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Biological control of the chestnut gall wasp with *T. sinensis*: A mathematical model

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1 Biological control of the chestnut gall wasp with *T.*
2 *sinensis*: a mathematical model.

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8 **Abstract**

The Asian chestnut gall wasp *Dryocosmus kuriphilus*, native of China, has become a pest when it appeared in Japan, Korea, and the United States. In Europe it was first found in Italy, in 2002. In 1982 the host-specific parasitoid *Torymus sinensis* was introduced in Japan, in an attempt to achieve a biological control of the pest. After an apparent initial success, the two species seem to have locked in predator-prey cycles of decadal length. We have developed a spatially explicit mathematical model that describes the seasonal time evolution of the adult insect populations, and the competition for finding egg deposition sites. In a spatially homogeneous situation the model reduces to an iterated map for the egg density of the two species. While, for realistic parameters, the map would support the hypothesis of biological control, the full model, in the same parameter range, does not give such a clear-cut answer. In particular, according to the spatially explicit model, the introduction of *T. sinensis* would spark a traveling wave of the parasitoid population that destroys the pest on its passage. Then, depending on the value of the diffusion coefficients of the two species, the pest may later be able to re-colonize the empty area left behind the wave. When this occurs the two populations do not seem to attain a state of spatial homogeneity, but produce an ever-changing pattern of traveling waves.

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9 1. Introduction

10 Since its first report in 2002 the Asian chestnut gall wasp *Dryocosmus*
11 *kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) is affecting many chestnut
12 ecosystems in Europe and its range is continuously expanding. Native of China,
13 it established as a pest in the mid 20th century in several countries, being re-
14 ported in Japan (1941) (Moriya et al., 2003), in Korea (1958) (Cho and Lee,
15 1963), in the United States (1974) (Rieske, 2007) in Nepal (1999) (Abe et al.,
16 2007), and in Canada (2012) (Huber and Read, 2012).

17 In Europe, *D. kuriphilus* was first found in Italy and reported only in 2002
18 (Brussino et al., 2002). It was added to the European Plant Protection Orga-
19 nization (EPPO) A2 Action list (EPPO, 2005) in 2003. Despite the European
20 Commission Decision 2006/464/EC of 27 June 2006 to put into place provisional
21 emergency measures to prevent the introduction into and the spread within the
22 community of *D. kuriphilus*, the pest is now widely distributed in Italy and
23 has become established in many other European countries including Austria
24 (2013), Croatia (2010), Czech Republic and Slovakia (2012), France (2005), Ger-
25 many (2013), Hungary (2013), Portugal (2014), Slovenia (2005), Spain (2012),
26 Switzerland (2009), Turkey (2014), the United Kingdom (2015) and Belgium
27 (2016) (EFSA, 2010; EPPO, 2013, 2015a, 2016). In the Netherlands it was acci-
28 dentally imported through nursery trees (2010) and then promptly detected and
29 eradicated by destroying the few affected plants (NPPO, 2013), but recently a
30 new outbreak has been detected close to the German border (EPPO, 2015b).
31 Since *D. kuriphilus* has shown its ability to spread rapidly and is successfully es-
32 tablished in several countries, further establishment is likely in Europe anywhere
33 there is availability of the host plants *Castanea* spp. (EFSA, 2010).

34 The chestnut gall wasp is a univoltine and thelytokous species (Moriya et
35 al., 1989), and lays eggs in buds during summer. The hatched larvae induce the
36 formation of greenish-red galls, which develop at the time of budburst in the
37 following early spring on new shoots (Ôtake, 1980), suppressing shoot elongation
38 and causing twig dieback. Severe reduction of fruiting with yield losses due to

39 insect attacks have been estimated to reach between 65% and 85% in northern
40 Italy (Bosio et al., 2013; Battisti et al., 2014). However, no evidence was found
41 to confirm tree mortality. A gradual reduction in vigor in the longer term is
42 the likely consequence of annual infestation by the gall wasp, causing a gradual
43 reduction in biomass (EFSA, 2010).

