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

1 **Dynamic role of grasslands as sources of soil-dwelling insect pests: new insights from *in silico***

2 **experiments for pest management strategies**

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14 **Highlights**:

15 - The role of grassland in field colonisation by insect pests is investigated in silico

16 - Population dynamics of wireworms is modelled, accounting for life cycle and dispersion

17 - Spatiotemporal effects of grassland in field history, field neighbourhood or their interaction,
18 depend on the pest life cycle and its dispersal capacity

19 - Grassy areas can act either as pseudo-sinks or as sources on neighbouring crops

20 - Control strategies based on grassland arrangements appear trait-specific

21

22 **Abstract**:

23 Sustainable pest control strategies hinge on the knowledge of movement ecology within the agricultural

24 landscape where contrasted habitat qualities intermingle, thereby influencing arthropod dispersal.

25 Hence, habitat manipulation in space and time can be a lever for action to control pests with regard to

26 landscape compositional constraints. In this study, we examined the role of grassland arrangements in

27 field colonisation by soil-dwelling pests within a dynamic agricultural landscape, and discussed the

28 implications for pest management with a focus on wireworms. For this purpose, we proposed a

29 framework combining (i) a spatially explicit and mechanistic model describing the pest population

30 dynamics in both aerial and soil compartments involved along its life cycle, and (ii) spatiotemporal

31 representations of various landscape contexts. We addressed the role of grassland in plot history, in plot

32 neighbourhood, or in both history and neighbourhood. Our results show that species with a short life

33 cycle are more responsive to changes in land use, and that the neighbourhood effect strongly relies on

34 dispersal mechanisms (random vs directed movements). We also highlight how the arrangement of

35 grassy landscape elements in space and time can mitigate crop infestation by soil-dwelling pests, thereby

36 emphasizing the relevance of managing grassland regimes. Once informed by critical pest life traits, our

37 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,

112 • the adult mortality,

113 • the larval development,

114 • and the larval density-dependent mortality.

115 Briefly, adults oviposit at a constant rate π, thereby increasing the belowground population that ages at

116 a constant velocity c, undergoing a density-dependent mortality. Wireworms reaching the critical age

117 m_c emerge as adults that disperse across the landscape to find resources and suitable habitat. The model

118 can be formalised as a system of partial differential equations: for $t > 0$ and $0 < m < m_c$

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

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

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

122 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

123 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

124 maturity dimension), where $\partial_x, \partial_y, \partial_m$ denote the partial derivatives with respect to x, y and m.

125 Model parameters and their meaning are described in Table 1. Model interpretation is fully presented in

126 the following paragraphs. The state variables A and B respectively denote the density of click beetles

127 aboveground, and the density of wireworms in soil. Actually, B encapsulates all belowground

128 development stages (larval instars, pupae) and is referred to as wireworms thereafter for the sake of

129 simplification. The dynamical condition at $m = 0$ (Eq. 3) reflects both the oviposition and the growth

130 of individuals who did not start to mature, while the condition in $m = m_c$ (Eq. 4) takes into account the

131 accumulation of individuals in the last class of maturation before emergence.. As initial conditions, the

132 aboveground population was set to zero and the age distribution of larvae was obtained from a

133 preliminary model simulation run over 15 years on a homogeneous landscape. The model was solved

134 using operator splitting (Press et al., 2007, Chapter 20.3.3). Alternating-direction implicit method solves

135 the diffusion (Press et al., 2007, Chapter 20.3.2), while a forward Euler scheme is used for the reaction

136 terms, and an upwind scheme for the advection terms (Press et al., 2007, Chapter 20.1). We considered

137 the spatial domain under study as a closed system (i.e. equal inflowing and outflowing pest

138 populations), thereby applying Neumann (reflecting) boundary conditions at the edges of the spatial

139 domain. All developments were made with the R programming language (R Core Team, 2018).

140

141 *Adult emergence and motions*

142 Click beetles emerge during spring. In accordance, we defined their emergence rate as a time-dependent

143 function $\tau(t)$ (cf. §2.2 and Suppl. Material 1) in Equation 1.

144 As recent findings suggested that wireworms do not move from field to field (Schallhart et al., 2011),

145 we considered that only adults contribute to the spatial redistribution of populations. We assumed that

146 adult motions included two components: a random component expressed through the diffusion term in

147 Equation 1, involving D the homogeneous diffusion coefficient; and a directed component expressed

148 through the advection term in Equation 1 and involving $\vec{u}$ the advection velocity. Regarding the latter

149 component, we assumed that click beetles move across the landscape based on the habitat quality they

150 perceive in their neighbourhood. We defined the local habitat quality $h(x,t)$ as a function of local

151 carrying capacities $K(x,t)$:

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

152 where K_{max} (resp. K_{min}) refers to the most favourable (resp. unfavourable) habitat for wireworms. As did

153 Bourhis et al. (2017), we derived the perception of the landscape habitat quality, noted $h_p(\boldsymbol{x},t)$, from a

154 convolution of a perception kernel (linear inverse distance weighting filter) with the mapping of local

155 habitat quality:

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

156 with Ω the whole spatial domain, and γ the distance beyond which habitat quality is no longer perceived

157 by click beetles. Finally, the advection velocity

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

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

159

160 *Oviposition*

161 Although the oviposition rate may vary among habitats (Brian, 1947), it was assumed here independent

162 of space (i.e. land use and associated carrying capacity) and constant over the whole duration of the

163 adult life. New-borns fall within the belowground population with age 0 (Eq. 3).

