac{\bar{B}(\boldsymbol{x},t)}{K(\boldsymbol{x},t)}\right)^{\beta} B(\boldsymbol{x},t,m_c) & (4) \end{cases}$$

Here, $\bar{B}(x,t) = \int_0^{m_c} B(x,t,m)dm$ represents the total belowground population, $\Delta_{\boldsymbol{x}} = \partial_x^2 + \partial_y^2$ is the Laplace operator (diffusion over **x**), $\nabla_{\boldsymbol{x}} = \begin{pmatrix}\partial_x \\ \partial_y\end{pmatrix}$ and ∂_m are the advection operators over **x** and *m* (the maturity dimension), where $\partial_x, \partial_y, \partial_m$ denote the partial derivatives with respect to *x*, *y* and *m*.

Model parameters and their meaning are described in Table 1. Model interpretation is fully presented in the following paragraphs. The state variables A and B respectively denote the density of click beetles aboveground, and the density of wireworms in soil. Actually, B encapsulates all belowground development stages (larval instars, pupae) and is referred to as wireworms thereafter for the sake of simplification. The dynamical condition at $m = 0$ (Eq. 3) reflects both the oviposition and the growth of individuals who did not start to mature, while the condition in $m = m_c$ (Eq. 4) takes into account the accumulation of individuals in the last class of maturation before emergence.. As initial conditions, the aboveground population was set to zero and the age distribution of larvae was obtained from a preliminary model simulation run over 15 years on a homogeneous landscape. The model was solved using operator splitting (Press et al., 2007, Chapter 20.3.3). Alternating-direction implicit method solves the diffusion (Press et al., 2007, Chapter 20.3.2), while a forward Euler scheme is used for the reaction terms, and an upwind scheme for the advection terms (Press et al., 2007, Chapter 20.1). We considered the spatial domain under study as a closed system (i.e. equal inflowing and outflowing pest populations), thereby applying Neumann (reflecting) boundary conditions at the edges of the spatial domain. All developments were made with the R programming language (R Core Team, 2018).

Adult emergence and motions

Click beetles emerge during spring. In accordance, we defined their emergence rate as a time-dependent function $\tau(t)$ (cf. §2.2 and Suppl. Material 1) in Equation 1.

As recent findings suggested that wireworms do not move from field to field (Schallhart et al., 2011), we considered that only adults contribute to the spatial redistribution of populations. We assumed that adult motions included two components: a random component expressed through the diffusion term in Equation 1, involving D the homogeneous diffusion coefficient; and a directed component expressed through the advection term in Equation 1 and involving $\vec{u}$ the advection velocity. Regarding the latter component, we assumed that click beetles move across the landscape based on the habitat quality they perceive in their neighbourhood. We defined the local habitat quality $h(\boldsymbol{x}, t)$ as a function of local carrying capacities $K(\boldsymbol{x}, t)$:

$$h(\boldsymbol{x}, t) = \frac{K(\boldsymbol{x}, t) - K_{min}}{K_{max} - K_{min}} \tag{5}$$

where K_{max} (resp. K_{min}) refers to the most favourable (resp. unfavourable) habitat for wireworms. As did Bourhis et al. (2017), we derived the perception of the landscape habitat quality, noted $h_p(\boldsymbol{x}, t)$, from a convolution of a perception kernel (linear inverse distance weighting filter) with the mapping of local habitat quality:

$$h_p(\mathrm{x}, t) = \int\limits_{\substack{x_i \epsilon \Omega \\ |x - x_i| < \gamma}} \left(1 - \frac{|\boldsymbol{x} - \boldsymbol{x_i}|}{\gamma}\right) h(\boldsymbol{x_i}, t) d\boldsymbol{x_i} \Bigg/ \int\limits_{\substack{x_i \epsilon \Omega \\ |x - x_i| < \gamma}} \left(1 - \frac{|\boldsymbol{x} - \boldsymbol{x_i}|}{\gamma}\right) d\boldsymbol{x_i} \tag{6}$$

with Ω the whole spatial domain, and γ the distance beyond which habitat quality is no longer perceived by click beetles. Finally, the advection velocity

$$\vec{u}(\boldsymbol{x}, t) = V_{max} \frac{\nabla_{\boldsymbol{x}} h_p(\boldsymbol{x}, t)}{max\left|\nabla_{\boldsymbol{x}} h_p(\boldsymbol{x}, t)\right|} \tag{7}$$

reaches its maximum speed V_{max} where the gradient of the potential function $h_p(\boldsymbol{x}, t)$ is maximum.

Oviposition

Although the oviposition rate may vary among habitats (Brian, 1947), it was assumed here independent of space (i.e. land use and associated carrying capacity) and constant over the whole duration of the adult life. New-borns fall within the belowground population with age 0 (Eq. 3).

Adult mortality

A constant mortality rate μ_A was applied to the aboveground compartment of the model.

Larval development

The belowground population distributes along an ageing axis. The population ages according to a constant coefficient c. When reaching the critical maturity m_c, larvae can emerge as click beetles.

Larval mortality

Uncultivated areas, such as grasslands or grassy strips, are acknowledged as favourable habitats for both adults and larvae of click beetles (Brian, 1947; Miles, 1942), providing sufficient food and humid conditions (Roebuck et al., 1947), therefore wireworm populations thrive in these areas. On the contrary, wireworm populations reach much lower infestation levels in cropped fields, where they nevertheless damage vulnerable crops (Miles, 1942). In our model, we assumed that the carrying capacity $K(x,t)$ is a proxy for habitat quality, and that larval mortality relies on a constant component μ_B weighted by a density-dependent factor. While the constant component provides a stationary annual dynamics within the landscape, the density-dependent term ensures that the population dynamics is centred on the carrying capacity. The exponent β controls the dynamics inertia, i.e. the speed at which the local population converges towards the local carrying capacity. For the sake of simplicity, larval mortality was independent of the age. Note that the reaction term departs from the canonical logistic growth model as the density dependence applies on larval mortality only rather than on larval population growth rate (which also depends on adult oviposition rate), emphasising that population is limited by larval competition for food rather than by adult competition for oviposition sites.

2.2. Model parameterisation

Land-use dependent carrying capacities (K_G and K_C)

We considered two types of land use: grasslands, known as favourable habitats (Furlan, 2004; Parker and Howard, 2001), and cropped fields.

Regarding grasslands, we set the carrying capacity K_G to 2000 individuals per square meter (thereafter ind/m^2) based on field studies carried out before the common access to chemical pesticides (Roebuck et al., 1947; Ross et al., 1947; Salt and Hollick, 1944). Based on a thorough study of two pastures at least 10-year old and regularly cut for hay, Salt and Hollick (1944) estimated densities about 850 and 2000 ind/m^2. Locally, they even observed densities reaching 6000 ind/m^2 in both pastures. Within other pastures less intensively sampled, they found about 2500 ind/m^2 on average. Roebuck et al. (1947) studied intensively the infestation level of an old meadow, and determined a density of about 300 ind/m^2 by the hand-sorting method. Following Salt and Hollick (1944) who consider that this method underestimates densities by two thirds, the actual infestation could be of about 1000 ind/m^2. Ross et al. (1947) studied six permanent pastures grazed and regularly hayed, and assessed a density of about 1000 ind/m^2.

In cropped fields, we set the carrying capacity K_C to 120 ind/m^2, i.e. about one order of magnitude smaller than K_G, and fairly close to values indicated by Roebuck (1924). Indeed, Roebuck (1924) studied the decline of wireworm populations in newly set up crop fields with repeated ploughing, and found average population density of 102, 80, 56 and 32 ind/m² the 1rst, 2nd, 3rd and 4rth year after ploughing from grass, respectively.

Belowground population maturation (c)

Wireworm species differ greatly from one another in their biology and ecology (Furlan, 2005; Ritter and Richter, 2013), in particular as regards the duration of their biological cycle. In France, four species from the genus *Agriotes* are responsible for most economical crop damage. Among them, *A. lineatus*, *A. obscurus* and *A. sputator*, predominantly present in the northern regions, exhibit a long life cycle (duration of larval stage of about 4 years), whereas *A. sordidus*, mainly found in south-western regions, exhibits a short life cycle (duration of larval stage of about 2 years). In our study, we set the duration of the larval stage (c^{-1}) at 2 years for short life-cycle species and at 4 years for long life-cycle species.

