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1 Short title: A billion dollar game of strategy

2 **The Effect of Farmers' Decisions on Pest Control**
3 **with *Bt* Crops: a Billion Dollar Game of Strategy**

4 Alice E. Milne^{1¶*}, James R. Bell^{2¶}, William D. Hutchison³, Frank van den Bosch¹, Paul D.
5 Mitchell⁴, David Crowder⁵, Stephen Parnell⁶ and Andrew P. Whitmore⁷

6

7 ¹Computational and Systems Biology, Rothamsted Research, Harpenden, UK

8 ²Rothamsted Insect Survey, Rothamsted Research, Harpenden, UK

9 ³Department of Entomology, University of Minnesota, St. Paul, USA

10 ⁴Department of Agricultural and Applied Economics, University of Wisconsin, Madison,
11 USA

12 ⁵Department of Entomology, Washington State University, Pullman, USA

13 ⁶School of Environment & Life Sciences, University of Salford, Manchester, UK

14 ⁷Sustainable Soils and Grassland Systems, Rothamsted Research, Harpenden, UK

15

16 *Corresponding author

17 E-mail: alice.milne@rothamsted.ac.uk

18

19 ¶ These authors contributed equally to this work.

20 **Abstract**

21 A farmer's decision on whether to control a pest is usually based on the perceived
22 threat of the pest locally and the guidance of commercial advisors. Therefore farmers in a
23 region are often influenced by similar circumstances, and this can create a coordinated
24 response for pest control that is effective at a landscape scale. This coordinated response is
25 not intentional, but is an emergent property of the system. We propose a framework for
26 understanding the intrinsic feedback mechanisms between the actions of humans and the
27 dynamics of pest populations, and demonstrate this framework using the European corn
28 borer, a serious pest in maize crops. We link a model of the European corn borer and a
29 parasite in a landscape with a model that simulates the decisions of individual farmers on
30 what type of maize to grow. Farmers chose whether to grow *Bt*-maize, which is toxic to the
31 corn borer, or conventional maize for which the seed is cheaper. The problem is akin to the
32 snow-drift problem in game theory; that is to say, if enough farmers choose to grow *Bt* maize
33 then because the pest is suppressed an individual may benefit from growing conventional
34 maize. We show that the communication network between farmers' and their perceptions of
35 profit and loss affects landscape scale patterns in pest dynamics. We found that although
36 adoption of *Bt* maize often brings increased financial returns, these rewards oscillate in
37 response to the prevalence of pests.

38

39 **Author summary**

40 A farmer's decision on whether to control a pest is usually based on the perceived threat of
41 the pest locally and the guidance of commercial advisors. Therefore farmers in a region are
42 often influenced by similar circumstances, and this can create a coordinated response to a
43 pest. This coordinated response, although not intentional, can affect ecological systems at the
44 landscape scale. Using the European corn borer as an exemplar system, we develop a
45 framework to explore the feedback mechanisms between pest populations and farmers'
46 decisions. We show that the form of communication network and the farmers' perceptions of
47 profit and loss influence the decisions made on pest control. Our work has implications for
48 other systems, whereby the ecology of a system is driven by individual decision makers
49 following similar heuristics and experiencing similar influences. Indeed, by understanding the
50 feedback mechanisms between pest populations and farmers' decisions we can predict
51 landscape-scale dynamics and determine how to manipulate these to sustain control.

52

53

54 **Introduction**

55 The European corn borer (*Ostrinia nubilalis*) (ECB), a serious pest of maize, cost the
56 American economy an estimated 1 billion US dollars annually at its worst in the early 1990s
57 [1, 2]. In 1996, *Bt* maize, a transgenic crop that expressed insecticidal proteins from the soil-
58 dwelling bacterium *Bacillus thuringiensis*, was introduced for control of the pest. Since then,
59 farmers have had to choose whether to plant conventional or *Bt* maize (Fig. 1). Their
60 decisions rest on the economic viability of *Bt*, given that future infestations of ECB cannot be
61 predicted. Specifically, farmers must predict whether increased returns from *Bt* will exceed
62 the technology fee, a financial premium for buying the transgenic seed [3, 4]. In some
63 situations, farmers believe that the economics favor conventional seed; more than half of
64 them believe that the price of *Bt* maize is too high to merit purchase [1, 5], particularly if their
65 crops have not recently been infested.

66

67 **Fig. 1. Influences on farmers' decisions and their impacts.** A schematic illustrating the
68 influences on farmers' decisions on what varieties of maize to grow, and how this impacts the
69 population dynamics of the European corn borer and the profitability of farming at a
70 landscape scale. The width of the green arrows indicates the approximate appropriation of
71 agricultural resources.

72

73 Hutchison *et al.* [1] showed that *Bt* maize generated an estimated \$230 million annual
74 benefit to maize growers in Illinois, Minnesota and Wisconsin. Much of this economic
75 benefit (75%) accrued to farmers who did not plant *Bt* maize; these farmers did not pay
76 technology fees but still benefitted from the area-wide suppression provided by those farmers

77 who cooperated to use *Bt* to reduce pest densities [1]. Other systems, such as cotton, have
78 shown similar benefits from area wide suppression of pests [6].