164

165 *Adult mortality*

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

167

168 *Larval development*

169 The belowground population distributes along an ageing axis. The population ages according to a

170 constant coefficient c. When reaching the critical maturity m_c, larvae can emerge as click beetles.

171

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/m²) 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/m². Locally, they even observed densities reaching 6000 ind/m² in both pastures. Within other pastures less intensively sampled, they found about 2500 ind/m² on average. Roebuck et al. (1947) studied intensively the infestation level of an old meadow, and determined a density of about 300 ind/m² 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/m². Ross et al. (1947) studied six permanent pastures grazed and regularly hayed, and assessed a density of about 1000 ind/m².

In cropped fields, we set the carrying capacity K_C to 120 ind/m², 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

207   average population density of 102, 80, 56 and 32 ind/m² the 1rst, 2nd, 3rd and 4rth year after ploughing

208   from grass, respectively.

209

210   *Belowground population maturation (c)*

211   Wireworm species differ greatly from one another in their biology and ecology (Furlan, 2005; Ritter and

212   Richter, 2013), in particular as regards the duration of their biological cycle. In France, four species

213   from the genus *Agriotes* are responsible for most economical crop damage. Among them, *A. lineatus*,

214   *A. obscurus* and *A. sputator*, predominantly present in the northern regions, exhibit a long life cycle

215   (duration of larval stage of about 4 years), whereas *A. sordidus*, mainly found in south-western regions,

216   exhibits a short life cycle (duration of larval stage of about 2 years). In our study, we set the duration of

217   the larval stage (c^{-1}) at 2 years for short life-cycle species and at 4 years for long life-cycle species.

218

219   *Emergence rate*

220   Studies relative to the date of emergence of *Agriotes* click beetles are fairly consistent. For instance, in

221   Austria, Landl et al. (2010) observed that the emergence of *A. lineatus* began at the end of April, which

222   is concordant with the observations of other authors from Eastern Europe and from western Canada

223   (Vernon et al., 2001). Regarding *A. ustulatus*, *A. lineatus* and *A. obscurus*, Parker and Howard (2001)

224   in United Kingdom reported emergences starting at mid-April and adults being captured until mid-July

225   (hence, they probably emerged until mid-June), while in Germany, Sufyan et al. (2007) observed that

226   the swarming period lasted from late April to the end of August (for *A. lineatus* and *A. obscurus*).

227   Although most authors reported two periods of adult activity, one main in May and one weaker in June-

228   July (Landl et al., 2010; Sufyan et al., 2007), we simply modelled adult emergence as a continuous

229   process spanning over a period governed by the cumulative degree days (see Supplementary Material

230   1). In our study, the emergence of click beetles spans from late April to the beginning of June, with a

231   peak of emergence located towards the middle of the period of emergence (i.e. mid-May). Over this

232   period, all wireworms at the critical age have emerged (see Supplementary Material 1, Fig. A1B).

233

234   *Belowground mortality (μ_B, β)*

235   Two main model parameters govern the larval mortality, namely the mortality rate μ_B and the inertia

236   exponent β. The mortality rate was determined by means of a preliminary optimisation procedure before

237   each simulation, given all other parameter values, such that larval density oscillated yearly around the

238   carrying capacity in any homogeneous landscape. β was estimated empirically to 0.2 from infestation

239   data collected in arable lands by Roebuck (1924) over 8 years. As shown in a sensitivity analysis (see

240   Supplementary Material 2), despite scarce knowledge on this parameter β, it has a significant effect on

241   the model output and its estimation would probably deserve further attention.

242

243 *Adult dispersion (D, V_{max})*

244 Literature provides a limited amount of information regarding click-beetle dispersal. In particular,

245 diffusion and advection processes can seldom be disentangled. Brian (1947) observed that *A. obscurus*

246 and *A. lineatus* (but not *A. sputator*) frequently flew in a glass cage experiment. Crozier et al. (2003)

247 reported that these species can be strong fliers, able to perform mass flights, travelling approximately 5

248 to 10 km/h for distances ranging from less than 1 m to 100 m on one occasion and with an average flight

249 covering 2 to 3 m. More recently, Blackshaw and Hicks (2013) concluded that *Agriotes spp.* disperse

250 widely and may originate from adjacent fields. Many studies have attempted to provide quantitative

251 estimates of click-beetle dispersal capacity, generally using mark-recapture experiments with

252 pheromone traps. Blackshaw et al. (2017) recaptured individuals (*A. lineatus*, *A. obscurus*, *A. sputator*)

253 at 1m from release point after 1h, and at 30m after 19h. Schallhart et al. (2009) studied the isotopic

254 signature of *A. obscurus* beetles captured in pheromone traps located in a grassland adjacent to a maize

255 field: 13% of individuals captured 80m inside the grassland plot had a signature characteristic of their

256 maize field origin. Based on this knowledge, we set the diffusion coefficient to 72 m²/day, hence

257 producing a mean dispersion radius of 15m in one day, 21m in two days, etc. (Shigesada and Kawasaki

258 (1997), page 38). The advection speed was set to 10 m/day.