44 Early attempts of biological control of the pest were performed in Japan
45 (Murakami et al., 1977; Murakami, 1981) and in the USA (Rieske, 2007) by
46 the introduction of *Torymus sinensis* Kamijo (Hymenoptera: Torymidae), a
47 chinese parasitoid described by Kamijo (1982). In its native environment it is
48 only one among many species of natural parasitoids of *D. kuriphilus* (Murakami
49 et al., 1980), but it appears to be very well synchronized with the life cycle of
50 the pest, making it a strong candidate as a biological control agent (Murakami,
51 1981). In addition, outside China, it was believed to be host-specific, although
52 its host range was never studied or tested in detail (Murakami et al., 1977;
53 Gibbs et al., 2011). Recently, a large-scale survey in northern Italy found a few
54 specimens of *T. sinensis* emerging from oak galls of the non-target host *Biorhiza*
55 *pallida* Olivier. All evidence, however, still suggests that *D. kuriphilus* is by far
56 the preferred host, and parasitism of other species occurs only exceptionally,
57 possibly as a response to scarcity of its primary host (Ferracini et al., 2015a).

58 *T. sinensis* reproduces sexually, and by arrhenotokous parthenogenesis if
59 there is lack of mating. It is reported as univoltine, like its host. However,
60 recent preliminary investigations highlighted that a very small fraction of the
61 insect population may undergo a prolonged diapause extended for 12 months,
62 mainly as late instar larva (Ferracini et al., 2015b). After emergence, which
63 takes place in early spring, and mating, the female lays eggs inside the larval
64 chamber of newly formed galls, one egg per host larva. Although in controlled
65 conditions occasional multiple eggs per host larva have been reported by an
66 early study (Piao and Moriya, 1992), we have never found more than one egg
67 per host larva while dissecting galls collected in the field. After hatching, the
68 larva feeds ectoparasitically on the host larva, and it pupates in the host larval
69 chamber during winter.

70 *T. sinensis* was introduced in Japan from China (Murakami et al., 1977,
71 1980; Moriya et al., 2003). After its release, it dispersed successfully alongside
72 expanding *D. kuriphilus* populations. In Japan *D. kuriphilus* may also be sub-
73 ject to varying levels of parasitism from native insects, most notably *Torymus*
74 *beneficus* Yasumatsu & Kamijo and several species of the genus *Eupelmus* (Mu-
75 rakami and Gyoutoku, 1995; Moriya et al., 2003) that, however, are unable to
76 control the pest. Monitoring of test orchards showed that after about 6–18 years
77 from the introduction of *T. sinensis*, the pest population declined to levels as
78 low as to be practically undetectable, giving rise to claims of success in bio-
79 logically controlling the infestation (Moriya et al., 1989; Murakami et al., 2001;
80 Moriya et al., 2003). However, continuous monitoring of the first release site
81 over 25 years shows three successive peaks in the population of *D. kuriphilus*,
82 shortly followed by peaks in the population of *T. sinensis* (Moriya, personal
83 communication). In the USA, several Asian *Torymus* species were released in
84 1977 in southeastern Georgia, but the release was not followed by any moni-
85 toring. The first accounts of the successful establishment of *T. sinensis* in the
86 United States were published only thirty years later (Cooper and Rieseke, 2007;
87 Rieseke, 2007). In spite of the abundant presence of *T. sinensis*, and of *Ormyrus*
88 *labotus* Walker (a native insect that was shown to easily parasitize *D. kuriphilus*
89 galls), the pest could be found in most of the southern Appalachian range, with
90 satellite infestations in Ohio and Pennsylvania.

91 The European chestnut (*Castanea sativa* Mill.) is one of the most important
92 broad-leaved species in Italy: chestnut stands amount to 788,400 hectares, which
93 represents 9% of the Italian forests (Graziosi and Santi, 2008). Due to the report
94 of the gall wasp in 2002 and in consideration of the long-established economic
95 importance of chestnut throughout the country for fruit and wood production,
96 a collaboration was started with Japanese researchers and a biological control
97 program was initiated in 2005 with the release in infested orchards of Japan-
98 imported *T. sinensis* specimens (Quacchia et al., 2008). Following the Japanese
99 and Italian experiences, reporting the establishment of a sizable population of
100 *T. sinensis* vigorously parasitizing the galls of *D. kuriphilus*, recent releasing

101 programs were performed in Croatia, France and Hungary (Borowiec et al.,
102 2014; Matošević et al., 2014), as well as test releases in Spain and Portugal (Juan
103 Ramón Boyero at Junta de Andalucía, personal communication, Associação
104 Portuguesa da Castanha, 2015).

105 Although in Europe there exist several native species of Hymenoptera capa-
106 ble of parasitizing *D. kuriphilus* galls, all of them have a very large host range,
107 and suffer by a mismatch between their emergence times and the development
108 of the galls. They are therefore unable to act effectively as biological control
109 agents (Aebi et al., 2006, 2007; Quacchia et al., 2013; Alma et al., 2014).