Emergence rate

Studies relative to the date of emergence of *Agriotes* click beetles are fairly consistent. For instance, in Austria, Landl et al. (2010) observed that the emergence of *A. lineatus* began at the end of April, which is concordant with the observations of other authors from Eastern Europe and from western Canada (Vernon et al., 2001). Regarding *A. ustulatus*, *A. lineatus* and *A. obscurus*, Parker and Howard (2001) in United Kingdom reported emergences starting at mid-April and adults being captured until mid-July (hence, they probably emerged until mid-June), while in Germany, Sufyan et al. (2007) observed that the swarming period lasted from late April to the end of August (for *A. lineatus* and *A. obscurus*). Although most authors reported two periods of adult activity, one main in May and one weaker in June-July (Landl et al., 2010; Sufyan et al., 2007), we simply modelled adult emergence as a continuous process spanning over a period governed by the cumulative degree days (see Supplementary Material 1). In our study, the emergence of click beetles spans from late April to the beginning of June, with a peak of emergence located towards the middle of the period of emergence (i.e. mid-May). Over this period, all wireworms at the critical age have emerged (see Supplementary Material 1, Fig. A1B).

Belowground mortality (μ_B,β)

Two main model parameters govern the larval mortality, namely the mortality rate μ_B and the inertia exponent β. The mortality rate was determined by means of a preliminary optimisation procedure before each simulation, given all other parameter values, such that larval density oscillated yearly around the carrying capacity in any homogeneous landscape. β was estimated empirically to 0.2 from infestation data collected in arable lands by Roebuck (1924) over 8 years. As shown in a sensitivity analysis (see Supplementary Material 2), despite scarce knowledge on this parameter β, it has a significant effect on the model output and its estimation would probably deserve further attention.

Adult dispersion (D, V_{max})

Literature provides a limited amount of information regarding click-beetle dispersal. In particular, diffusion and advection processes can seldom be disentangled. Brian (1947) observed that *A. obscurus* and *A. lineatus* (but not *A. sputator*) frequently flew in a glass cage experiment. Crozier et al. (2003) reported that these species can be strong fliers, able to perform mass flights, travelling approximately 5 to 10 km/h for distances ranging from less than 1 m to 100 m on one occasion and with an average flight covering 2 to 3 m. More recently, Blackshaw and Hicks (2013) concluded that *Agriotes spp.* disperse widely and may originate from adjacent fields. Many studies have attempted to provide quantitative estimates of click-beetle dispersal capacity, generally using mark-recapture experiments with pheromone traps. Blackshaw et al. (2017) recaptured individuals (*A. lineatus*, *A. obscurus*, *A. sputator*) at 1m from release point after 1h, and at 30m after 19h. Schallhart et al. (2009) studied the isotopic signature of *A. obscurus* beetles captured in pheromone traps located in a grassland adjacent to a maize field: 13% of individuals captured 80m inside the grassland plot had a signature characteristic of their maize field origin. Based on this knowledge, we set the diffusion coefficient to 72 m²/day, hence producing a mean dispersion radius of 15m in one day, 21m in two days, etc. (Shigesada and Kawasaki (1997), page 38). The advection speed was set to 10 m/day.

Perceptual range (γ)

We assumed that adult click beetles could perform directed motions as responses to distant stimuli (e.g. olfactory stimuli). Advection processes may result from foraging for food or laying sites, from searching for a sexual partner, etc. In our model, we described advection at the population level as a tendency to move along a gradient of increasing habitat quality expressed in terms of carrying capacities. In particular, as wireworms thrive in grasslands, we expect adult click beetles to disperse preferentially towards nearby grassy areas. We set the perceptual range (i.e. the distance beyond which habitat quality is no longer perceived by click beetles) to 10 m. This estimated value mainly stems from studies dealing with pheromone attractiveness for click beetles, since it is the only advection process for which literature provides some guidance. Sufyan et al. (2007) assessed the range of attractiveness of pheromone traps (for both species *A. lineatus* and *A. obscurus*) through a mark – recapture experiment. They recaptured > 60% and < 10% of beetles in pheromone traps placed at 2 and 60 m from their release point, respectively. In a later experiment, Sufyan et al. (2011) estimated the maximum distance of perception of a pheromone trap to be around 15-20 m. Blackshaw et al. (2018) studied the attractive range of traps baited with *A. obscurus* pheromone to male beetles in both still air and wind conditions. They found that the attraction distance was less than 5m in still air but increased with airflow.

Aboveground population mortality (μ_A)

Adult life expectancy varies among studies. Brian (1947) observed that longevity of *A. obscurus* on various crops ranged from 69 to 84 days for females and from 45 to 75 days for males. Regarding *A.*

ustulatus, Hinkin (1983) reported an average longevity of 28 days for females and 19 days for males, while Furlan (1996) measured an adult lifespan of 24 (SD=5) days for females. More recently, Hicks and Blackshaw (2008) as well as Blackshaw et al. (2017) performed mark–release experiments on click beetles ; they showed respectively that adults (males and females combined) can survive for at least 45 and 25 days. Accordingly, in our model, based on these elements and in accordance with our own field observations, we set the adult average lifespan to 25 days for both sexes.

Oviposition rate (π)

Most authors have studied oviposition under laboratory conditions. Brian (1947) found an average fecundity ranging from 30 to 150 (*A. obscurus*) depending on the crop (flax, potato and wheat were associated with low fecundity while grasslands of *Lolium*, *Festuca* and *Agrostis* were associated with high fecundity). Miles and Cohen (1941), Cohen (1942), and Furlan (1996), reported an average number of eggs laid per female of 109 in *A. obscurus* (min=78, max=186), 103 in *A. obscurus* and 78 in *A. ustulatus* (SD=27.9, min=52, max=140). Accordingly, we considered fecundity to be of 80 eggs per female over its lifespan (25 days as mentioned in the previous paragraph). Considering that sex ratio tends towards 1:1 (Blackshaw et al., 2017; Furlan, 1996), the oviposition rate was set to (80/2)/25=1.6 eggs per capita per day.

2.3. Landscape contexts

We defined four landscape contexts (Fig. 2 and Fig. 3) to investigate the processes driving the colonisation of vulnerable habitats (arable crops) characterised by a habitat quality lower than the one associated with grasslands (favourable habitats). The first three contexts are shown in Fig.2: a homogeneous cropped field cultivated over 2 years (Fig. 2A), a grassland in the field history (Fig. 2B) or in the neighbourhood of the cropped field (Fig. 2C). Finally, Fig. 3 describes the fourth context where we compared two dynamic landscapes Ω_1 and Ω_2 exhibiting the same duration of land use over time (landscape composition) but through contrasted spatial configurations.

3. Results

3.1. Population dynamics in a homogeneous landscape context

Fig. 4 shows the dynamics of above- and belowground populations in the simple case of a homogeneous landscape (Fig. 2A) comprising vulnerable cropped fields only. Simulation starts in winter with a null aboveground population and a larval density at equilibrium, hence 120 individuals per square meter.

Until the emergence of adults, the only process at stake is larval mortality, which reduces the belowground population to about 90 individuals per square meter. Adults emerge in early spring producing an increase in the aboveground population density with a peak value determined by (i) the density of mature larvae at the onset of the emergence period, (ii) climate and (iii) adult life expectancy. It is followed by a decrease resulting from the constant mortality rate μ_A. About 65 days after the last emergence, the aboveground population becomes extinct. This pattern repeats over the years.

After adults have emerged, they disperse and lay eggs, thus refilling the belowground population compartment that increases, reaches a maximum at the end of the oviposition period, and then decreases due to larval mortality. After a few years a stationary pattern occurs.

3.2. Wireworm dynamics with grassland in field history

The effect of a grassland in field history (Fig. 2B) on the wireworm population density is illustrated on Fig. 5 for two pest life cycle durations: 2 years (short life cycle) and 4 years (long life cycle). Both dynamics exhibit the periodic behaviour described in the previous section (§3.1). At time 0, the field is converted to grassland, which translates into an important rise in habitat quality resulting in a subsequent wireworm population increase.

In Fig. 5, we compare the dynamics of a short life cycle population and a long life cycle population. The amplitudes of intra-annual oscillations are more important for the former. On one hand, the proportion of the belowground population that emerges as adults is larger in the case of a short life cycle (about half the population emerges each year) than in that of a long life cycle (about a quarter emerges each year). Given that oviposition rate is independent from life-cycle duration in our model, the increase in wireworm density is greater for short cycle species. On the other hand, once the aboveground population has vanished, high larval density results in a strong mortality until the next laying period.

In summary, short life cycle wireworms react more promptly to changes in habitat quality, thereby leading to higher infestation levels in temporary grasslands. Conversely, after grassland conversion into crop, wireworm density reaches more quickly the new current carrying capacity K_C in the case of short cycle species. Note that these conclusions stem from our model hypotheses, where a difference in life cycle duration results in different mortality rates (land-use carrying capacities and oviposition rates being unchanged).

3.3. Wireworm dynamics in a field with a newly set-up grassland in its neighbourhood

We simulated the effect of the conversion of half of a crop field into permanent grassland (Fig. 2C). Fig. 6 shows the wireworm density along a direction orthogonal to the grassland/crop field border (40 meters on both sides), over a period of 10 years, and for a range of values of the diffusion coefficient D, the maximal advection speed V_{max} and the perceptual range γ. Diffusion tends to homogenise wireworm densities in space, while advection entails population movements from low towards high carrying capacity places.