259

260 *Perceptual range (γ)*

261 We assumed that adult click beetles could perform directed motions as responses to distant stimuli (e.g.

262 olfactory stimuli). Advection processes may result from foraging for food or laying sites, from searching

263 for a sexual partner, etc. In our model, we described advection at the population level as a tendency to

264 move along a gradient of increasing habitat quality expressed in terms of carrying capacities. In

265 particular, as wireworms thrive in grasslands, we expect adult click beetles to disperse preferentially

266 towards nearby grassy areas. We set the perceptual range (i.e. the distance beyond which habitat quality

267 is no longer perceived by click beetles) to 10 m. This estimated value mainly stems from studies dealing

268 with pheromone attractiveness for click beetles, since it is the only advection process for which literature

269 provides some guidance. Sufyan et al. (2007) assessed the range of attractiveness of pheromone traps

270 (for both species *A. lineatus* and *A. obscurus*) through a mark – recapture experiment. They recaptured

271 > 60% and < 10% of beetles in pheromone traps placed at 2 and 60 m from their release point,

272 respectively. In a later experiment, Sufyan et al. (2011) estimated the maximum distance of perception

273 of a pheromone trap to be around 15-20 m. Blackshaw et al. (2018) studied the attractive range of traps

274 baited with *A. obscurus* pheromone to male beetles in both still air and wind conditions. They found that

275 the attraction distance was less than 5m in still air but increased with airflow.

276

277 *Aboveground population mortality (μ_A)*

278 Adult life expectancy varies among studies. Brian (1947) observed that longevity of *A. obscurus* on

279 various crops ranged from 69 to 84 days for females and from 45 to 75 days for males. Regarding *A.*

280 *ustulatus*, Hinkin (1983) reported an average longevity of 28 days for females and 19 days for males,
281 while Furlan (1996) measured an adult lifespan of 24 (SD=5) days for females. More recently, Hicks
282 and Blackshaw (2008) as well as Blackshaw et al. (2017) performed mark–release experiments on click
283 beetles ; they showed respectively that adults (males and females combined) can survive for at least 45
284 and 25 days. Accordingly, in our model, based on these elements and in accordance with our own field
285 observations, we set the adult average lifespan to 25 days for both sexes.
286
287 *Oviposition rate (π)*
288 Most authors have studied oviposition under laboratory conditions. Brian (1947) found an average
289 fecundity ranging from 30 to 150 (*A. obscurus*) depending on the crop (flax, potato and wheat were
290 associated with low fecundity while grasslands of *Lolium*, *Festuca* and *Agrostis* were associated with
291 high fecundity). Miles and Cohen (1941), Cohen (1942), and Furlan (1996), reported an average number
292 of eggs laid per female of 109 in *A. obscurus* (min=78, max=186), 103 in *A. obscurus* and 78 in *A.*
293 *ustulatus* (SD=27.9, min=52, max=140). Accordingly, we considered fecundity to be of 80 eggs per
294 female over its lifespan (25 days as mentioned in the previous paragraph). Considering that sex ratio
295 tends towards 1:1 (Blackshaw et al., 2017; Furlan, 1996), the oviposition rate was set to (80/2)/25=1.6
296 eggs per capita per day.
297
298 **2.3. Landscape contexts**
299 We defined four landscape contexts (Fig. 2 and Fig. 3) to investigate the processes driving the
300 colonisation of vulnerable habitats (arable crops) characterised by a habitat quality lower than the one
301 associated with grasslands (favourable habitats). The first three contexts are shown in Fig.2: a
302 homogeneous cropped field cultivated over 2 years (Fig. 2A), a grassland in the field history (Fig. 2B)
303 or in the neighbourhood of the cropped field (Fig. 2C). Finally, Fig. 3 describes the fourth context where
304 we compared two dynamic landscapes Ω_1 and Ω_2 exhibiting the same duration of land use over time
305 (landscape composition) but through contrasted spatial configurations.
306
307 **3. Results**
308
309 **3.1. Population dynamics in a homogeneous landscape context**
310 Fig. 4 shows the dynamics of above- and belowground populations in the simple case of a homogeneous
311 landscape (Fig. 2A) comprising vulnerable cropped fields only. Simulation starts in winter with a null
312 aboveground population and a larval density at equilibrium, hence 120 individuals per square meter.
313 Until the emergence of adults, the only process at stake is larval mortality, which reduces the
314 belowground population to about 90 individuals per square meter. Adults emerge in early spring
315 producing an increase in the aboveground population density with a peak value determined by (i) the

316   density of mature larvae at the onset of the emergence period, (ii) climate and (iii) adult life expectancy.

317   It is followed by a decrease resulting from the constant mortality rate μ_A. About 65 days after the last

318   emergence, the aboveground population becomes extinct. This pattern repeats over the years.

319   After adults have emerged, they disperse and lay eggs, thus refilling the belowground population

320   compartment that increases, reaches a maximum at the end of the oviposition period, and then decreases

321   due to larval mortality. After a few years a stationary pattern occurs.

322

323   **3.2. Wireworm dynamics with grassland in field history**

324   The effect of a grassland in field history (Fig. 2B) on the wireworm population density is illustrated on

325   Fig. 5 for two pest life cycle durations: 2 years (short life cycle) and 4 years (long life cycle). Both

326   dynamics exhibit the periodic behaviour described in the previous section (§3.1). At time 0, the field is

327   converted to grassland, which translates into an important rise in habitat quality resulting in a subsequent

328   wireworm population increase.

329   In Fig. 5, we compare the dynamics of a short life cycle population and a long life cycle population. The

330   amplitudes of intra-annual oscillations are more important for the former. On one hand, the proportion

331   of the belowground population that emerges as adults is larger in the case of a short life cycle (about

332   half the population emerges each year) than in that of a long life cycle (about a quarter emerges each

333   year). Given that oviposition rate is independent from life-cycle duration in our model, the increase in

334   wireworm density is greater for short cycle species. On the other hand, once the aboveground population

335   has vanished, high larval density results in a strong mortality until the next laying period.