79 As such, the control of ECB can be evaluated through game theory because the
80 mechanisms of cooperation, such as reciprocity, reputation and spatial structure are
81 embedded in the farmer networks that mediate the population dynamics of the pest [7–10].
82 The system is akin to a ‘snow drift’ game [8]. The snow drift game is a metaphor for a
83 situation whereby the benefit that an individual, in this case a farmer, obtains for a given
84 strategy depends on the actions of others. In particular, if a farmer chooses to grow
85 conventional maize in a landscape where the pest is suppressed by other farmers growing *Bt*
86 maize, then this individual will benefit from the pest suppression without paying the
87 technology fee. On the other hand, in a situation where the pest is not suppressed at landscape
88 scale it is likely to be more profitable for an individual to grow *Bt* maize.

89 When deciding whether to plant *Bt* maize, farmers negotiate between ‘expert’ and
90 ‘local’ knowledge (Fig. 1). For example, Kaup’s [5] hierarchy of influences showed maize-
91 seed dealers and crop consultants appeared to have substantial influence, neighbors had
92 moderate influence, and extension agents had little influence on the farmers’ decisions to
93 plant *Bt* maize. More than 50% of farmers who anticipated having ECB problems chose to
94 plant *Bt* maize. The results emphasize an important principle in pest control: farmers’
95 perceived risks, rather than actual losses, play an important role in pest management [5, 11,
96 12]. This principle of ‘risk perception’ is crucial. If farmers’ underestimate the risk of
97 infestation and grow conventional maize then the pest will flourish and diminish yields. If on
98 the other hand farmers exaggerate the risk and plant too much *Bt* maize then there is an
99 increased risk that the pest will adapt to its new host and threaten the long-term production of
100 maize.

101 Here we build a framework for exploring understanding of the intrinsic feedback
102 mechanisms between the actions of humans and the dynamics of pest populations in a
103 structured landscape, and use the European corn borer in maize as an example. Our example
104 is intended to demonstrate the plausibility of the framework and so is illustrative rather than
105 predictive. Our models are kept simple to both aid the elucidation of our results and to reduce
106 the runtimes of the simulations. This particular example was chosen because there is a rich
107 source of data to support it. We build a mechanistic model of the population dynamics of
108 ECB in a 700-km long strip of the US Corn Belt. The models are parameterised to reflect a
109 maize system similar to that in the part of the US Corn Belt that passes through Minnesota
110 and Wisconsin. The model of the population dynamics includes the life cycle, dispersal and
111 ecology of the pest including its relationship with the pathogen *Nosema pyrausta*
112 (Microsporidia: Nosematidae), which is one of the most important natural enemies of the
113 ECB; this parasite reduces the number of surviving offspring, and is cited as the primary
114 reason for the observed cycle in the population density [13–16]. The landscape model is
115 spatially-explicit and parameterized so that one half has similar county sizes, farm sizes, and
116 density of maize crops to those in Minnesota and the other to those in Wisconsin. We show
117 how this model captures the behavior of the ECB-population dynamics in the observed
118 empirical data at a coarse spatial scale. Importantly, analysis of the model shows that even
119 when the infected population is reduced to small numbers, it retains the capacity to recover
120 and so the natural control persists.

121 We then introduce a sociological layer to the model. We simulate the processes by
122 which individual farmers decide whether to grow *Bt* maize or conventional maize. The
123 decision is based predominantly on likely profit: the probability that a farmer will chose a
124 given strategy is based on the information that he or she has on the profits achieved under *Bt*
125 maize and conventional maize in recent seasons. For any given farmer, the source of this

126 information will depend on the network of communication. Here we explicitly model four
127 different networks of communication. In particular we explore how the form of the network
128 affects the uptake of *Bt* maize over time, the pest population dynamics and the long term
129 profits of the farmers in the landscape. We show that the form of the network impacts the
130 feedback mechanism between pest populations and farmers' decisions that affect landscape-
131 scale dynamics. We show that independent decision makers that follow similar heuristics and
132 are influenced by the same circumstances can create an apparent coordinated response which
133 affects ecological systems at landscape scales. This coordinated response is not intentional,
134 but is an emergent property of the system.

135

136 **Methods**

137 Below we present the components of the model framework, including the pest dynamics
138 model, the farmer decision model and four different communication networks. We then use
139 this framework to explore the effect of the different communication networks and the
140 responsiveness of the farmers to loss on (i) the pest dynamics, (ii) the uptake of *Bt* maize and
141 (iii) the long term losses of the farmers.

142 **European corn borer and *Nosema pyrausta* model**

143 We developed a model to explore the population dynamics of ECB and its natural
144 enemy, the pathogen *Nosema pyrausta*, and the impact of ECB on maize crops in a
145 landscape. This landscape was based on national agricultural census statistics from 1997,
146 2002 and 2007 on county sizes, farm sizes and numbers, harvested areas and the area of
147 maize grown in Wisconsin and Minnesota [17–19]. We used a grid of 300 x 1400 cells that
148 equates to a 150km x 700km strip. Each cell represents 25 ha (0.5km x 0.5km), similar to the

149 typical size of maize fields in the region. One half of the simulated landscape was
150 parameterised to be similar to Wisconsin and the other to Minnesota. We partitioned the two
151 states into counties, with county sizes reflecting the actual distribution of county sizes in each
152 state. We defined farms as connected cells in which arable crops could be grown. The
153 number of farms in each simulated county, and the distribution of their sizes, reflected the
154 true distribution of arable land on farms in each state. Simulated farms were fitted into the
155 county, along with uncropped areas at random (see S1). The landscape was generated
156 stochastically and so is a realisation of a random process.