110 In the present paper we develop a mathematical model of the interaction
111 between *T. sinensis* and *D. kuriphilus*. aiming at developing a tool for under-
112 standing and evaluating the effectiveness of biological control programs based
113 on the release of *T. sinensis* in woods and orchards infested by *D. kuriphilus*.

114 In particular we would like to investigate whether *T. sinensis* should be
115 expected to be able, alone, to maintain its population to levels at least as low as
116 to produce no harm, or if such expectations are over optimistic. The fact that *T.*
117 *sinensis* is extremely well synchronized with *D. kuriphilus*, that outside China it
118 acts almost perfectly as host-specific, and that in Europe its abundance appears
119 to be limited only by the availability of its host, with a very low mortality during
120 all its life stages, allows hopes for a rapid, complete, and permanent control of
121 the pest. However, the experiences of both Japan and the USA warn that the
122 effectiveness of *T. sinensis* might be less perfect than one would wish it to be.
123 In the case of Japan the imperfect control of *D. kuriphilus* has been ascribed to
124 a high mortality of *T. sinensis* by hyperparasitism (Murakami and Gyoutoku,
125 1991). In Europe hyperparasitism is only occasional (Quacchia et al., 2013),
126 which leaves more room for hopes of obtaining a control.

127 In order to have a flexible tool, our model, in its full form, is hybrid discrete-
128 continuous in time and spatially explicit. In an abstract setting, a class of models
129 of this sort for a single species has been discussed by Lewis and Li (2012).
130 Our model describes the host-parasitoid interplay of two species (namely *T.*
131 *sinensis* and *D. kuriphilus*). For both species the time-continuous part of the

132 model describes the seasonal dispersal of the adult insect population, and the
133 inter-specific competition for finding egg deposition sites. The time-discrete
134 (or “impulsive”) part describes the overwintering of the larvae. In a spatially-
135 homogeneous situation the model may be rigorously reduced to an iterated map
136 quantifying the egg density of the two species, whose properties are studied
137 with a combination of analytic and numerical techniques. The full, spatially-
138 explicit model is studied by means of numerical simulations in one and two
139 spatial dimensions. The comparison between the dynamics of the iterated maps
140 and of the full model suggests a diffusion-based mechanisms that may give rise,
141 under certain conditions, to repeated waves of full infestation followed by near
142 disappearance of the pest and of its parasitoid, on time scales that depend **not**
143 only on the physiological and ecological parameters, but also on the size and
144 geometry of the wood.

145 The rest of the paper is organized as follows: the mathematical model is
146 developed in section 2; the results obtained from the model are reported in
147 detail in section 3; finally they are summarized in section 4, together with some
148 speculative considerations. Section 5 is an appendix containing mathematical
149 analyses in support of statements appearing in sections 2 and 4.

150 2. The model

151 2.1. Equations for the gall wasp

152 We aim at describing the population of adult gall wasps on spatial scales
153 much larger than those of an individual tree. Thus the population of adult gall
154 wasps during the summer of the year n is quantified as a vertically-integrated
155 density field U_n (that is, the number of insects per unit area as a function of time
156 and space) of egg-carrying *D. kuriphilus* adults. By “density of egg-carrying
157 adults” we mean that an adult that has not yet laid any eggs contributes by
158 a whole unit in the computation of this density, an adult that has laid, say,
159 half its eggs contributes by half a unit, and one that has laid all its eggs does
160 not contribute at all, even if it is still alive. Thus, calling N_D the maximum
161 number of eggs that can be laid by a typical *D. kuriphilus* adult under optimal

162 conditions, then $N_D U_n(\mathbf{x}, t)$ is the number of eggs per unit area present at the
 163 location \mathbf{x} and time t that can still potentially be laid.

164 We shall also need a second field, V_n , that quantifies the density of eggs laid
 165 in chestnut buds. Because *D. kuriphilus* may only lay eggs on chestnuts buds,
 166 and at most M eggs per bud, then the density of laid eggs in any location \mathbf{x} is
 167 always at most $M\beta_n(\mathbf{x})$, where β_n is the density of chestnut buds on the n -th
 168 year. In any case, the maximum density of laid eggs cannot exceed the quantity

$$V_{max} = M\beta_{max} \quad (1)$$

169 where the constant β_{max} is the maximum density of buds attainable in a chest-
 170 nut wood under optimal conditions.