336   In summary, short life cycle wireworms react more promptly to changes in habitat quality, thereby

337   leading to higher infestation levels in temporary grasslands. Conversely, after grassland conversion into

338   crop, wireworm density reaches more quickly the new current carrying capacity K_C in the case of short

339   cycle species. Note that these conclusions stem from our model hypotheses, where a difference in life

340   cycle duration results in different mortality rates (land-use carrying capacities and oviposition rates

341   being unchanged).

342

343   **3.3. Wireworm dynamics in a field with a newly set-up grassland in its neighbourhood**

344   We simulated the effect of the conversion of half of a crop field into permanent grassland (Fig. 2C). Fig.

345   6 shows the wireworm density along a direction orthogonal to the grassland/crop field border (40 meters

346   on both sides), over a period of 10 years, and for a range of values of the diffusion coefficient D, the

347   maximal advection speed V_{max} and the perceptual range γ. Diffusion tends to homogenise wireworm

348   densities in space, while advection entails population movements from low towards high carrying

349   capacity places.

350   In Fig. 6A, only diffusion applies. Wireworm densities increase from K_C (120 ind/m²) towards K_G (2000

351   ind/m²) along the 10 years on the side covered with grassland. Adult click beetle diffusion results in an

352 increase in wireworm density in the adjacent cropped field with an intensity that vanishes away from

353 the ecotone.

354 In the next six panels (Figs. 6B-G), diffusion and advection have antagonistic effects. Advection fosters

355 population displacements from low towards high quality habitat, whereas diffusion promotes a

356 homogenisation of the densities.

357 During the transient period before reaching equilibrium density in the grassland, the set-up of a grassland

358 can have opposite effects on wireworm density in crop, depending on the advection strength (Figs. 6B-

359 D). Indeed, a high maximal advection speed V_{max} results in a reduction of wireworm density inside the

360 cropped field due to advection effect exceeding diffusion effect. For low maximal advection speed, the

361 opposite occurs. Thus, 5 years after grassland set-up, wireworm density can be greater (Fig. 6B), similar

362 (Fig. 6C) or lower (Fig. 6D) than the initial density in the crop. Changes in perceptual range have similar

363 effects than changes in maximal advection speed (Figs. 6B-G).

364 A mechanistic effect of the population redistribution must be noted here. Unlike advection, diffusion is

365 an inherently density-dependent process. As population increases within the grassland, so does the

366 diffusion intensity, mechanically. The neighbourhood effect of grassland is therefore changing

367 throughout the season, as diffusion takes more control over the redistribution.

368

369 **3.4. Effect of spatiotemporal distribution of grasslands on wireworm densities**

370 We considered two dynamic landscape contexts Ω_1 and Ω_2 spanning over four years (Fig. 3). Landscape

371 composition over time (i.e. the proportions of cropped field and grassland over the duration of the virtual

372 experiment) remains unchanged, while spatial configurations differ. The land cover within plot A is

373 identical over the years in Ω_1 and Ω_2, however the mean wireworm densities differ all along the four-

374 year period. Final densities deviate by 10%. Indeed, in Ω_1, wireworm density increases in plot B the first

375 two years due to a favourable habitat (grassland). Subsequently, when plot A turns into grassland

376 whereas plot B switches to cropped field, both advection and diffusion induce aboveground population

377 movements from plot B to plot A, resulting in a meaningful wireworm increase once oviposition has

378 been completed, that combines with the expansion of wireworm density due to the high carrying capacity

379 associated with grassland. In Ω_2, simultaneous evolution of densities in plots A and B do not favour any

380 population flows.

381

382 **4. Discussion**

383

384 **4.1. Model relevance and novelty**

385 Insect pests inflict severe damage to agricultural crops, in spite of the intense use of agrochemical inputs.

386 In fragmented and changing environment, as most agricultural landscapes are, the movement of insect

387 pests has a strong influence on their abundance and spatiotemporal distribution, hence the extent of the

388 inflicted crop damage (Mazzi and Dorn, 2012). Thus, understanding dispersal mechanisms may help
389 design effective pest management strategies. Here, we developed a spatially explicit mechanistic model
390 to describe the population dynamics of insect pests inflicting crop damage while developing in soil, and
391 spreading across the landscape as adults. We accounted for both aboveground and belowground
392 population dynamics. To date, few studies have considered the link between both compartments though
393 many species of ecological and economic importance have both above- and belowground life cycle
394 stages (Benefer et al., 2012). Therefore, our developments could serve in investigations dealing with a
395 wide variety of soil-dwelling insect pests.
396 Combined with spatial representations of dynamic landscape contexts, our population dynamics model
397 enables the investigation of the spatial redistribution of populations over time given the spatial
398 distribution of habitat quality and species life-history traits (dispersal ability, life cycle duration, etc.).
399 We thus provide an appropriate framework to study how the arrangement of grassy landscape elements
400 in space and time can mitigate crop infestation by soil-dwelling pests.
401
402 **4.2. The dynamics of grassland as reservoirs or sources of pests**
403 In our results, we highlight (§3.2) the influence of the legacy of previous land uses on the current
404 wireworm infestation level. This is well documented in plant sciences, e.g. regarding soil
405 suppressiveness (Bailey et al., 2009; Postma et al., 2010), effects of biofumigation (Matthiessen and
406 Kirkegaard, 2006), etc. Here we show that given its habitat favourability, the presence of a grassland in
407 plot history entails the build-up of wireworm populations, and acts as a reservoir (Fig. 5). Interestingly,
408 species life-history traits mitigate the changes in population density in response to land use change.
409 Indeed, short life cycle species may be more responsive to land use change (Fig. 5).
410 At a broader spatial scale (landscape context, §3.3), the wireworm population response to the presence
411 of a grassland in an adjacent field relies on the pest life-traits (dispersal ability, life cycle duration),
412 habitat quality, and habitat patch dynamics. Local habitat quality governs the wireworm density in the
413 field core, whereas density in borders results from the diffusion and advection of click beetles between
414 habitats over time (Fig. 6). When advection is high, the inner edge of a low-quality habitat is temporary
415 depleted at the expense of the adjacent higher quality habitat. However, diffusion (which tends to
416 homogenise density) usually plays the opposite effect. Hence, wireworm density is ruled by the trade-
417 off between these two antagonistic dispersal mechanisms. In a grassland where wireworm density has
418 reached the local carrying capacity, diffusion at the ecotones will be high and sustain the colonisation
419 of neighbouring crops. Therefore, the presence of a temporary versus permanent grassland in the
420 neighbourhood may significantly change the outcome in terms of spatial distribution of wireworm
421 populations. If advection is strong and grasslands highly favourable, temporary grasslands may act as
422 pseudo-sinks, while permanent grasslands act as sources for click beetle populations. This clearly
423 emphasizes the relevance of managing grassland regimes.
424