157 Crops were assigned county by county. On average, maize accounted for 44% of the
158 cropped area in Minnesota and 37% in Wisconsin [17–19]. Cropped cells were then allocated
159 at random as maize or other. Each year, the proportion of maize in a given county was
160 resampled, and cropped cells allocated again at random to maize or other. This process
161 allowed for a proportion of fields to have maize crops grown consecutively and others to
162 have rotations with a non-host crop for ECB. We made the simplifying assumption that ECB
163 only develops in grid cells with maize. In each of these cells we use an abundance-based
164 population model to describe the development of a population of ECB that is susceptible to
165 the pathogen *N. pyrausta* and one that is infected. Our model did not include the effect of
166 other natural enemies of ECB or climate, and so was not expected to accurately describe the
167 historic dynamics of the ECB. Rather, its purpose was to capture the population cycle
168 attributed to *N. pyrausta* and to simulate the effect of *Bt* maize on larval survival.

169 In the model, eggs hatch into larvae that pass through five instar stages. The survival
170 of the larvae through to pupation is density dependent. We assume that the *Bt* toxin reduces
171 the number of larvae that reach instar 3 by 99.9% [20]. We do not consider insecticides as a
172 control measure as these are considered largely ineffective because after the neonate stage,
173 the ECB larvae are concealed within the maize plant, thus avoiding direct contact with an

174 insecticide's active ingredients. Adults emerge following pupation, then disperse and mate,
175 and then females disperse before oviposition and the cycle starts again. We assume two
176 generations of ECB per year, as is typical in Minnesota and Wisconsin. The larvae from the
177 second generation overwinter in stalks, and so their survival rate is lower than that of the first
178 generation. Infection by *N. pyrausta* travels through both horizontal and vertical pathways.
179 We assume that infected adult males do not pass infection to their young, but that females
180 pass on infection to 85% of their eggs [21]. Infection passes horizontally through the
181 population during the larvae stage when susceptible (uninfected) larvae come into contact
182 with frass from infected larvae. The infection rate is modelled as density dependent. The
183 survival of the infected population at each stage is smaller than the healthy population. The
184 parameter values of the model were based on the body of work by Onstad and colleagues [12,
185 21, 22] (see S2 for full model description).

186 We modelled the dispersal of the populations in four stages: pre-mating dispersal,
187 mating, post-mating dispersal of females, and oviposition. The dispersal functions represent
188 the integration of the movement of moths over a period of days. The dispersal of insects is
189 often modelled with an exponential dispersal kernel which has a mode at the origin. The
190 literature [23–24] suggest that in the case of the corn borer, however, this may not be
191 appropriate as instinct and environmental factors force large numbers of adults from their
192 natal fields. For this reason, and for computational efficiency we chose to model dispersal
193 using a beta distribution, which has a flexible mode. We assume dispersal is the same in all
194 directions, and that at the boundary of the landscape the moths are reflected back.

195 We base our dispersal estimates on observations in the literature which demonstrate
196 seasonal differences in the dispersal of spring and summer adults [23–26]. Crop rotation and
197 lack of adequate humidity in crops during the day time can force newly emerged adults to
198 move from their overwintering field before initiating sexual activity [27]. The probability

199 density function (PDF) that describes the pre-mating dispersal in spring has a mode of 10km
200 and 90% of the population travelling less than 30 km. The dispersal of infected moths is
201 reduced by 80%. Dispersal in summer is more conservative with a mode of 1km and 90% of
202 the adult moths fly less than 15km. Under typical conditions, the pre-oviposition period has a
203 mean of 3.6 days [14]. Thereafter the mean oviposition period is approximately 10 days with
204 oviposition decreasing with time. During this time a female could cover a considerable area.
205 We assumed that for spring the mode of the post-mating PDF was 35 km and that 90% of the
206 population travel less than 60 km, and that in summer the mode was 5 km with 90% of the
207 population traveling less than 30 km (see Fig. 2).

208

209 **Fig. 2. The functions used to model the dispersal of the European corn borer.** The
210 dispersal functions for adult moths pre- and post- mating in spring and summer.

211 The model of the ECB population density expresses the cycle of infestation caused by *N.*
212 *pyrausta* observed in the field data with a similar wavelength [2]. When *Bt* was introduced
213 into the landscape, the cycle collapsed and the pest was suppressed in a way similar to
214 observed patterns [2] (Fig. 3).

215

216 **Fig. 3. Overwintering larvae.** Average numbers of overwintering larvae from Minnesota
217 over time (solid black line) during a period where the proportion of *Bt* maize broadly
218 increased (dashed red line). Our simulation model (solid blue line) captures the behavior
219 observed in the field with a cycle in the population of similar wavelength to that observed in
220 the data. The introduction of *Bt* maize results in this cycle being damped but still persisting
221 (the cycle is under-damped in this case — see S2).

222 **Modelling the decision process**

223 In the model, farmers growing maize face the decision of whether to plant *Bt* or
224 conventional maize. As described above, the decisions on which type of maize to grow
225 directly impacts the survival of the ECB larvae and so the population dynamics of the pest.
226 Kaup [5] surveyed 4000 farmers in Wisconsin and Minnesota and found that the most
227 common reasons for growing *Bt* maize were: (i) to increase yield; (ii) to control insects
228 better; and (iii) they anticipated ECB problem. The most common reasons for not using *Bt*
229 maize were (i) the price of *Bt* seed was too high; or (ii) no ECB problem was anticipated.
230 Although growers may misconceive the financial impact of the drivers described above, these
231 drivers imply a profit-based decision. Other factors including farm size, age, education and
232 available market information have been shown to influence the adoption of GM crops and
233 complex empirical models have been proposed to describe these effects on farmer decisions
234 [28]. To both ensure the easy interpretation of our results, we chose to use a simple model
235 based on perceived profit.