In Fig. 6A, only diffusion applies. Wireworm densities increase from K_C (120 ind/m^2) towards K_G (2000 ind/m^2) along the 10 years on the side covered with grassland. Adult click beetle diffusion results in an increase in wireworm density in the adjacent cropped field with an intensity that vanishes away from the ecotone.

In the next six panels (Figs. 6B-G), diffusion and advection have antagonistic effects. Advection fosters population displacements from low towards high quality habitat, whereas diffusion promotes a homogenisation of the densities.

During the transient period before reaching equilibrium density in the grassland, the set-up of a grassland can have opposite effects on wireworm density in crop, depending on the advection strength (Figs. 6B-D). Indeed, a high maximal advection speed V_{max} results in a reduction of wireworm density inside the cropped field due to advection effect exceeding diffusion effect. For low maximal advection speed, the opposite occurs. Thus, 5 years after grassland set-up, wireworm density can be greater (Fig. 6B), similar (Fig. 6C) or lower (Fig. 6D) than the initial density in the crop. Changes in perceptual range have similar effects than changes in maximal advection speed (Figs. 6B-G).

A mechanistic effect of the population redistribution must be noted here. Unlike advection, diffusion is an inherently density-dependent process. As population increases within the grassland, so does the diffusion intensity, mechanically. The neighbourhood effect of grassland is therefore changing throughout the season, as diffusion takes more control over the redistribution.

3.4. Effect of spatiotemporal distribution of grasslands on wireworm densities

We considered two dynamic landscape contexts Ω_1 and Ω_2 spanning over four years (Fig. 3). Landscape composition over time (i.e. the proportions of cropped field and grassland over the duration of the virtual experiment) remains unchanged, while spatial configurations differ. The land cover within plot A is identical over the years in Ω_1 and Ω_2, however the mean wireworm densities differ all along the four-year period. Final densities deviate by 10%. Indeed, in Ω_1, wireworm density increases in plot B the first two years due to a favourable habitat (grassland). Subsequently, when plot A turns into grassland whereas plot B switches to cropped field, both advection and diffusion induce aboveground population movements from plot B to plot A, resulting in a meaningful wireworm increase once oviposition has been completed, that combines with the expansion of wireworm density due to the high carrying capacity associated with grassland. In Ω_2, simultaneous evolution of densities in plots A and B do not favour any population flows.

4. Discussion

4.1. Model relevance and novelty

Insect pests inflict severe damage to agricultural crops, in spite of the intense use of agrochemical inputs. In fragmented and changing environment, as most agricultural landscapes are, the movement of insect pests has a strong influence on their abundance and spatiotemporal distribution, hence the extent of the inflicted crop damage (Mazzi and Dorn, 2012). Thus, understanding dispersal mechanisms may help design effective pest management strategies. Here, we developed a spatially explicit mechanistic model to describe the population dynamics of insect pests inflicting crop damage while developing in soil, and spreading across the landscape as adults. We accounted for both aboveground and belowground population dynamics. To date, few studies have considered the link between both compartments though many species of ecological and economic importance have both above- and belowground life cycle stages (Benefer et al., 2012). Therefore, our developments could serve in investigations dealing with a wide variety of soil-dwelling insect pests.

Combined with spatial representations of dynamic landscape contexts, our population dynamics model enables the investigation of the spatial redistribution of populations over time given the spatial distribution of habitat quality and species life-history traits (dispersal ability, life cycle duration, etc.). We thus provide an appropriate framework to study how the arrangement of grassy landscape elements in space and time can mitigate crop infestation by soil-dwelling pests.

4.2. The dynamics of grassland as reservoirs or sources of pests

In our results, we highlight (§3.2) the influence of the legacy of previous land uses on the current wireworm infestation level. This is well documented in plant sciences, e.g. regarding soil suppressiveness (Bailey et al., 2009; Postma et al., 2010), effects of biofumigation (Matthiessen and Kirkegaard, 2006), etc. Here we show that given its habitat favourability, the presence of a grassland in plot history entails the build-up of wireworm populations, and acts as a reservoir (Fig. 5). Interestingly, species life-history traits mitigate the changes in population density in response to land use change. Indeed, short life cycle species may be more responsive to land use change (Fig. 5).

At a broader spatial scale (landscape context, §3.3), the wireworm population response to the presence of a grassland in an adjacent field relies on the pest life-traits (dispersal ability, life cycle duration), habitat quality, and habitat patch dynamics. Local habitat quality governs the wireworm density in the field core, whereas density in borders results from the diffusion and advection of click beetles between habitats over time (Fig. 6). When advection is high, the inner edge of a low-quality habitat is temporary depleted at the expense of the adjacent higher quality habitat. However, diffusion (which tends to homogenise density) usually plays the opposite effect. Hence, wireworm density is ruled by the trade-off between these two antagonistic dispersal mechanisms. In a grassland where wireworm density has reached the local carrying capacity, diffusion at the ecotones will be high and sustain the colonisation of neighbouring crops. Therefore, the presence of a temporary versus permanent grassland in the neighbourhood may significantly change the outcome in terms of spatial distribution of wireworm populations. If advection is strong and grasslands highly favourable, temporary grasslands may act as pseudo-sinks, while permanent grasslands act as sources for click beetle populations. This clearly emphasizes the relevance of managing grassland regimes.

4.3. Implications in terms of pest management strategies

Our study outlines the complex link between pest colonisation patterns within the agricultural mosaic and the entanglement of habitats. The results presented in §3.4 (also Fig. 3 and Fig. 7) clearly support that the spatiotemporal arrangement of grasslands opens avenues for the management of soil-dwelling insect pests. As stated in previous studies, habitat manipulation can be successfully implemented to enhance the effectiveness of natural enemies (Landis et al., 2000), and mitigate the impacts of invasive arthropod pests (Jonsson et al., 2010). Yet here we emphasize the importance of the dynamics of land use spatial configurations. For example, click beetle spillover between a grassland and a neighbouring cropped field depends on the population replenishment in the favourable habitat: a recently installed grassland may act as a pseudo-sink, whereas a permanent grassland may act as a source. This finding evidences that depending on the spatiotemporal dynamics of habitat distribution, the role of a particular landscape element can switch from favourable to detrimental to pest population in fields. Consequently, pest management strategies relying on habitat spatial connectivity also call for the consideration of spatiotemporal continuity (or discontinuity).

Our modelling framework helps apprehending the effects of agroecological infrastructures (green veins, grassy strips, etc.) on pest communities. Grassy landscape elements are well known reservoirs for beneficial organisms (Blackshaw et al., 2017) but can also increase wireworm pressure. Our modelling approach is precious to identify the appropriate grassland management regime that provides the best trade-off to balance wireworm damage and a bundle of ecosystem services such as sustaining natural pest control, prevention against soil erosion, etc. (Hermann et al., 2013). Regarding the broad spatial and temporal scales related to the functioning of agroecosystems, frameworks enabling virtual experiments provide a relevant, if not unique, way to anticipate the complex trade-off between beneficial and detrimental effects associated with the adoption of agri-environmental schemes.

4.4. Limitations and perspectives

The reaction-diffusion-advection model we conceived to explore the main mechanisms at stake in the colonisation of vulnerable crops at the landscape scale is parsimonious. Model parameters were set based on a comprehensive review of literature dealing with the biology and the ecology of click beetles and their larvae. Nevertheless, knowledge gaps complicated the parameterisation step. For instance, knowledge on click beetle dispersal is still rudimentary, and though it has been evidenced that they can move across adjacent plots (Schallhart et al., 2009), some unpublished research suggest they may disperse on a much wider scale than currently mentioned (Lorenzo Furlan, personal communication). Dispersal patterns between uncultivated areas (grasslands) and cropped fields remain insufficiently documented. Moreover, in our approach we used the carrying capacity as a proxy for habitat quality. However, most experimental data we found date back to the first half of the twentieth century (Roebuck, 1924; Roebuck et al., 1947; Ross et al., 1947; Salt and Hollick, 1949, 1944) and limit to grasslands. Their current accuracy can be questioned given changes in habitat properties and possibly in pest life-history traits that have occurred since then. Further experiments to assess the carrying capacities associated with the main land uses occurring in the current agricultural landscapes are definitely required.

Furthermore, we did not explicitly consider crop management practices within our modelling framework, but rather treated them as an implicit component of the habitat quality associated with each land use. However, there is clear evidence that farming practices influence insect abundance (see for example Puech et al., 2014 and Kladivko, 2001). Soil cultivation directly affects the number and size of wireworms (Salt and Hollick, 1949). Interestingly, Furlan et al. (2020) demonstrated that an accurate ploughing timing of meadows, when rotation includes meadows, provides an efficient management tactic to prevent soil-pest damage to maize crops. Thus, combining virtuous cropping practices and a relevant strategy for the spatiotemporal arrangement of grasslands derived from our modelling framework may provide a holistic integrated pest management approach, as well as a credible alternative to chemical pesticides, in accordance with the principles of the European Directive 2009/128/EC on the sustainable use of pesticides (Barzman et al., 2015; Lorenzo Furlan et al., 2017).