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

498 framework offering exciting perspectives for the management of the trade-offs in a bundle of services
499 and to identify situations or practices that allow switching from antagonism to synergy.
500

509
510

511 **Sample CRediT author statement**
512 **Sylvain Poggi:** Conceptualization, Methodology, Software, Writing – Original Draft, Funding
513 acquisition, Supervision **Mike Sergent:** Methodology, Software, Writing – Original Draft,
514 Visualization **Youcef Mammeri:** Methodology, Software, Formal Analysis, Writing – Review &
515 Editing **Manuel Plantegenest:** Conceptualization, Methodology, Writing – Review & Editing **Ronan
516 Le Cointe:** Conceptualization, Writing – Review & Editing, Funding acquisition **Yoann Bourhis:**
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723 **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	-

724 [#]d: day and y: year.

725 † See Supplementary Material 1.

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

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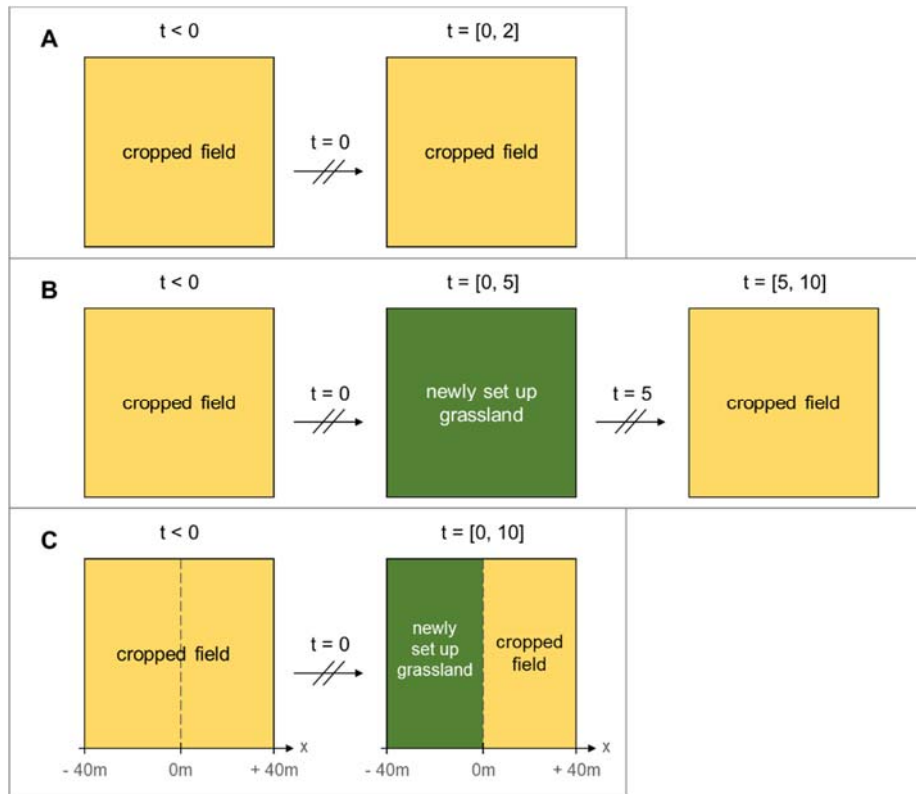
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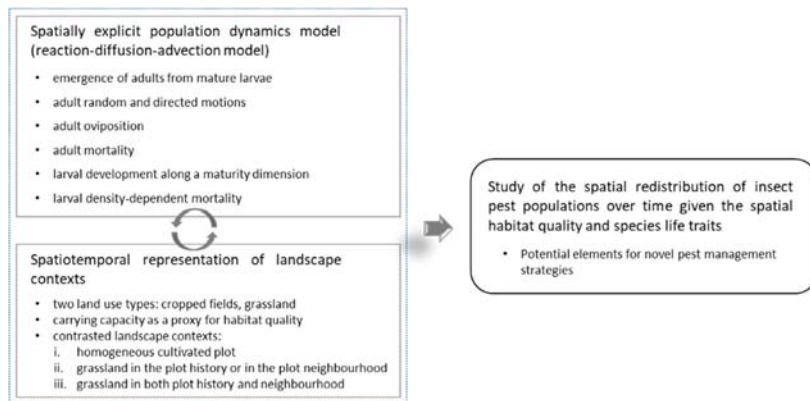
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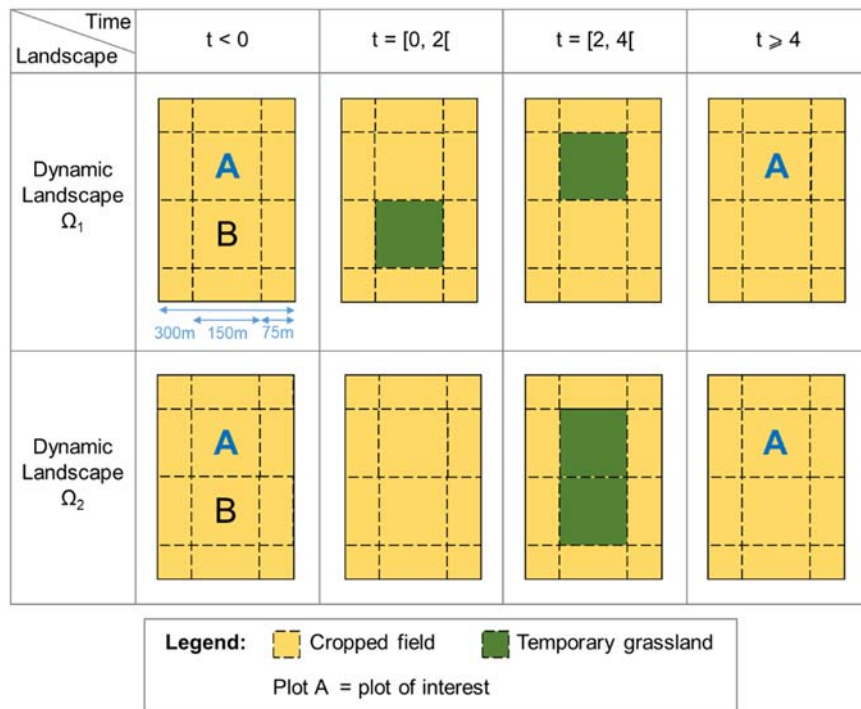730   **Fig. 1:** Conceptual diagram of the modelling framework.