236 We assumed that the decision process is driven by the financial impact of ECB, and
237 that farmers make decisions based on recent years' experience [5]. We used data from
238 Wisconsin and Minnesota on the estimated benefit ($\$ \text{ ha}^{-1}$) from *Bt* maize and the increase in
239 the area of *Bt* maize grown (as a percentage of total maize grown) between 1995 and 2009 to
240 model the probability (p) of farmers changing cropping strategy (Hutchison et al., [1]). The
241 following exponential function was used based on empirical and theoretical considerations:

$$242 \quad p = 1 - \exp\left[-\beta(r_A - r_f)\right] \text{ where } r_A > r_f$$

$$243 \quad p = 0 \text{ otherwise.}$$

$$244 \quad (1)$$

245 Here β is a parameter, r_F is the reward the farmer perceives was attained under the chosen
246 strategy and r_A is the reward the farmers perceives would have been attained under the
247 alternative strategy, so that the difference $r_A - r_F$ measures the perceived net benefit for *Bt*
248 maize adoption. This model is not only more parsimonious than a more traditional logistic
249 model, but also has better goodness of fit criteria (S3). Furthermore, the exponential model is
250 a constant absolute risk aversion utility function for the representative farmer with parameters
251 estimated to fit the observed state-level *Bt* maize adoption data and estimated benefit [29, 30].
252 The parameter β quantifies farmer responsiveness to the perceived gain from *Bt* maize
253 adoption (or equivalently, ECB loss). The regression estimate for β was 0.0055 with a
254 standard error of 0.00174 with no evidence to support separate parameters for each state. In
255 practice it would be possible to influence farmer responsiveness (i.e. β) through subsidy,
256 taxation or education. For example if farmers were encouraged to be cautious about returning
257 to conventional maize then farmers growing *Bt* maize would be less responsive when they
258 experienced an apparent benefit reduction. We used the fitted value \pm three standard errors to
259 define the range of values for β that we explored in our analysis.

260 For each season, we sample an individual farmer's decision from a distribution whereby
261 the probability of changing strategy is p (as defined in Equation 1). This allows us to
262 implicitly include a range of individual behaviors from the intransigent farmer who finds a
263 preferred strategy and will not change, to the receptive farmer who will try new practices. It
264 also implicitly includes other social factors which we do not explicitly account for.

265

266 The farmer's reward is given by the average financial reward from his maize fields
267 calculated as

268
$$r = (Y - Y_L)m_p - F, \quad (2)$$

269 Where Y is the expected yield in a ECB-free crop (t ha^{-1}), Y_L is the loss in yield due to the
 270 ECB (t ha^{-1}), m_p is the crop price ($\text{\$ t}^{-1}$) and F is the technology fee ($\text{\$}$), which is the seed
 271 price difference between conventional and *Bt* maize. We do not include varietal effects that
 272 could modify yields slightly, but assume that all maize crops have the same expected yield
 273 (10 t ha^{-1}). We assume that this yield is reduced by ECB according to the function given in
 274 the supplementary information of Hutchison et al., [1]:

275
$$Y_L = Y \frac{0.021(2.56x + 5.65\sqrt{x})^{1.16}}{[(2.56x + 5.65\sqrt{x})^2 + (3.4 + 1.73x)^2]^{0.29}}, \quad (3)$$

276 Where x is the average number of overwintering larvae per plant. To be consistent with the
 277 data used to parameterise the landscape model we assume $F = 16 \text{ \$ ha}^{-1}$ and a crop price (m_p)
 278 of $99 \text{ \$ t}^{-1}$ which are averages for Minnesota and Wisconsin between 1996 and 2009 [1].

279 **Communication networks**

280 Given that we can calculate the reward (r) for growing maize in any particular field we
 281 must consider how to calculate the reward the farmer perceives was attained under each
 282 strategy (i.e. r_F and r_A). The reward for a given strategy may be calculated from the rewards
 283 obtained for this strategy over a given area of the landscape, i.e. a farmer's perceived reward
 284 depends on the network of communication and how much credence the farmer gives to the
 285 information available to them. Kaup [5] showed that growers who had reported an insect
 286 problem in one year were likely to grow *Bt* maize in the next, which is consistent with
 287 farmers who grow other *Bt* crops [31]. In Kaup's study the state-reported insect levels did not
 288 significantly influence behavior. Therefore we assume that a farmer perceives that the reward

289 for their chosen strategy (r_F) is given by the average reward from across their fields, taking
290 no account of the success of that strategy in their neighborhood.

291 To inform on the perceived reward from the alternative strategy we consider four
292 networks of communication that we shall refer to as: (i) landscape-network; (ii) neighbor-
293 network; (iii) Kaup-network and (iv) varying-response-network. There are two theoretical
294 extremes: the first is where each farmer has information from across the whole landscape,
295 akin to accessing web-based crop data. In this scenario the perceived reward for the
296 alternative strategy is the average of the rewards for the alternative strategy across the
297 landscape. We call this the ‘landscape-network’. The second is where each farmer has
298 information only from farms that neighbor their own, which may reflect how traditional
299 farming decisions are made alone or within cooperatives. In this scenario the reward for the
300 alternative strategy is given by the average reward that this strategy attains in farms that
301 neighbor the farmer. We call this the ‘neighbor-network’.