171 At the beginning of each season, the density of both the gall wasps and of
 172 their laid eggs are zero:

$$\begin{cases} U_n(\mathbf{x}, 0) = 0 \\ V_n(\mathbf{x}, 0) = 0 \end{cases} \quad (2)$$

173 As the season progresses, from the galls formed during the previous season, the
 174 wasps gradually emerge. For simplicity we shall assume a constant emergence
 175 rate:

$$\text{emergence rate} = \frac{\eta V_{n-1}(\mathbf{x}, T_D)}{T_D} \quad (3)$$

176 where T_D is the length of the egg deposition season, and the non-dimensional
 177 parameter $\eta \in (0, 1]$ is the survival rate during the overwintering. More pre-
 178 cisely, $\eta V_{n-1}(\mathbf{x}, T_D) dA$ is the number of *D. kuriphilus* adults that emerge dur-
 179 ing the n -th season from an area dA centered around the location \mathbf{x} . Taking
 180 into account that chestnut gall wasps reproduce by thelytokous parthenogene-
 181 sis (Murakami, 1981), and have a low natural mortality of eggs and larvae, we
 182 expect the numerical value of η to be close to one. More in detail, the primary
 183 mortality factors for *D. kuriphilus* are parasitism, gall-chamber invading fungi
 184 and failure of adult gall wasp to emerge (Cooper and Rieske, 2010), but from
 185 our experience all these processes have effects so mild to be almost negligible
 186 (authors' personal observation).

187 Individual gall wasps do not survive for more than a few days. Therefore
188 we need to introduce a sink term representing their mortality rate. We are not
189 aware of any evidence in the literature of important exogenous factors affecting
190 the mortality of adult gall wasps. Thus, taking individual deaths as independent
191 from each other, the rate of deaths per unit area is likely to be proportional to
192 the density of the population, suggesting the following simple choice for the
193 death rate term

$$\text{death rate} = -\frac{U_n(\mathbf{x}, t)}{a} \quad (4)$$

194 where a is the typical adult life span (up to ten days: EFSA, 2010).

195 We shall assume that during the egg-laying season the gall wasps move ran-
196 domly, diffusing isotropically in the forest. Although there is evidence of a
197 response of *D. kuriphilus* to olfactory cues in the choice of a host twig, this was
198 observed at spatial scales shorter than a meter (Germinara et al., 2011). On
199 much larger scales there is no evidence of anisotropic motion of the gall wasps,
200 nor it should be expected. Following olfactory cues in a turbulent environment,
201 such as a wood canopy, is a very challenging task when there is a single odor
202 source (Balkowsky and Shraiman, 2002). In the presence of multiple sources
203 it is very unlikely that an insect can consistently and reliably exploit olfactory
204 cues on long range. For example, in the case of the parasitoid wasp *Diachas-*
205 *mimorpha juglandis* Muesebeck, it was verified that it preferred to use visual
206 cues rather than olfactory ones for locating the walnut fruit husks where its host
207 may be found (Henneman et al., 2002). In the case of *D. kuriphilus*, the avail-
208 able visual cues are also short-range: chestnut buds are not visible from more
209 than a few meters away. Therefore, we consider reasonable to assume that the
210 large-scale motion (that is, on distances larger than the size of individual trees)
211 of *D. kuriphilus* adults is aimless and random, and thus it should be modeled
212 by a Laplacian diffusion operator (we shall further discuss this issue in section
213 4).

214 When the egg-carrying adults find available buds (that is buds that are not
215 already fully saturated by other eggs), they quickly lay one or more eggs, thus

216 reducing the number of available deposition sites. The rate of egg deposition
 217 of an individual will be proportional to the density of available eggs deposition
 218 sites, which, in the model, is expressed as $M\beta_n(\mathbf{x}) - V_n(\mathbf{x}, t)$. It would be more
 219 accurate to assume that the egg deposition rate is a Holling's type II function of
 220 the available egg deposition sites. However, our observations suggest that, for
 221 *D. kuriphilus*, the handling time (the time actually spent laying eggs) is just a
 222 tiny fraction of the search time (which is comparable with the adult life span).
 223 When the handling time is negligible, the Holling's type II function tends to a
 224 simple proportionality between the deposition rate and the density of available
 225 deposition places (see e.g. Vandermeer and Goldberg, 2013, p.163). Accordingly,
 226 the egg deposition rate of the whole population is taken as proportional to the
 227 product of the density of available sites by the density of the adult population,
 228 as in the following expression

$$\text{egg deposition rate} = r_D \frac{M\beta_n(\mathbf{x}) - V_n(\mathbf{x}, t)}{V_{max}} U_n(\mathbf{x}, t). \quad (5)$$