Finally, in our study we examined various situations dealing with the presence of grassland in plot history (legacy effect) or neighbourhood (neighbourhood effect), as well as in dynamic landscape contexts (spatiotemporal effect). Such analytic landscape contexts allowed to address the role of grassland as sources of soil-dwelling pests, yet clearly do not reflect the real complexity of the agricultural mosaic, that stems from stakeholder decisions under agronomical, economical, socio-technical constraints. The representation of agroecosystems is still a research issue (Poggi et al., 2018b), and some model representations encompass more or less explicitly these constraints (Bareille et al., 2020; Martel et al., 2017; Ricci et al., 2018). Hence, a next research avenue consists in the exploration of suppressive patterns in simplified but realistic agricultural landscapes, generated under agronomic constraints at the farm or landscape scales.

5. Conclusion

Using mechanistic modelling, we illustrated how species life-history traits interact with spatiotemporal arrangement of habitats in agricultural landscape to shape pest abundances in vulnerable crops. Through neighbouring effect, legacy effect or their interaction, the distribution of grassy elements across the landscape has discernible effects on wireworm abundance in crops. We showed here that such endeavour is knowledge-hungry as it must be informed by some critical pest traits, but also a measurable alternative to a chemically driven crop protection. Our modelling framework allowed us to explore the ecosystem service of crop pest reduction that grasslands could provide through their ecological role on legacy effect and movements of pest populations (pseudo-sink vs source). Obviously, other ecosystem services provided by grasslands, such as biological control conservation, could be integrated in a common framework offering exciting perspectives for the management of the trade-offs in a bundle of services and to identify situations or practices that allow switching from antagonism to synergy.

Acknowledgements

This study was carried out as a part of the project STARTAUP “Design of alternative strategies for controlling wireworm damage in maize crops” with financial support from The Foundation for Research on Biodiversity (FRB, project neonic-33). SP and MS acknowledge the INRAE metaprogramme “Sustainable Management of Crop Health” for funding the ESPACE project. YM thanks the Institute for Genetics, Environment and Plant Protection (IGEPP, INRAE) for welcoming him as a temporary researcher during the year 2017-2018. SP, RLC and MP thank partners of the ElatPro project (ERA-NET C-IPM, 2016-2019, grant no.:618110) for meaningful discussions.

Sample CRediT author statement

Sylvain Poggi: Conceptualization, Methodology, Software, Writing – Original Draft, Funding acquisition, Supervision **Mike Sergent:** Methodology, Software, Writing – Original Draft, Visualization **Youcef Mammeri:** Methodology, Software, Formal Analysis, Writing – Review & Editing **Manuel Plantegenest:** Conceptualization, Methodology, Writing – Review & Editing **Ronan Le Cointe:** Conceptualization, Writing – Review & Editing, Funding acquisition **Yoann Bourhis:** Methodology, Software, Formal Analysis, Writing – Review & Editing

References

Aviron, S., Lalechère, E., Duflot, R., Parisey, N., Poggi, S., 2018. Connectivity of cropped vs. semi-natural habitats mediates biodiversity: A case study of carabid beetles communities. Agriculture, Ecosystems & Environment 268, 34–43. https://doi.org/10.1016/j.agee.2018.08.025

Bailey, D.J., Paveley, N., Spink, J., Lucas, P., Gilligan, C.A., 2009. Epidemiological analysis of take-all decline in winter wheat. Phytopathology 99, 861–868.

Balachowsky, A., Mesnil, L., 1935. Les taupins, in: Les Insectes Nuisibles Aux Plantes Cultivées. Balachowsky A., Paris, pp. 754–787.

Bareille, F., Boussard, H., Thenail, C., 2020. Productive ecosystem services and collective management: Lessons from a realistic landscape model. Ecological Economics 169, 106482. https://doi.org/10.1016/j.ecolecon.2019.106482

Barzman, M., Bàrberi, P., Birch, A.N.E., Boonekamp, P., Dachbrodt-Saaydeh, S., Graf, B., Hommel, B., Jensen, J.E., Kiss, J., Kudsk, P., Lamichhane, J.R., Messéan, A., Moonen, A.-C., Ratnadass, A., Ricci, P., Sarah, J.-L., Sattin, M., 2015. Eight principles of integrated pest management. Agronomy for Sustainable Development 35, 1199–1215. https://doi.org/10.1007/s13593-015-0327-9

Benefer, C.M., Knight, M.E., Ellis, J.S., Hicks, H., Blackshaw, R.P., 2012. Understanding the relationship between adult and larval *Agriotes* distributions: The effect of sampling method, species identification and abiotic variables. Applied Soil Ecology 53, 39–48. https://doi.org/10.1016/j.apsoil.2011.11.004

Blackshaw, R.P., Hicks, H., 2013. Distribution of adult stages of soil insect pests across an agricultural landscape. Journal of Pest Science 86, 53–62. https://doi.org/10.1007/s10340-012-0413-6

Blackshaw, R.P., van Herk, W.G., Vernon, R.S., 2018. Determination of *Agriotes obscurus* (Coleoptera: Elateridae) sex pheromone attraction range using target male behavioural responses: Pheromone attraction range of *Agriotes obscurus*. Agr Forest Entomol 20, 228–233. https://doi.org/10.1111/afe.12249

Blackshaw, R.P., Vernon, R.S., 2006. Spatiotemporal stability of two beetle populations in non-farmed habitats in an agricultural landscape: *Agriotes* distribution in an agricultural landscape. Journal of Applied Ecology 43, 680–689. https://doi.org/10.1111/j.1365-2664.2006.01167.x

Blackshaw, R.P., Vernon, R.S., Thiebaud, F., 2017. Large scale *Agriotes* spp. click beetle (Coleoptera: Elateridae) invasion of crop land from field margin reservoirs: Click beetle dispersal. Agricultural and Forest Entomology. https://doi.org/10.1111/afe.12228

Bourhis, Y., Poggi, S., Mammeri, Y., Cortesero, A.-M., Le Ralec, A., Parisey, N., 2015. Perception-based foraging for competing resources: Assessing pest population dynamics at the landscape scale from heterogeneous resource distribution. Ecological Modelling 312, 211–221. https://doi.org/10.1016/j.ecolmodel.2015.05.029

Bourhis, Y., Poggi, S., Mammeri, Y., Le Cointe, R., Cortesero, A.-M., Parisey, N., 2017. Foraging as the landscape grip for population dynamics—A mechanistic model applied to crop protection. Ecological Modelling 354, 26–36. https://doi.org/10.1016/j.ecolmodel.2017.03.005

Bressan, A., Moral Garcia, F.J., Sémétey, O., Boudon-Padieu, E., 2010. Spatio-temporal pattern of *Pentastiridius leporinus* migration in an ephemeral cropping system. Agricultural and Forest Entomology 12, 59–68. https://doi.org/10.1111/j.1461-9563.2009.00450.x

Brian, M.V., 1947. On the Ecology of Beetles of the Genus Agriotes with Special Reference to A. Obscurus. The Journal of Animal Ecology 16, 210. https://doi.org/10.2307/1496

Cohen, M., 1942. Observations on the biology of Agriotes Obscurus L.: I. The adult insect. Annals of Applied Biology 29, 181–196. https://doi.org/10.1111/j.1744-7348.1942.tb07586.x

Crozier, S., Tanaka, A., Vernon, R.S., 2003. Flight activity of Agriotes lineatus L. and A. obscurus L. (Coleoptera: Elateridae) in the field. Journal of the Entomological Society of British Columbia 100, 91–92.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65, 169. https://doi.org/10.2307/3544901

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x

Furlan, L., 2005. An IPM approach targeted against wireworms: What has been done and what has to be done. IOBC/WPRS Bull. 28, 91–100.

Furlan, L., 2004. The biology of *Agriotes sordidus* Illiger (Col., Elateridae). Journal of Applied Entomology 128, 696–706. https://doi.org/10.1111/j.1439-0418.2004.00914.x

Furlan, L., 1998. The biology of *Agriotes ustulatus* Schaller (Col., Elateridae). II. Larval development, pupation, whole cycle description and practical implications. Journal of Applied Entomology 122, 71–78.