302 Research shows that when farmers decide which varieties to grow they may consult
303 family and friends, other farmers, commercial newsletters, county extension agents and
304 university specialists. Kaup [5] reports that 40.2% of farmers acknowledged that a major
305 reason to grow *Bt* was that it was recommended by their seed dealers or consultants.
306 Similarly 7.9% of farmers acknowledged recommendation by a neighbor, and 3.4%
307 acknowledged recommendation by university or extension agencies. Normalizing these
308 percentages to sum to 100%, we simulate a communication network whereby a farmer has a
309 probability of 0.78 of being influenced by a consultant, a probability 0.15 of being influenced
310 by a neighbour and a probability of 0.07 of being influenced by a university. According to
311 those probabilities each farm is assigned a communication network type. For those assigned
312 to be neighbor-influenced we calculate the reward of the alternative strategy by averaging the

313 scores of this strategy from farms within 1km. We assume consultants operate over a county,
314 and so for farmers assigned to be consultant-influenced we calculated the reward as the
315 average reward across a county. Finally we assume universities operate at the state level and
316 so the reward for those assigned to be university-influenced is given by the average reward
317 across the state. This network, which we refer to as the ‘Kaup-network’, is arguably more
318 common in today's farming environment than the two former scenarios. For each network we
319 set the responsiveness parameter β (Equation 1) to 0.0055, 0.0003 and 0.0108, which are the
320 value fitted to the data, and that value \pm three standard errors.

321 Kaup [5] showed that if farmers had planted *Bt* in the past then they were more likely
322 to use it in the future. This tendency is incorporated into the model by scaling β in Equation
323 (1) so that farmers who have used *Bt* maize in the past are more responsive to loss of profit.
324 Our final network, the ‘varying-response-network’, incorporates a reluctance for farmers to
325 change back from *Bt*-maize to conventional maize. It assumes a Kaup-network with the
326 probability of a farmer switching to *Bt* maize, having previously tried it given by Equation (1)
327 with $\beta=0.0055$ otherwise $\beta=0.0003$.

328

329 **Implementing the model**

330 We ran each simulation for 100 seasons. At the end of each season the reward $r_F(i)$ is
331 calculated for each farm i along with the perceived reward for the alternative strategy $r_A(i)$.
332 The probability that the farm strategy will change is calculated according to the farmer’s
333 responsiveness to loss. This probability is used to determine if they change strategy. Crops
334 are rotated and fields growing maize are assigned to *Bt* or conventional maize according to
335 the calculated strategy.

336

337 Results

338 Analysis of the European corn borer and *Nosema pyrausta* model

339 To explore the behavior of the solutions of the model we considered the equations
340 without the spatial component. Ignoring dispersal, the model equations listed in S2 reduce to
341 the following set of difference equations:

$$342 \quad \tilde{S}(t) = \frac{a(S(t) + cP(t))e^{-\alpha P(t)}}{\nu + S(t) + P(t)}$$

$$343 \quad \tilde{P}(t) = \frac{k[P(t) + b(S(t) + cP(t))(1 - e^{-\alpha P(t)})]}{\nu + S(t) + P(t)}$$

$$344 \quad S(t+1) = \omega_1 \frac{a(\tilde{S}(t) + c\tilde{P}(t))e^{-\alpha \tilde{P}(t)}}{\nu + \tilde{S}(t) + \tilde{P}(t)}$$

$$345 \quad P(t+1) = \frac{k[\tilde{P}(t) + b(\tilde{S}(t) + c\tilde{P}(t))(1 - e^{-\alpha \tilde{P}(t)})]}{\nu + \tilde{S}(t) + \tilde{P}(t)}$$

346 (4)

347 where $S(t)$ and $P(t)$ represent the number of susceptible and infected eggs in year t , for the
348 first generation respectively and $\tilde{S}(t)$ and $\tilde{P}(t)$ are for the second generation. The first pair of
349 equations describes the summer generation and the second pair the autumn-spring generation.
350 Many of the parameters result from combinations of biologically meaningful parameters from
351 the full model (see S2). Parameters $a = 929.8$ and $k = 85.6$ capture the population increase
352 from births modulated by survival rates for susceptible and healthy populations respectively.
353 Parameter $c = 0.15$ is the proportion of susceptible eggs produced by an infected female. The
354 term $(1 - e^{-\alpha P(t)})$ determines the proportion of the healthy population that becomes infected,

355 where $\alpha=0.72$ controls the infection transfer from the infected to susceptible population.
 356 Parameter $b=2.31$ relates to the survival of this recently infected population. The carrying
 357 capacity parameter $v=130.7$ controls the density dependent survival of the larvae, parameters
 358 $\omega_1=0.081$ and $\omega_2=0.02835$ relate to the overwintering survival of the susceptible and infected
 359 populations respectively.