229 It is possible to give a reasonable estimate for the proportionality constant r_D
 230 that appears in the expression above. In fact, we must assume that in optimal
 231 conditions (that is, if $V_n = 0$, $\beta_n(\mathbf{x}) = \beta_{max}$ and thus the deposition rate reduces
 232 to $r_D U_n$) every adult gall wasp must be able to lay all its N_D eggs in a time
 233 interval roughly equal to its adult life span a . This would imply that

$$r_D = \frac{N_D}{a} \quad (6)$$

234 By adding together all the processes discussed in this section we arrive to
 235 the following model that describes the time evolution of the U_n and V_n fields
 236 during the n -th season.

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} U_n(\mathbf{x}, t) = D_D \nabla^2 U_n(\mathbf{x}, t) - \frac{1}{a} \frac{M\beta_n(\mathbf{x}) - V_n(\mathbf{x}, t)}{V_{max}} U_n(\mathbf{x}, t) \\ \quad - \frac{1}{a} U_n(\mathbf{x}, t) + \frac{\eta V_{n-1}(\mathbf{x}, T_D)}{T_D} \\ \frac{\partial}{\partial t} V_n(\mathbf{x}, t) = \frac{N_D}{a} \frac{M\beta_n(\mathbf{x}) - V_n(\mathbf{x}, t)}{V_{max}} U_n(\mathbf{x}, t) \end{array} \right. \quad (7)$$

237 where D_D is the diffusivity of the gall wasps, and all other symbols have already
 238 been defined. Note that the egg deposition rate, that appears as the only term
 239 in the right-hand side of the equation for V_n , also appears in the equation for
 240 U_n with a minus sign and divided by N_D . This is because, as discussed above,
 241 the contribution of each individual to the density U_n is weighted by the fraction
 242 of eggs that it carries.

243 The problem (7) with the initial conditions (2) is not closed, because no rule
 244 was specified for the time evolution of the bud density β_n . In the presence of a
 245 developed infestation the health of the chestnut trees progressively deteriorates,
 246 and the bud density may decrease. This is a slow process, whose details are
 247 largely unknown (Kato and Hijii, 1997). If the model were used to perform
 248 detailed, realistic year-by-year forecasts of the spreading of *D. kuriphilus*, the
 249 best results would be obtained by measuring the density β_n by means of direct
 250 surveys of the orchards and coppices under study. In this paper, in order to
 251 assess and understand the main features of the solutions of the model's equa-
 252 tions, we shall use the strong simplifying assumption that the density of buds
 253 is always constant, and equal to β_{max} .

254 It is convenient to make non-dimensional the dependent variables, by defin-
 255 ing $u_n = U_n/(\eta V_{max})$ and $v_n = V_n/V_{max}$. Note that $v_n \in [0, 1]$ and that
 256 $M\beta_n/V_{max} = 1$, because of the simplifying assumption $\beta_n = \beta_{max}$. Likewise, it
 257 is convenient to use non-dimensional variables also for time and space. These
 258 are defined as: $\tilde{t} = t/T_D$ and $\tilde{\mathbf{x}} = \mathbf{x}/\sqrt{D_D T_D}$. Thus the equations (7) be-
 259 come (for typographical brevity in the following we shall omit the tildes on the
 260 non-dimensional independent variables)

$$\begin{cases} \frac{\partial}{\partial t} u_n(\mathbf{x}, t) &= \nabla^2 u_n(\mathbf{x}, t) - \mu(2 - v_n(\mathbf{x}, t))u_n(\mathbf{x}, t) + v_{n-1}(\mathbf{x}, t) \\ \frac{\partial}{\partial t} v_n(\mathbf{x}, t) &= E_D \mu(1 - v_n(\mathbf{x}, t))u_n(\mathbf{x}, t) \end{cases} \quad (8)$$

261 where $\mu = T_D/a$, $E_D = \eta N_D$ and $t \in [0, 1]$. For each n , the equations (8) are
 262 subject to the conditions

$$\begin{cases} u_n(\mathbf{x}, 0) &= 0 \\ v_n(\mathbf{x}, 0) &= 0 \end{cases} \quad (9)$$