Furlan, L., 1996. The biology of *Agriotes ustulatus* Schäller (Col., Elateridae). I. Adults and oviposition. Journal of Applied Entomology 120, 269–274. https://doi.org/10.1111/j.1439-0418.1996.tb01605.x

Furlan, L., Benvegnù, I., Chiarini, F., Loddo, D., Morari, F., 2020. Integrated Pest Meadow-ploughing timing as an integrated pest management tactic to prevent soil-pest damage to maize. European Journal of Agronomy 112, 125950. https://doi.org/10.1016/j.eja.2019.125950

Furlan, L., Contiero, B., Chiarini, F., Colauzzi, M., Sartori, E., Benvegnù, I., Fracasso, F., Giandon, P., 2017. Risk assessment of maize damage by wireworms (Coleoptera: Elateridae) as the first step in implementing IPM and in reducing the environmental impact of soil insecticides. Environmental Science and Pollution Research 24, 236–251. https://doi.org/10.1007/s11356-016-7692-z

Furlan, Lorenzo, Vasileiadis, V.P., Chiarini, F., Huiting, H., Leskov?ek, R., Razinger, J., Holb, I.J., Sartori, E., Urek, G., Verschwele, A., Benvegn?, I., Sattin, M., 2017. Risk assessment of soil-pest damage to grain maize in Europe within the framework of Integrated Pest Management. Crop Protection 97, 52–59. https://doi.org/10.1016/j.cropro.2016.11.029

Hermann, A., Brunner, N., Hann, P., Wrbka, T., Kromp, B., 2013. Correlations between wireworm damages in potato fields and landscape structure at different scales. Journal of Pest Science 86, 41–51. https://doi.org/10.1007/s10340-012-0444-z

Hicks, H., Blackshaw, R.P., 2008. Differential responses of three *Agriotes* click beetle species to pheromone traps. Agricultural and Forest Entomology 10, 443–448. https://doi.org/10.1111/j.1461-9563.2008.00397.x

Hinkin, S., 1983. Biology and ecology of western click beetle Agriotes ustulatus Schall (Elateridae, Coleoptera). Rasteniev dni nauki 20.

Jonsson, M., Wratten, S.D., Landis, D.A., Tompkins, J.-M.L., Cullen, R., 2010. Habitat manipulation to mitigate the impacts of invasive arthropod pests. Biol Invasions 12, 2933–2945. https://doi.org/10.1007/s10530-010-9737-4

Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil and Tillage Research 61, 61–76. https://doi.org/10.1016/S0167-1987(01)00179-9

Kozina, A., Lemic, D., Bazok, R., Mikac, K.M., Mclean, C.M., Ivezić, M., Igrc Barčić, J., 2015. Climatic, edaphic factors and cropping history help predict click beetle (Coleoptera: Elateridae) (*Agriotes* spp.) abundance. Journal of Insect Science 15, 100. https://doi.org/10.1093/jisesa/iev079

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45, 175–201.

Landl, M., Furlan, L., Glauninger, J., 2010. Seasonal fluctuations in Agriotes spp. (Coleoptera: Elateridae) at two sites in Austria and the efficiency of bait trap designs for monitoring wireworm populations in the soil. Journal of Plant Diseases and Protection 117, 268–272. https://doi.org/10.1007/BF03356372

Martel, G., Aviron, S., Joannon, A., Lalechère, E., Roche, B., Boussard, H., 2017. Impact of farming systems on agricultural landscapes and biodiversity: From plot to farm and landscape scales. European Journal of Agronomy. https://doi.org/10.1016/j.eja.2017.07.014

Martensen, A.C., Saura, S., Fortin, M.-J., 2017. Spatio-temporal connectivity: assessing the amount of reachable habitat in dynamic landscapes. Methods Ecol Evol 8, 1253–1264. https://doi.org/10.1111/2041-210X.12799

Matthiessen, J.N., Kirkegaard, J.A., 2006. Biofumigation and enhanced biodegradation: Opportunity and challenge in soilborne pest and disease management. Critical Reviews in Plant Sciences 25, 235–265.

Mazzi, D., Dorn, S., 2012. Movement of insect pests in agricultural landscapes. Annals of Applied Biology 160, 97–113.

Men, X., Ge, F., Yardim, E., Parajulee, M., 2004. Evaluation of winter wheat as a potential relay crop for enhancing biological control of cotton aphids. BioControl 49, 701–714. https://doi.org/10.1007/s10526-004-5278-z

Miles, H.W., 1942. Wireworms and agriculture, with special reference to *Agriotes obscurus* L. Annals of Applied Biology 29, 176–180. https://doi.org/10.1111/j.1744-7348.1942.tb07585.x

Miles, H.W., Cohen, M., 1941. Investigations on Wireworms and their Control. Report for the Years 1939 and 1940., J. Lanes, agric. Soc. ed. Preston.

Milosavljević, I., Esser, A.D., Crowder, D.W., 2016. Effects of environmental and agronomic factors on soil-dwelling pest communities in cereal crops. Agriculture, Ecosystems & Environment 225, 192–198. https://doi.org/10.1016/j.agee.2016.04.006

Moilanen, A., Hanski, I., 2001. On the use of connectivity measures in spatial ecology. Oikos 95, 147–151. https://doi.org/10.1034/j.1600-0706.2001.950116.x

Parisey, N., Bourhis, Y., Roques, L., Soubeyrand, S., Ricci, B., Poggi, S., 2016. Rearranging agricultural landscapes towards habitat quality optimisation: In silico application to pest regulation. Ecological Complexity 113–122. https://doi.org/10.1016/j.ecocom.2016.07.003

Parker, W.E., Howard, J.J., 2001. The biology and management of wireworms (*Agriotes* spp.) on potato with particular reference to the U.K. Agricultural and Forest Entomology 3, 85–98. https://doi.org/10.1046/j.1461-9563.2001.00094.x

Poggi, S., Le Cointe, R., Riou, J.-B., Larroudé, P., Thibord, J.-B., Plantegenest, M., 2018a. Relative influence of climate and agroenvironmental factors on wireworm damage risk in maize crops. Journal of Pest Science 91, 585–599. https://doi.org/10.1007/s10340-018-0951-7

Poggi, S., Papaïx, J., Lavigne, C., Angevin, F., Le Ber, F., Parisey, N., Ricci, B., Vinatier, F., Wohlfahrt, J., 2018b. Issues and challenges in landscape models for agriculture: from the representation of agroecosystems to the design of management strategies. Landscape Ecol 33, 1679–1690. https://doi.org/10.1007/s10980-018-0699-8

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biological Conservation 141, 1505–1524. https://doi.org/10.1016/j.biocon.2008.03.022

Postma, J., Scheper, R.W.A., Schilder, M.T., 2010. Effect of successive cauliflower plantings and Rhizoctonia solani AG 2-1 inoculations on disease suppressiveness of a suppressive and a conducive soil. Soil Biology & Biochemistry 42, 804–812.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 2007. Numerical recipes, 3rd ed. Cambridge University Press.

Puech, C., Baudry, J., Joannon, A., Poggi, S., Aviron, S., 2014. Organic vs. conventional farming dichotomy: Does it make sense for natural enemies? Agriculture, Ecosystems & Environment 194, 48–57. https://doi.org/10.1016/j.agee.2014.05.002

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricci, B., Petit, S., Allanic, C., Langot, M., Parisey, N., Poggi, S., 2018. How effective is large landscape-scale planning for reducing local weed infestations? A landscape-scale modelling approach. Ecological Modelling 384, 221–232. https://doi.org/10.1016/j.ecolmodel.2018.06.029

Ritter, C., Richter, E., 2013. Control methods and monitoring of *Agriotes* wireworms (Coleoptera: Elateridae). Journal of Plant Diseases and Protection 120, 4–15. https://doi.org/10.1007/BF03356448

Roebuck, A., 1924. Destruction of wireworms. The Journal of Agricultural Science 30, 47–51.

Roebuck, A., Broadbent, L., Redman, R.F.W., 1947. The behaviour of adult click beetles of the genus Agriotes (A. obscurus L., A. lineatus L., and A. sputator L.). Ann Applied Biology 34, 186–196. https://doi.org/10.1111/j.1744-7348.1947.tb06354.x

Roques, L., Hamel, F., 2007. Mathematical analysis of the optimal habitat configurations for species persistence. Mathematical Biosciences 210, 34–59. https://doi.org/10.1016/j.mbs.2007.05.007

Ross, D.M., Stapley, J.H., Cockbill, G.F., 1947. Wireworm populations in relation to crop production; population changes in grassland. Ann Appl Biol 34, 66–82.

Salt, G., Hollick, F.S.J., 1949. Studies of wireworm population: III. Some effects of cultivation. Annals of Applied Biology 36, 169–186. https://doi.org/10.1111/j.1744-7348.1949.tb06407.x

Salt, G., Hollick, F.S.J., 1944. Studies of wireworm populations: I. A census of wireworms in pasture. Annals of Applied Biology 31, 52–64. https://doi.org/10.1111/j.1744-7348.1944.tb06208.x

Saussure, S., Plantegenest, M., Thibord, J.-B., Larroudé, P., Poggi, S., 2015. Management of wireworm damage in maize fields using new, landscape-scale strategies. Agronomy for Sustainable Development 35, 793–802. https://doi.org/10.1007/s13593-014-0279-5

Schallhart, N., Tusch, M.J., Staudacher, K., Wallinger, C., Traugott, M., 2011. Stable isotope analysis reveals whether soil-living elaterid larvae move between agricultural crops. Soil Biology and Biochemistry 43, 1612–1614. https://doi.org/10.1016/j.soilbio.2011.03.024

Schallhart, N., Wallinger, C., Juen, A., Traugott, M., 2009. Dispersal abilities of adult click beetles in arable land revealed by analysis of carbon stable isotopes. Agricultural and Forest Entomology 11, 333–339. https://doi.org/10.1111/j.1461-9563.2009.00428.x

Shigesada, N., Kawasaki, K., 1997. Biological invasions: theory and practice, 1st ed. ed, Oxford series in ecology and evolution. Oxford University Press, Oxford ; New York.