360 Analysis of these equations shows three steady-states, i.e. solutions where the rates of change
 361 of healthy population (S) and the infected population (P) are zero: (C1) [$P^* = 0, S^* = 0$], (C2)

362 [$P^* = 0, S^* = \frac{a^2\omega_1 - v^2}{a + v}$], and (C3) [$P^* = P_0, S^* = S_0$], where both P_0 and S_0 are positive real

363 values. Linearization around these points determines the behavior of the solutions of the
 364 equations [32]. The first steady-state (C1) relates to the trivial solution whereby both healthy
 365 and infected populations become extinct; the second (C2) relates to the solution where the
 366 infected population becomes extinct; and the third steady-state (C3) relates to the solutions
 367 where both the healthy and the infected population densities are larger than zero and the total
 368 population cycles. It can be shown that (C3) exists, implying that *N. pyrausta* survives in the

369 system, for parameter combinations such that $\sqrt{\omega_2} \left(\frac{k + ab\hat{S}}{v + \hat{S}} \right) > 1$, where $\hat{S} = \frac{a^2\omega_1 - v^2}{a + v}$. For

370 the model parameters used, and a wide range around these parameters, the steady-state (C3)
 371 always exists supporting the hypothesis that even if ECB is suppressed to low levels, the
 372 infected population will survive and the natural control given by *N. pyrausta* persists.

373

374 **The snow-drift game**

375 Under the landscape-network simulation shown in Figs 4a and 4b, the percentage of
 376 *Bt* maize oscillates between approximately 1% and 95% over time. Larval populations are

377 driven by the *Bt* adoption and oscillate similarly, with the largest levels prior to the maxima
378 in the *Bt* cycle. Increasing farmer responsiveness to economic loss (i.e. increasing the
379 parameter β in Equation 1) increases the frequency and amplitude of the oscillation;
380 reducing farmer responsiveness reduces the frequency and amplitude of the oscillation. The
381 average larval density is held near or below the economic threshold (0.06 larvae per plant for
382 the model parameterization reported here), however, in some parts of the landscape the
383 density was much higher. The results from the Kaup-network are similar to the landscape-
384 network, but with a slightly higher oscillation frequency and slight dampening (see S4).

385

386 **Fig. 4. Results from the landscape-network, neighbor-network, and varying-response-**
387 **network simulations.** The top pane of each pair shows the proportion of *Bt* maize and
388 bottom panes show the average number of overwintering larvae per plant across the two areas
389 of the landscape, one in Wisconsin and the other in Minnesota. The simulation was started
390 with 1% of the maize as *Bt* distributed randomly in the landscape.

391

392 In the neighbor network the solution slowly converges to a state where the proportion
393 of *Bt* maize is approximately 0.67 in Minnesota and 0.24 in Wisconsin (Fig 4c). The
394 difference in adoption rate results because the neighborhood connections are stronger in
395 Minnesota than in Wisconsin due to a greater density of farms in Minnesota. Indeed, in the
396 simulated Wisconsin landscape, more farms are likely to be isolated and so have no
397 neighbors growing *Bt* maize to compare profits with (see Fig 5a). Simulated ECB populations
398 in Minnesota are lower than those in Wisconsin, where adoption of *Bt* maize was smaller (Fig
399 4d). Figure 5b shows the average number of overwintering larvae per plant in each cell for a
400 single year of the simulation. The average numbers of larvae in Wisconsin reach larger levels,

401 and even for isolated farms in Minnesota the pest is suppressed by the larger amount of *Bt*
402 maize grown in the surrounding area. For example between years 30 and 50 of the simulation
403 shown in Fig. 4 the maximum number of ECB in any cell was 8.12 larvae per plant for
404 Wisconsin and 2.69 for Minnesota. The responsiveness of the farmer to loss (parameter β)
405 affects the convergence rate with smaller values of β taking longer to converge.

406 Results from the simulation where farmers were more responsive to loss from
407 conventional maize if they had experience of growing *Bt* maize (varying-response-network
408 simulations) are shown in Figs 4e and 4f. The simulation illustrates that adoption of *Bt* maize
409 is more rapid than that of conventional maize.

410

411 **Fig. 5. The spatial distribution of crops and larvae in a single year of the simulation.** (a)

412 The land use in year 73 of simulated landscape under the neighbor-network. The left half of
413 the landscape represents Minnesota (abscissa from 0 to 350 km) and the right Wisconsin
414 (abscissa from 350 to 700 km); (b) shows the corresponding average number of
415 overwintering larvae per plant. Enlarged sections show the spatial distributions in more
416 detail.

417

418 Table 1 lists the average losses ($\$ \text{ ha}^{-1} \text{ year}^{-1}$) across the landscape between year 20
419 and 100 under each simulation, and the average proportion of the maize that is *Bt*. Initial
420 years were excluded to allow the simulation to stabilize. Losses (L) were calculated from a
421 baseline whereby conventional maize was grown in an ECB-free landscape, i.e.,
422 $L = Y_L m_p + F$, where Y_L is the yield loss caused by the ECB, m_p is the crop price and F is
423 the technology fee. These results are based on 10 realisations of each simulation. The average

424 proportions of *Bt* maize are similar across the networks ranging between 0.41 (when
 425 $\beta = 0.0108$) and 0.67 (when $\beta = 0.0003$). The standard deviation of the proportions of *Bt*
 426 maize were generally smaller for the less responsive farmers ($\beta = 0.0003$). For the values β
 427 considered, mean losses are least in the varying-response-network scenario and greatest in the
 428 neighbor-network scenario. We also simulated losses under scenarios where the proportion of
 429 *Bt* in the landscape was fixed at a given proportion, with the smallest simulated losses
 430 averaging 11 \$ ha⁻¹ year⁻¹ with a proportion of *Bt* of 0.61. The sensitivity of our results to
 431 model assumptions is discussed in S5.