263 This is a piecewise smooth initial value problem, characterized by two free pa-
 264 rameters: E_D and μ . The first one is the maximum number of eggs that can be
 265 laid by a *D. kuriphilus* adult, multiplied by the overwintering mortality (which
 266 does not appear elsewhere in the non-dimensional equations); the second is the
 267 reciprocal of the adult life span, measured in the non-dimensional time units.
 268 A further important parameter is the size, in non-dimensional units, of the
 269 domain Ω , that is the chestnut-covered area on which U_n and V_n are defined.
 270 The equations (8) and the conditions (9) must be complemented by suitable
 271 boundary conditions describing the behavior of the gall wasps when they find
 272 themselves at the edge of the wood. We are not aware of any published work
 273 on this issue. It is very likely that a small fraction of the gall wasps would ven-
 274 ture outside a chestnut orchard or coppice, spilling over adjacent regions. For
 275 simplicity, here we assume that any gall-wasp that were to leave the domain
 276 Ω would promptly change its course, returning inside the chestnut-populated
 277 area. In this idealized situation there would be no flux of wasps across the edges
 278 of Ω , and therefore the appropriate boundary conditions for U_n would be

$$\hat{\mathbf{n}} \cdot \nabla u_n|_{\partial\Omega} = 0 \quad (10)$$

279 where $\partial\Omega$ denotes the line delimiting the boundary of Ω , and $\hat{\mathbf{n}}$ represents the
 280 outward unit vector perpendicular to $\partial\Omega$.

281 The no-flux boundary condition (10) is of particular interest because it al-
 282 lows for homogeneous solutions, that is, solutions in which the densities u_n and
 283 v_n are constant in space (but not in time). In particular, it is straightforward to
 284 verify that if s_0 is taken as a constant, then at all later times t and seasons n , u_n
 285 and v_n do not depend on \mathbf{x} , and the problem (8,9,10) reduces to the following
 286 chain of ordinary differential equations:

$$\begin{cases} \dot{u}_n(t) &= v_{n-1}(1) - \mu(2 - v_n(t)) u_n(t) \\ \dot{v}_n(t) &= E_D \mu (1 - v_n(t)) u_n(t) \\ u_n(0) &= 0 \\ v_n(0) &= 0 \end{cases} \quad (11)$$

287 where the dot denotes differentiation with respect to time. The solution of these
 288 nonlinear equations cannot be expressed in terms of simple functions. However,
 289 a formal calculation shows that the year-over-year dynamics of the egg density
 290 can be well approximated by the following simple map (see Appendix 5.1 for
 291 details)

$$v_n = 1 - e^{-kv_{n-1}} \quad (12)$$

292 where the egg densities v_n, v_{n-1} are evaluated at time $t = 1$ (corresponding
 293 to the end of the n -th and $(n - 1)$ -th seasons). The positive constant k that
 294 appears in the exponential is given by one of the following two expressions

$$\begin{cases} k_+ = \frac{ED}{\mu} (e^{-\mu} + \mu - 1) & \text{approx. from above,} \\ k_- = \frac{ED}{4\mu} (e^{-2\mu} + 2\mu - 1) & \text{approx. from below.} \end{cases} \quad (13)$$

295 On choosing $k = k_-$ we obtain an approximation from below, which is highly
 296 accurate when the previous year egg density v_{n-1} is appreciably smaller than
 297 1. Choosing $k = k_+$ one has an approximation from above, that captures the
 298 dynamics more accurately when the egg density v_{n-1} is close to 1. (see Appendix
 299 5.1 for details, and Figure 1).

300 We observe that the iterated map (12) is the well-known model of Skellam
 301 (Skellam, 1951; Brännström and Sumpter, 2005), that describes the population
 302 dynamics of univoltine insects in a regime of contest competition.

303 2.2. Equations for *T. sinensis*

304 *Torymus* adults emerge from vacated galls in spring. There appears to be a
 305 good degree of synchronism in the emergence process, so that the great majority
 306 of all the individuals appear in a time span of a few days (authors' personal
 307 observation). After mating, the egg-carrying females look for intact galls into
 308 which they lay (usually) one egg per chamber (Piao and Moriya, 1992). Each
 309 female initially carries about $N_T \approx 70$ eggs. In outdoor conditions the adult
 310 lifetime of *T. sinensis* is at least 37 days (Piao and Moriya, 1992). For modeling