Sufyan, M., Neuhoff, D., Furlan, L., 2013. Effect of male mass trapping of *Agriotes* species on wireworm abundance and potato tuber damage. Bulletin of Insectology 66, 135–142.

Sufyan, M., Neuhoff, D., Furlan, L., 2011. Assessment of the range of attraction of pheromone traps to Agriotes lineatus and Agriotes obscurus. Agricultural and Forest Entomology 13, 313–319. https://doi.org/10.1111/j.1461-9563.2011.00529.x

Sufyan, M., Neuhoff, D., Furlan, L., 2007. Investigations on click beetles using pheromone traps. IOBC/WPRS Bull. 30, 83–87.

Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. Oikos 68, 571. https://doi.org/10.2307/3544927

Traugott, M., Benefer, C.M., Blackshaw, R.P., van Herk, W.G., Vernon, R.S., 2015. Biology, Ecology, and Control of Elaterid Beetles in Agricultural Land. Annual Review of Entomology 60, 313–334. https://doi.org/10.1146/annurev-ento-010814-021035

Tscharntke, T., Brandl, R., 2004. Plant-insect interactions in fragmented landscapes. Annual Review of Entomology 49, 405–430. https://doi.org/10.1146/annurev.ento.49.061802.123339

Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.M., Baudry, J., 2013. The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? Agriculture Ecosystems & Environment 166, 3–14.

Vernon, B., Lagasa, E., Philip, H., 2001. Geographic and temporal distribution of Agriotes obscurus and A. lineatus (Coleoptera: Elateridae) in British Columbia and Washington as determined by pheromone trap surveys. Journal of the Entomological Society of British Columbia. 98, 257–266.

With, K.A., King, A.W., 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biological Conservation 100, 75–88. https://doi.org/10.1016/S0006-3207(00)00209-3

Table 1: List of variables and parameters.

Name	Description	Unit#	Nominal value	Range (see Suppl. Mat. 2)
τ	Emergence rate of adults	d^{-1}	†	-
D	Diffusion coefficient	m^2/d	72	-
π	Oviposition rate	d^{-1}	1.6	[1.2, 3.5]
c	Advection coefficient along the maturity dimension	y^{-1}	0.25	[1/6, 1/2]
μ_A	Aboveground mortality rate	d^{-1}	0.04	[1/35, 1/15]
μ_B	Belowground mortality rate	d^{-1}	*	
K_G	Grassland carrying capacity	m^{-2}	2000	[800, 3000]
K_C	Crop carrying capacity	m^{-2}	120	
β	Exponent associated with belowground density-dependent mortality	-	0.2	[0.05, 0.4]
γ	Perception radius	m	10	-
V_{max}	Maximum advection speed	m/d	10	-

[#] d: day and y: year.

[†] See Supplementary Material 1.

[*] Assessed using an optimisation procedure (see §2.2).

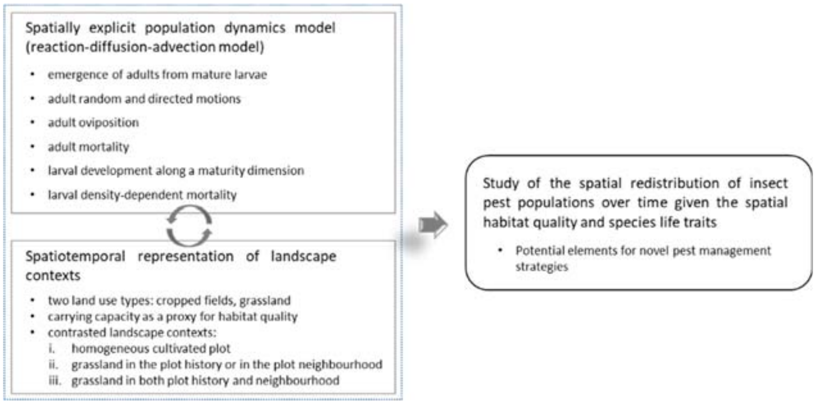

Fig. 1: Conceptual diagram of the modelling framework.

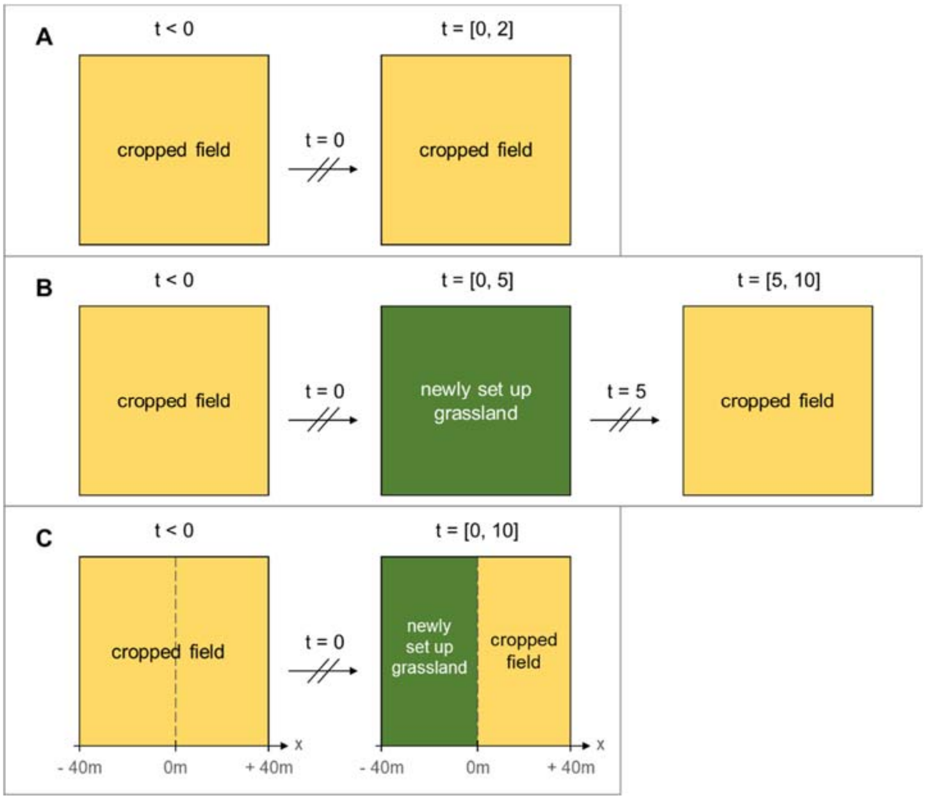

Fig. 2: Three landscape contexts investigated along the study. Initial conditions correspond to stationary populations within a long-term homogeneous cropped field; initial wireworm densities correspond to the crop carrying capacity. (A) Homogeneous area studied over 2 years. (B) Five-year unmanaged area (grassland) followed by a five-year cultivated area (cropped field). (C) Heterogeneous area resulting from the conversion of a cropped field into two neighbouring plots, one cultivated and the other unmanaged.

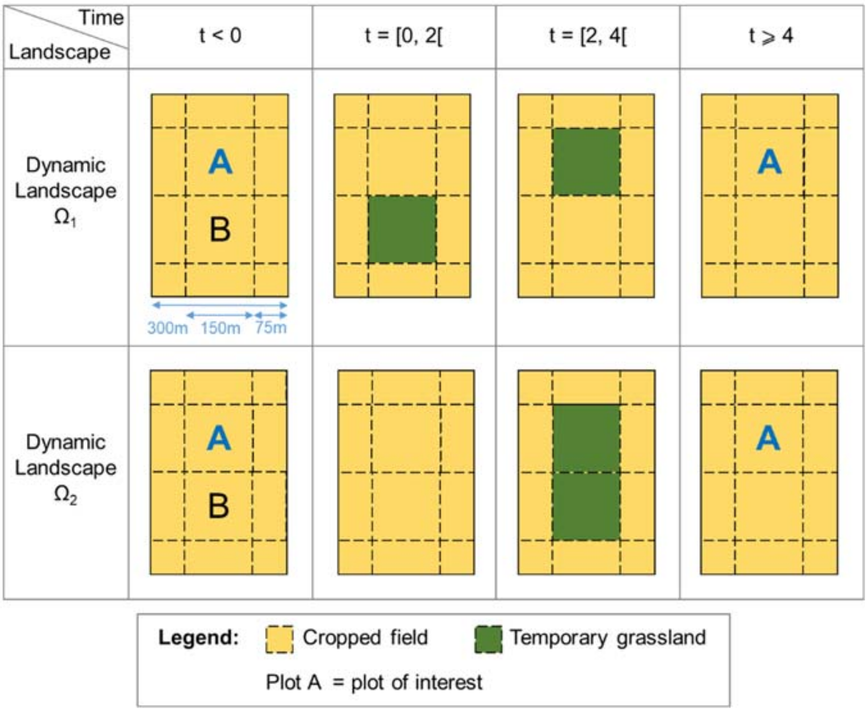

Fig. 3: Dynamic landscapes Ω_1 and Ω_2 exhibiting the same composition in terms of landscape features over the period under study but contrasted spatial configurations.