432

433 **Table 1.** The average losses and the average proportion of the crop that is *Bt* between year 20
 434 and 100 under each simulation according to communication network type and value of the
 435 parameter β , which changes the responsiveness of the farmer to loss. The standard deviations
 436 are given in parentheses.

Network type	Value of β	Loss/\$ ha ⁻¹ year ⁻¹	Proportion of <i>Bt</i>
Landscape-network	0.0003	15.63 (0.182)	0.67 (0.073)
	0.0055	14.28 (0.302)	0.45 (0.319)
	0.0108	14.02 (0.216)	0.51 (0.312)
Neighbor-network	0.0003	30.02 (0.420)	0.50 (0.045)
	0.0055	27.51 (0.548)	0.51 (0.043)
	0.0108	27.64 (0.749)	0.50 (0.039)
Kaup-network	0.0003	17.15 (0.132)	0.58 (0.089)

	0.0055	16.12 (0.141)	0.43 (0.304)
	0.0108	15.96 (0.278)	0.42 (0.275)
Varying-response-network	–	13.90 (0.285)	0.56 (0.088)

437

438 **Comparison of the dynamics of farmer behaviour with data**

439

440 To test the plausibility of the results from our model, we compared the observed and
441 simulated dynamics of the relationships between loss incurred by growing conventional
442 maize (calculated as above) and the percentage of maize that was *Bt* (Fig. 6). The relationship
443 between these two variables changes year on year depending on the corn borer population in
444 the landscape. The dynamics observed in the data from Minnesota and the simulations for the
445 varying-response-network are broadly similar (Fig. 6a and e). The percentage of *Bt* maize
446 grown increases until it is not profitable to grow *Bt*, then farmers start to move back to
447 conventional maize only to return to *Bt* maize as losses increase later. The period of dis-
448 adoption shown in Fig 6a is unlikely to be solely driven by the farmers’ perceptions of loss
449 from corn borer infestation as it coincides with a period where there was a drop in confidence
450 for the marketability of *Bt* maize, however our analysis gives support to the hypothesis that
451 farmers’ perceptions of loss might explain dynamics. The Minnesotan data shows a second
452 small drop in adoption over a two year period when the losses reach $-13 \text{ \$ ha}^{-1}$ thereafter
453 there is a steady increase in the percentage of *Bt* maize grown with no relationship to loss.
454 Observed dynamics for Wisconsin show slower uptake of *Bt* maize compared with Minnesota
455 (Fig. 6b). This may reflect the fact that maize is grown on a much larger scale in Minnesota
456 compared to other states including Wisconsin, which in turn may have implications for the

457 way in which information is shared and how fields are managed in these states [33]. Similar
458 to the neighbor network we also see that levels of *Bt* maize that initially control losses are
459 subsequently less effective at the landscape scale and so the use of *Bt* is increased. No ECB
460 resistance to *Bt* maize has been reported and so these changes in loss result from other factors
461 such as climate or *N. pyrausta*.

462

463 **Fig. 6.** The loss in profit incurred by growing conventional maize compared with growing *Bt*
464 maize plotted against the percentage of maize that is *Bt*. The arrow indicates the direction of
465 time. Subplots (a) and (b) are based on data from states in the Corn Belt and subplots (c) to
466 (e) are based on simulations.

467

468 Discussion

469 Liu et al. [34] highlighted the importance of linking sociological influences to ecological
470 systems. In our simulation we show how economic conditions can result in the suppression of
471 a pest throughout a landscape. Our results accord with the findings of Bell et al. [2] who
472 observed the impact of a coordinated response to ECB, and showed the planting of *Bt* maize
473 in Minnesota led to a collapse in the cycle of ECB caused by *N. pyrausta*. In Wisconsin,
474 however, where less *Bt* maize was grown, the cycle persisted. Similarly, Hutchison *et al.* [1]
475 showed that farmers who grew conventional maize benefited from the area-wide suppression
476 from *Bt* maize in the region. Our model shows a similar phenomenon, particularly
477 exemplified in the neighbor-network simulation where a smaller proportion of *Bt* maize in
478 Wisconsin resulted in a larger density of ECB compared with Minnesota, so that ECB
479 population density continued to exhibit the *N. pyrausta* driven cycle. The landscape scale

480 effects of the decisions made by individuals have been observed in other agricultural systems
481 in which farmers' decisions are influenced by social or economic factors or both and appear
482 to be coordinated. The farmers' behaviors results in substantial impacts on the population
483 dynamics of species across landscapes. For example, Bianchi et al. [35] reported that
484 coordinated changes in landscape composition negatively impact natural pest control, and
485 Klein et al. [36] showed how agricultural intensification threatens wild bee pollination
486 services at the landscape scale.

487 In our example, we show that decisions made by farmers on an individual basis impact
488 ECB populations and the profitability of growing maize in the landscape. These decisions are
489 driven by a range of external influences, from the advice of neighbors to information from
490 extension specialists. We showed that the form of the network and the farmer responsiveness
491 to loss substantially impact the dynamics of the system at all trophic levels. Generally we
492 found that *Bt*-maize adoption oscillated in response to the prevalence of ECB in the
493 landscape, and that the communication network and responsiveness of the farmer to loss
494 influenced the amplitude and frequency of this oscillation. As the scale of communication
495 networks increased so did the rate at which change occurred. This phenomenon was observed
496 by Lambin et al. [37] who reported that rapid land-use changes often result when global
497 influences replace local drivers. For example the global markets demand for certain
498 commodities may rapidly change landscapes from longstanding diverse land-use patterns to
499 more uniform cropping.