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.

740

Time / Landscape	t < 0	t = [0, 2[	t = [2, 4[	t ⩾ 4
Dynamic Landscape Ω_1	A B (300m 150m 75m)			A
Dynamic Landscape Ω_2	A B			A

Legend: ▢ Cropped field ▪ Temporary grassland
Plot A = plot of interest

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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.
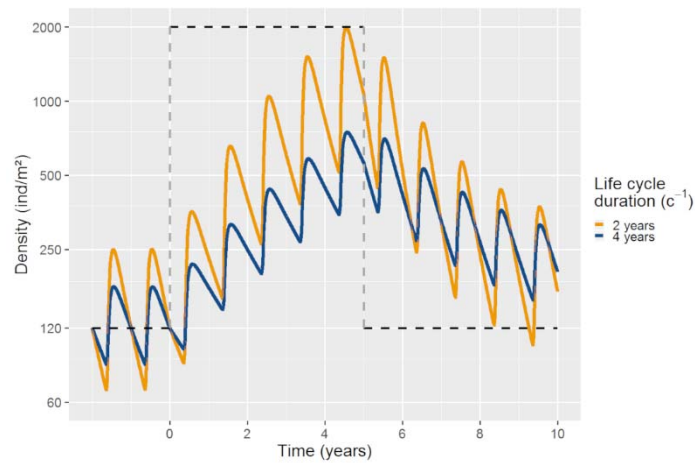
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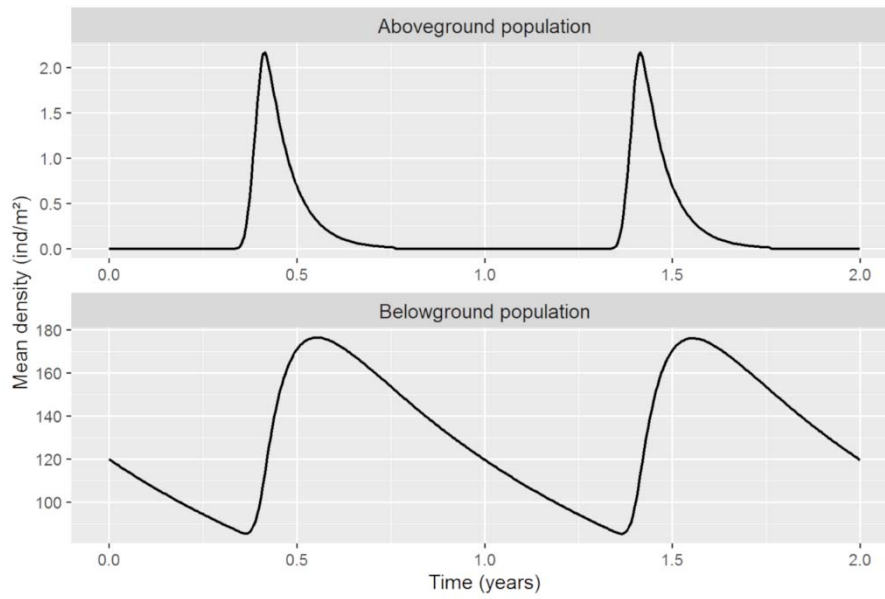
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749 **Fig. 4:** Above- and belowground population dynamics in a homogeneous landscape context (as depicted

750 in Fig. 2A). Simulations obtained by setting model parameters to their nominal values reported in Table

751 1.