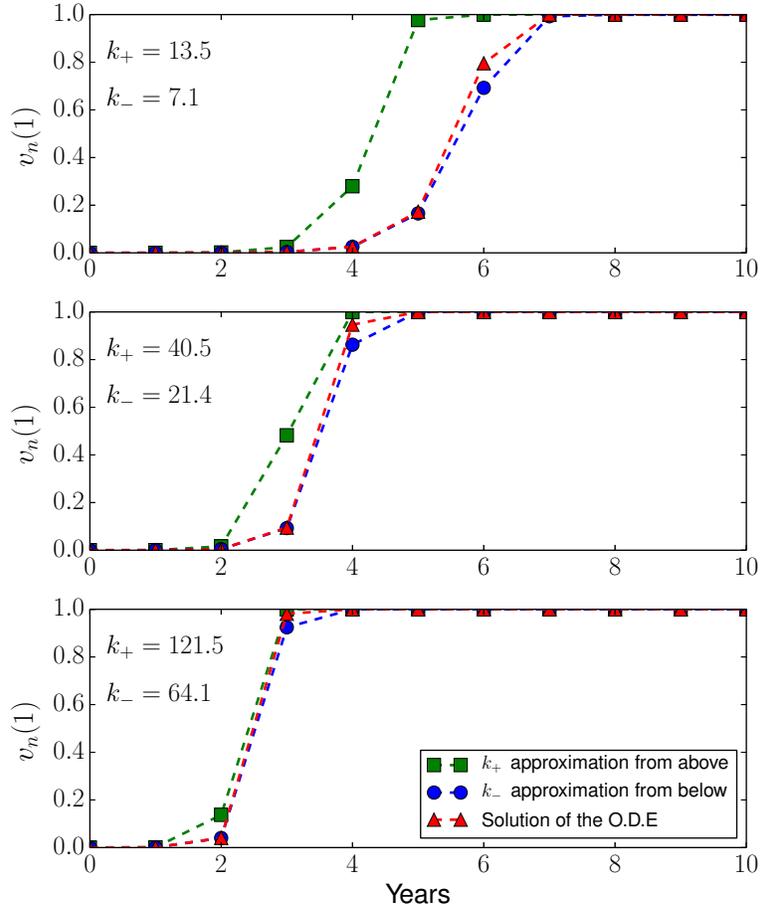


Figure 1: Comparison of the end-of-season egg densities given by Skellam's map (12) and by a numerical solution of the spatially-homogeneous model (11) for different values of the parameter k_{\pm} defined in (13). In all the computations we have used $N_D = 150$, $\mu = 10$, $v_0(1) = 10^{-5}$. The overwintering survival rates are, from top to bottom, $\eta = 0.1, 0.3, 0.9$. The first two values are unrealistically low and are meant just to illustrate the properties of the two approximations. The last value is considered to be realistic in the European setting.

311 purposes we shall take the emergence as an instantaneous process, and attribute
 312 the same life-span to all the individuals, so that they all die together.

313 In the following we will denote with P_n the density of the egg-carrying T .
 314 *sinensis* females and with Q_n the density of the eggs already laid, during the
 315 n -th season. Just as in our model of *D. kuriphilus*, we shall use the following
 316 expression for the egg deposition rate of *T. sinensis*

$$\text{egg deposition rate} = r_T \frac{\eta V_{n-1}(\mathbf{x}, T_D) - Q_n(\mathbf{x}, t)}{V_{max}} P_n(\mathbf{x}, t) \quad (14)$$

317 Also in this case, in principle, the rate should be expressed through a Holling's
 318 type II functional response. But the oviposition time of *T. sinensis* is very
 319 short (a few minutes, authors' personal observation) in comparison with its
 320 search time. Thus, as we argued in the case of the gall wasp, the deposition rate
 321 must be proportional to the product of the density of egg-carrying *T. sinensis*
 322 females with the density of the sites where oviposition is possible. The latter
 323 is given by the difference between the density of gall wasp eggs laid during
 324 the previous season and turned into larvae (namely ηV_{n-1}) and the density of
 325 *T. sinensis* eggs already laid. Here r_T/V_{max} is the proportionality constant.
 326 As for the gall-wasp we should assume that every female *Torymus*, in optimal
 327 conditions (that is, $\eta V_{n-1} = V_{max}$ and $Q_n = 0$), should be able to lay all its N_T
 328 eggs during its life span T_T . Thus, we assume

$$r_T = \frac{N_T}{T_T}. \quad (15)$$

329 Also for *T. sinensis* it is known that it responds to olfactory and visual cues
 330 at short ranges (Graziosi and Rieske, 2013). On longer distances, the same
 331 considerations already mentioned for the gall-wasp apply: the overall motion
 332 of an adult *T. sinensis* during its life span should be random and aimless, and
 333 therefore a Laplacian diffusion process, characterized by a constant diffusivity
 334 D_T , should be the appropriate model.