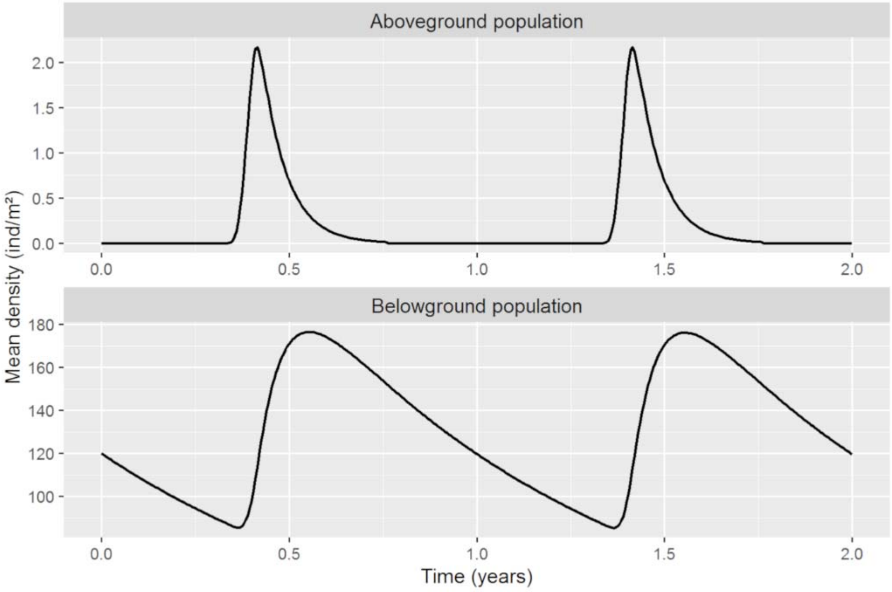

Fig. 4: Above- and belowground population dynamics in a homogeneous landscape context (as depicted in Fig. 2A). Simulations obtained by setting model parameters to their nominal values reported in Table 1.

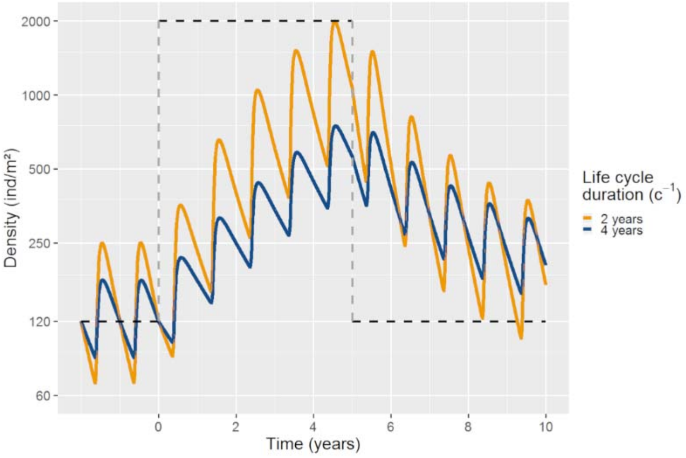

Fig. 5: Wireworm population dynamics in a landscape with grassland in the plot history (as depicted in Fig. 2B). The orange and blue lines are associated with two different values of the life cycle duration (2 and 4 years respectively); other model parameters set to their nominal values. The dashed step curve indicates current values of the carrying capacity (K_G=2000 ind/m² and K_C=120 ind/m²).

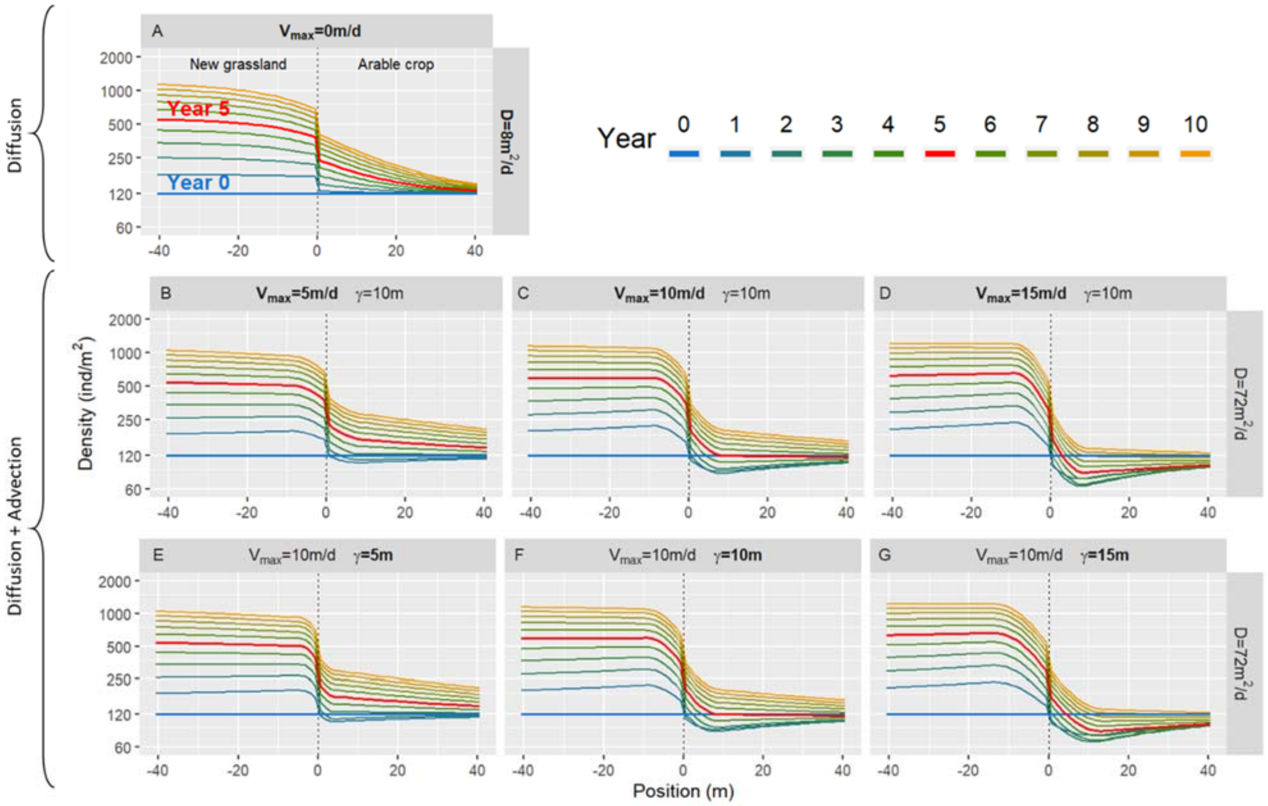

Fig. 6: Wireworm density along the spatial dimension orthogonal to the boundary between the cropped field (right side) and the newly set up grassland (left side) (40 meters on both sides of the ecotone, as depicted in Fig. 2C), over a period of 10 years, and for different values of the diffusion coefficient *D*, the maximal advection speed V_{max} and the perception radius γ. Values assigned to carrying capacities are K_G=2000 ind/m² and K_C=120 ind/m² for the grassland and the cropped field respectively.