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757 **Fig. 5:** Wireworm population dynamics in a landscape with grassland in the plot history (as depicted in

758 Fig. 2B). The orange and blue lines are associated with two different values of the life cycle duration (2

759 and 4 years respectively); other model parameters set to their nominal values. The dashed step curve

760 indicates current values of the carrying capacity (K_G=2000 ind/m² and K_C=120 ind/m²).

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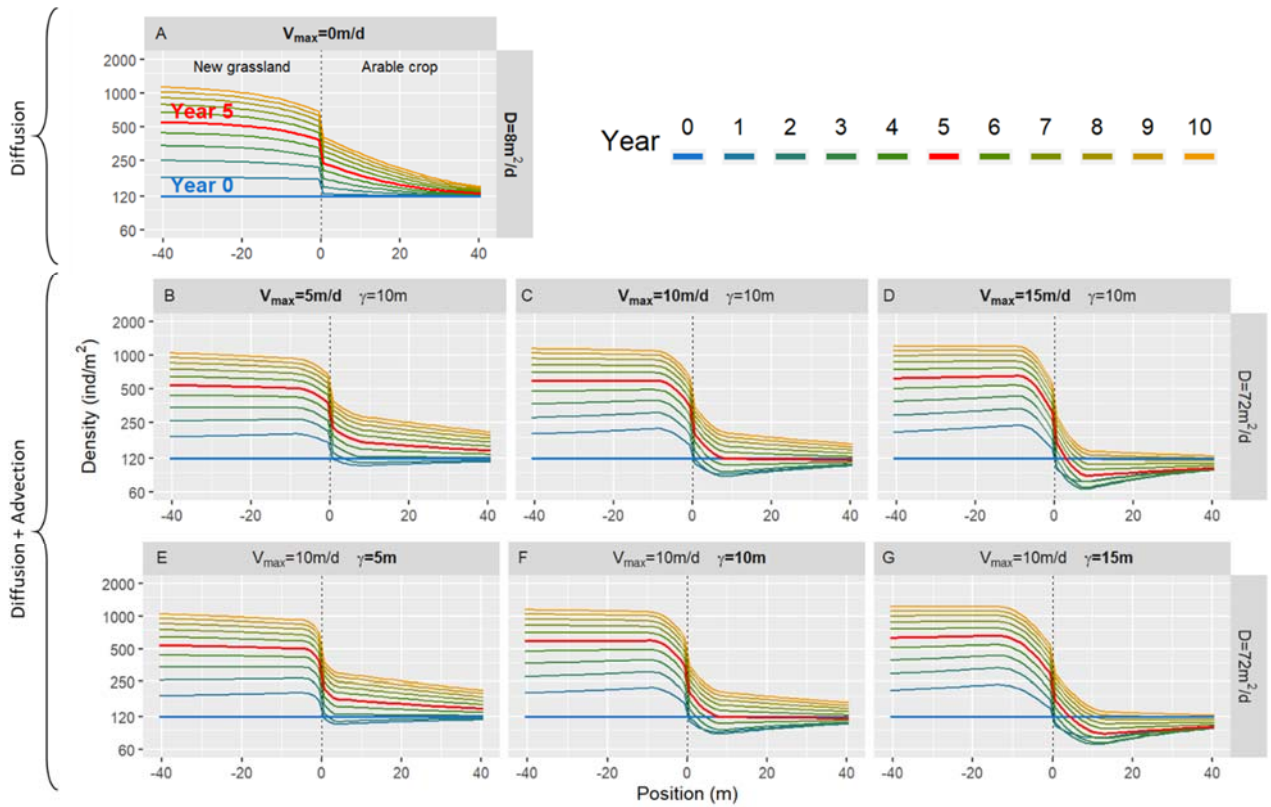
Fig. 6: Wireworm density along the spatial dimension orthogonal to the boundary between the cropped
field (right side) and the newly set up grassland (left side) (40 meters on both sides of the ecotone, as
depicted in Fig. 2C), over a period of 10 years, and for different values of the diffusion coefficient 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.

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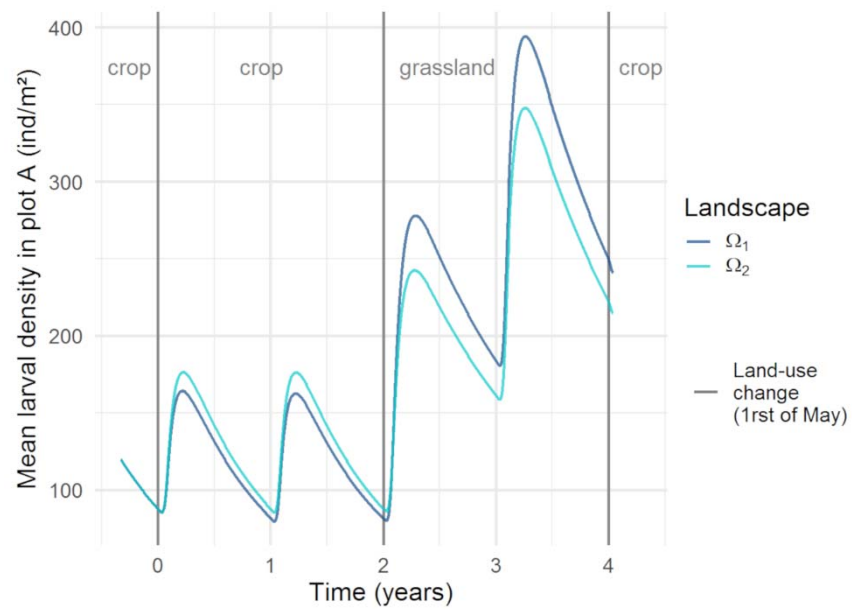
Fig. 7: Mean wireworm densities in plot A of dynamic landscape contexts Ω_1 and Ω_2 (as depicted in Fig. 3) over four years. Simulations obtained by setting model parameters to their nominal values reported in Table 1.