500 Of the networks we considered, the varying-response-network performed the best in
501 terms of minimising losses and showed a reasonably constant proportion of *Bt* maize grown
502 across time (Table 1). The farmers in this simulation had good access to information from
503 across the landscape and were quicker to re-adopt *Bt* maize at the first sign of losses from
504 ECB, yet slower to return to the more risky strategy of growing conventional maize.

505 Importantly, our simulations show that to avoid extreme events some resistance to change
506 must be inherent in the system. The varying-response-network did not outcompete the
507 simulation with a fixed percentage of 61% *Bt* maize however. This outcome is compatible
508 with the initial US-EPA resistance management requirements for ECB of at least 20% non-*Bt*
509 maize planted each year, to serve as a refuge to maintain non-*Bt* selected susceptible moths in
510 the landscape [1].

511 One aspect that we did not consider is that seed companies use market power to protect
512 against the sales of *Bt* maize oscillating by selling the ECB-*Bt* maize seed bundled with other
513 desirable seed traits and by reducing ECB-*Bt* maize prices so that farmers continue to buy the
514 ECB-*Bt*-maize [38]. Similarly, seed dealers may promote *Bt* maize seed over conventional
515 because they themselves receive a better rate of commission for *Bt* maize. The effect of such
516 actions would be to inflate the reward farmers perceive is obtained from growing *Bt* maize,
517 and so increase the adoption of *Bt* maize and drive the trajectories shown in Fig. 4 to the
518 right. Indeed any volatility in the price of seed or the harvested crop will impact the dynamics
519 of the system. Increases in the price of maize or a reduction in the technology fee result
520 would result in a lower tolerance to corn borer larvae. Another area not included in our
521 analysis is the effect of farmer decisions on the evolution of resistance ECB to *Bt* maize. A
522 recent review by Tabashnik et al.[39] found no evidence of a decrease in the susceptibility of
523 ECB to Cry1Ab in *Bt* maize in the field. Others have used modelling to evaluate the effect of
524 refuge planting strategies and including two or more toxins within a cultivar (pyramided
525 toxins) on the rate of resistance evolution [22, 40–42]. These studies aim to guide regulatory
526 policy designed to mitigate the threat of resistance. It is generally held that the greater the
527 density of *Bt* maize in the landscape the faster the evolution of resistance. It follows that
528 within the context of farmer behaviour, social factors that increase the use of *Bt* maize in the
529 landscape would increase the rate of the evolution of resistance. Increased resistance of ECB

530 to *Bt* maize would in turn result in farmers seeking alternative methods of control perhaps in
531 the form of new toxins, or cropping strategies.

532 Our work has implications for other systems, whereby the ecology of a system is driven
533 by individual decision makers following similar heuristics and experiencing similar
534 influences. Examples include important systems where co-ordinated control can result in
535 area-wide suppression of a pest or diseases. These systems typically involve insect pests that
536 either cause damage to crops by herbivory (e.g. *Meligethes aeneus* F, *Spodoptera exempta*
537 *Walker*) or act as a vector for disease [43]. The model framework presented here also has
538 application to other areas such as disease prevention in a public health setting. There are clear
539 parallels between landscape suppression of pests and diseases, and the herd immunity
540 afforded when sufficient numbers of the population vaccinate. A number of modelling studies
541 have been done to explore behaviour in the context of vaccination to try to understand the
542 conditions that cause vaccine coverage to fall [44–46]. The conceptual difference between
543 the vaccination studies and our study is that in our study the host of the insect pest is fixed in
544 space and the insect moves across space, whereas in the case of human diseases the hosts
545 move and transmit disease to one another. Our decision model was based on the farmers’
546 perceived profits. However, other social factors such as perceived food safety, the threat to
547 non-target species and resistance management can effect decisions [47]. These factors often
548 do manifest as economic factors but where they do not, they could be included in a model
549 framework such as the one described by using opinion dynamics models [48]. Vaccination
550 uptake is an example of a situation where often decisions are based on a perception of the
551 safety rather than financial incentives (44). By understanding the dynamics of farmer
552 decisions we can determine how to manage better the system, through improved
553 communication, subsidy or taxation, to achieve robust and cost effective area-wide control,
554 while minimizing the risk of the evolution of resistance to control strategies.

555

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560

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686

687 **Supporting Information**

688 **S1 The Landscape Model.**

689 **S2 The European Corn Borer Model**

690 **S3 Figure of the data used to support the decision model.** The increase in area of *Bt* grown
691 as a proportion of the area of non-transgenic maize between year t and $t+1$ plotted against the
692 net benefit of growing *Bt* calculated for year t (Hutchison et al., Science 2010; 330: 222).

693 **S4 Figure of the results from Kaup-network simulation.** (a) the percentage of maize
694 grown in the landscape that is *Bt* and (b) the average number of larvae per plant across the
695 two areas of the landscape. The parameter $\beta = 0.0055$.

696 **S5 Sensitivity of Results from Snow Drift Game to Model Assumptions**

697 **S6 Data on the maize yields, *Bt* uptake, average ECB per plant.** Data on maize yields, *Bt*
698 uptake and average ECB per year for Minnesota and Wisconsin with estimates of loss due to
699 ECB. These data and calculations were reported in Hutchison et al., Science 2010; 330: 222.