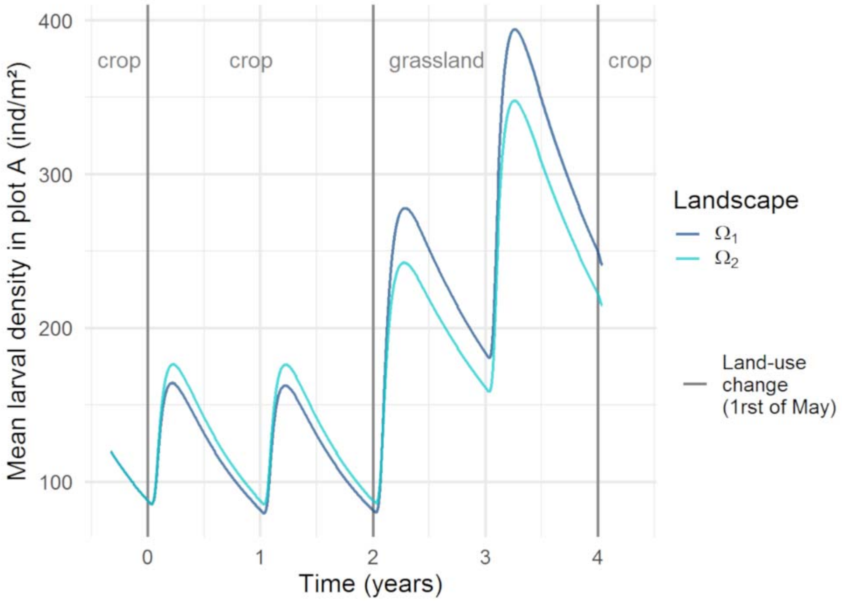

Fig. 7: Mean wireworm densities in plot A of dynamic landscape contexts Ω_1 and Ω_2 (as depicted in Fig. 3) over four years. Simulations obtained by setting model parameters to their nominal values reported in Table 1.

Appendix 1: Emergence rate of click beetles

In our study, we modelled adult emergence as a continuous process spanning over a period governed by the cumulative degree-days. We formalised the emergence rate as a temperature-dependent functional response. Let's note

$$\theta_{cum}(t) = \sum_{\substack{j=0 \\ \theta(j)>\theta_{base}}}^{t} (\theta(j) - \theta_{base}) \qquad (A1.1)$$

where θ_{cum} stands for the cumulated number of degree-days starting arbitrarily in January, θ_{base} is the temperature below which degree-days are not accounted for, set to 10°C in accordance with findings from Furlan (2004, 1998) who showed that no larval development happened below this threshold value. Denoting θ_{start} (resp. θ_{end}) the minimal (resp. maximal) number of cumulated degree-days above (resp. below) which emergence starts (resp. ends with the entire pool of mature larvae having emerged), the emergence rate writes

$$\tau(t) = \begin{cases} 0 & if\ \theta_{cum}(t) < \theta_{start} \\ \left(\dfrac{\theta_{cum}(t) - \theta_{start}}{\theta_{end} - \theta_{start}}\right)^{\alpha} & if\ \theta_{start} \leq \theta_{cum}(t) \leq \theta_{end} \\ 0 & if\ \theta_{cum}(t) > \theta_{end} \end{cases} \qquad (A1.2)$$

with α set empirically to 2.5 to ensure that the peak of emergence occurs in the middle of the emergence window. As the effect of temperature was not in the scope of this study, we averaged the daily temperatures in Le Rheu (Brittany, France) over a 10-year period (2008 to 2017), and we chose the values of θ_{start} and θ_{end} that corresponded to late April and beginning of June (April 23rd and June 8th), in accordance with published studies (Landl, 2010; Parker & Howard, 2001; Sufyan, 2007; Villeneuve & Latour, 2011). The functional response for the emergence rate and the proportion of emerged adults along time (applied to our temperature dataset) are illustrated on Fig. A1.

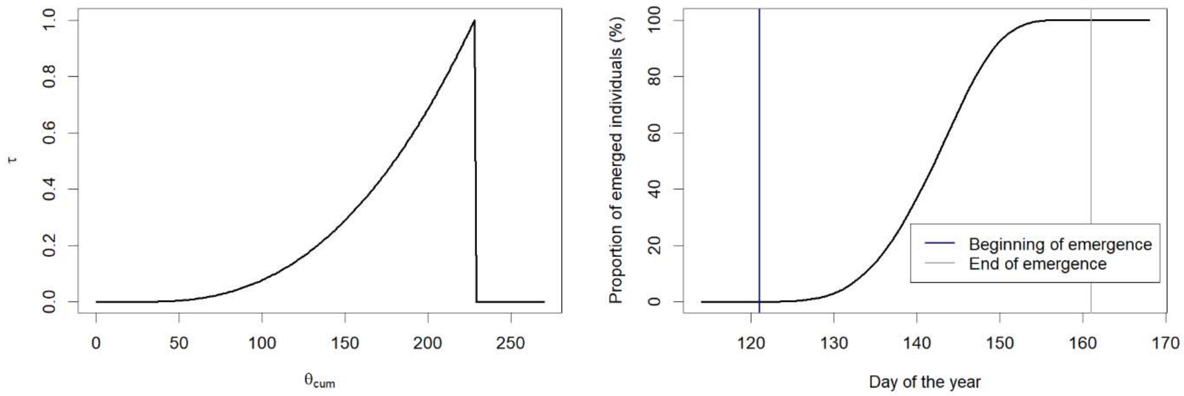

Fig. A1: (A) Functional response for the emergence rate: emergence rate vs cumulative degree-days. (B) Proportion of emerged adults along time.

References

Landl, M., Furlan, L., Glauninger, J., 2010. Seasonal fluctuations in Agriotes spp. (Coleoptera: Elateridae) at two sites in Austria and the efficiency of bait trap designs for monitoring wireworm populations in the soil. Journal of Plant Diseases and Protection 117, 268–272. https://doi.org/10.1007/BF03356372

Parker, W.E., Howard, J.J., 2001. The biology and management of wireworms (Agriotes spp.) on potato with particular reference to the U.K. Agricultural and Forest Entomology 3, 85–98. https://doi.org/10.1046/j.1461-9563.2001.00094.x

Sufyan, M., Neuhoff, D., Furlan, L., 2007. Investigations on click beetles using pheromone traps. IOBC/WPRS Bull. 30, 83–87.

Villeneuve, F., Latour, F., 2011. Taupins et légumes: le casse-tête du piégeage. Phytoma 643, 24–28.

Appendix 2: Sensitivity analysis

We carried out a Morris sensitivity analysis (Morris, 1991) to study the effect of model parameters on the speed at which the wireworm population density converges toward the carrying capacity of a given land cover. For this purpose, we considered the situation where a cultivated crop (with carrying capacity K_C) is converted to grassland (with carrying capacity K_G). Initially, the wireworm density equals the crop carrying capacity K_C. We applied our population dynamics model (§2.1) and defined as an output metric the time required for the wireworm density to reach the mean density between K_C and K_G.

Among the model parameters, five were suspected of influencing the process of interest: the oviposition rate (π), the advection coefficient along the maturity dimension (c), the aboveground mortality rate (μ_A), the grassland carrying capacity (K_G), and the exponent associated with the belowground density-dependent mortality (β). Ranges of value assigned to these parameters are reported in Table 1 (last column). Other parameters were set to their nominal value (Table 1), except μ_B that was assessed using a preliminary optimisation procedure as mentioned in §2.2.

Figure A2 shows the standard deviation (σ) versus the absolute mean (μ^*) of the elementary effects associated with each of the five parameters investigated. Parameters K_G and μ_A have a very low overall influence on the output metric. On the contrary, the parameter c has a significant linear influence, while parameters π and β exhibit a non-linear influence, possibly with interactions, on the output metric.

Thus, despite scarce knowledge on this parameter β (driving the strength of the legacy effect), it has a significant effect on the output metric we investigated, and its estimation would probably deserve further attention.

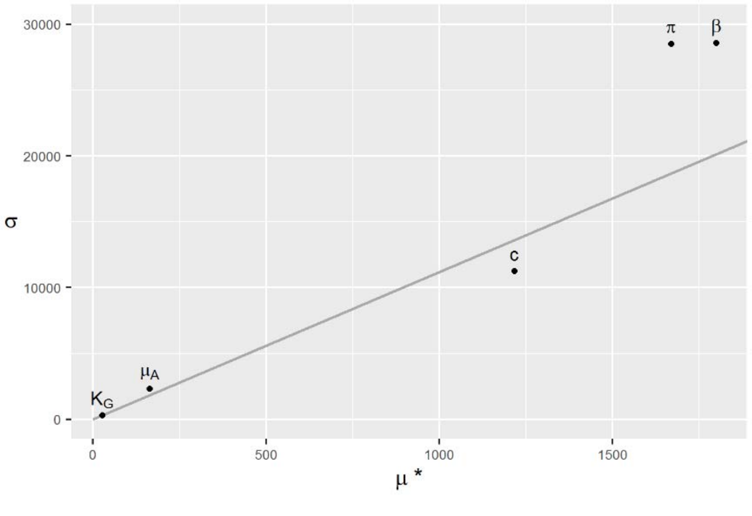

Fig. A2: Standard deviation (σ) vs. absolute means (μ^*) of elementary effects obtained from the Morris method. Elementary effects of five parameters on the time required to reach the mean density between K_C and K_G. The oblique grey line corresponds to $\mu^*= 2SEM$ (Standard Error of the Mean $SEM = \sigma/\sqrt{r}$, number of trajectories r = 200).

Reference

Morris, M.D., 1991. Factorial Sampling Plans for Preliminary Computational Experiments. Technometrics 33, 161–174. https://doi.org/10.1080/00401706.1991.10484804