Appendix 1: Emergence rate of click beetles

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779   In our study, we modelled adult emergence as a continuous process spanning over a period governed by

780   the cumulative degree-days. We formalised the emergence rate as a temperature-dependent functional

781   response. Let's note

782
$$\theta_{cum}(t) = \sum_{\substack{j=0 \\ \theta(j) > \theta_{base}}}^{t} (\theta(j) - \theta_{base}) \qquad (A1.1)$$

783   where θ_{cum} stands for the cumulated number of degree-days starting arbitrarily in January, θ_{base} is the

784   temperature below which degree-days are not accounted for, set to 10°C in accordance with findings

785   from Furlan (2004, 1998) who showed that no larval development happened below this threshold value.

786   Denoting θ_{start} (resp. θ_{end}) the minimal (resp. maximal) number of cumulated degree-days above (resp.

787   below) which emergence starts (resp. ends with the entire pool of mature larvae having emerged), the

788   emergence rate writes

789
$$\tau(t) = \begin{cases} 0 & if\ \theta_{cum}(t) < \theta_{start} \\ \left(\dfrac{\theta_{cum}(t) - \theta_{start}}{\theta_{end} - \theta_{start}}\right)^{\alpha} & if\ \theta_{start} \leq \theta_{cum}(t) \leq \theta_{end} \\ 0 & if\ \theta_{cum}(t) > \theta_{end} \end{cases} \qquad (A1.2)$$

790   with α set empirically to 2.5 to ensure that the peak of emergence occurs in the middle of the emergence

791   window. As the effect of temperature was not in the scope of this study, we averaged the daily

792   temperatures in Le Rheu (Brittany, France) over a 10-year period (2008 to 2017), and we chose the

793   values of θ_{start} and θ_{end} that corresponded to late April and beginning of June (April 23rd and June 8th),

794   in accordance with published studies (Landl, 2010; Parker & Howard, 2001; Sufyan, 2007; Villeneuve

795   & Latour, 2011). The functional response for the emergence rate and the proportion of emerged adults

796   along time (applied to our temperature dataset) are illustrated on Fig. A1.

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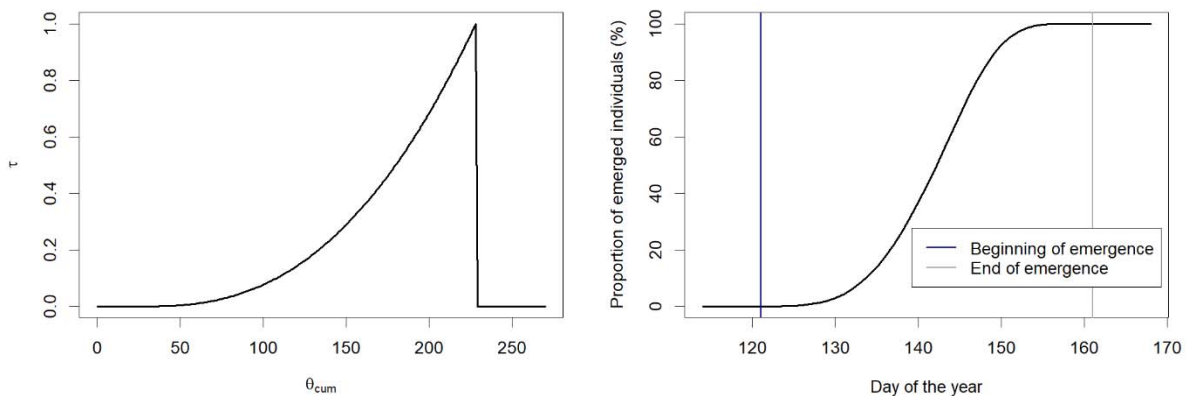
Fig. A1: (A) Functional response for the emergence rate: emergence rate vs cumulative degree-days. (B) Proportion of emerged adults along time.

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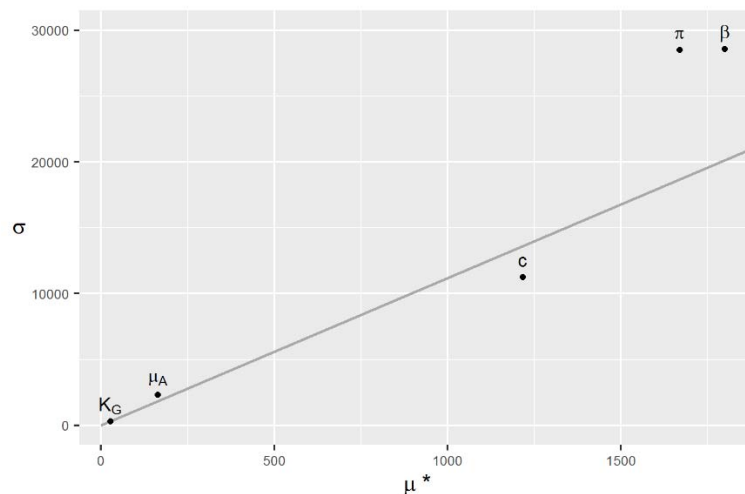
Fig. A2: Standard deviation (σ) vs. absolute means (μ^*) of elementary effects obtained from the Morris method. Elementary effects of five parameters on the time required to reach the mean density between K_C and K_G. The oblique grey line corresponds to $\mu^* = 2SEM$ (Standard Error of the Mean $SEM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

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Reference

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