335 Therefore we may describe the dynamics of a population of *T. sinensis* dur-
 336 ing the n -th season with the following equations:

$$\begin{cases} \frac{\partial}{\partial t} P_n(\mathbf{x}, t) &= D_T \nabla^2 P_n(\mathbf{x}, t) - \frac{1}{T_T} \frac{\eta V_{n-1}(\mathbf{x}, T_D) - Q_n(\mathbf{x}, t)}{V_{max}} P_n(\mathbf{x}, t) \\ \frac{\partial}{\partial t} Q_n(\mathbf{x}, t) &= \frac{N_T}{T_T} \frac{\eta V_{n-1}(\mathbf{x}, T_D) - Q_n(\mathbf{x}, t)}{V_{max}} P_n(\mathbf{x}, t) \end{cases}. \quad (16)$$

337 Here the time $t = 0$ corresponds to the simultaneous emergence of the adult
 338 *Torymus*. The equations are valid up to $t = T_T$, corresponding to the end of
 339 the *Torymus* season, when all the adults die. Just as we did for the gall wasp,
 340 the rate of change of the laid egg density Q_n is equal to the egg deposition rate.
 341 This rate is also divided by N_T and subtracted from the equation for the rate
 342 of change of the density P_n of the *T. sinensis* females, because the density of
 343 adult females is weighted by the number of eggs that each adult carries.

344 The equations (16) are subject to the initial conditions

$$\begin{cases} P_n(\mathbf{x}, 0) &= \gamma Q_{n-1}(\mathbf{x}, T_T) \\ Q_n(\mathbf{x}, 0) &= 0 \end{cases} \quad (17)$$

345 The initial density of *T. sinensis* females is not zero because we assumed the
 346 instantaneous emergence of all the adults. The constant γ accounts for the
 347 sex ratio of *T. sinensis*, and for the mortality rate of the overwintering larvae.
 348 Male and female have roughly the same probability to emerge from a fertilized
 349 egg of *T. sinensis* (Ferracini et al., 2015b) and the overwintering mortality is
 350 believed to be very low (author's personal observation), thus we shall use values
 351 of γ smaller than, but close to $1/2$. *T. sinensis* females that are not able to
 352 mate may still lay their unfertilized eggs, from which will emerge males, by
 353 arrhenotokous parthenogenesis. Therefore, if the density of *T. sinensis* drops
 354 to very low levels, in the next season the sex ratio will be skewed in favor of the
 355 males, resulting in an improved mating probability for the remaining females.
 356 In its present form, our model does not include this mechanism. However, we
 357 also do not model explicitly the mating process: all the females are implicitly
 358 considered to be fertilized at the moment of their emergence. Thus we are
 359 already overestimating the mating probability of the females, and we feel that,
 360 at this stage, further complications may be unnecessary. For the same reason,

361 *T. sinensis* is modeled as a strictly univoltine species. The recent observations
 362 of an extended diapause of a few *Torymus* individuals, in a controlled setting
 363 (Ferracini et al., 2015b), does not yet allow a quantitative assessment of the
 364 importance (if any) of this process for the dynamics of the population in the wild.
 365 Thus we postpone the inclusion of these processes for a possible future improved
 366 version of the model. [However, in section 4 we present some additional results](#)
 367 [that allow us to argue that, as long as the fraction of individuals undergoing](#)
 368 [extended diapause remains very low, the overall effects should be negligible.](#)

369 It is convenient to rewrite the model by using the non-dimensional densities
 370 $p_n = P_n/(\gamma\eta V_{max})$, $q_n = Q_n/(\eta V_{max})$, and the same non-dimensional space
 371 and time variables already used for the gall-wasp equations. The equations
 372 (16) then become

$$\begin{cases} \frac{\partial}{\partial t} p_n(\mathbf{x}, t) = \delta \nabla^2 p_n(\mathbf{x}, t) - \tau^{-1} (v_{n-1}(\mathbf{x}, 1) - q_n(\mathbf{x}, t)) p_n(\mathbf{x}, t), \\ \frac{\partial}{\partial t} q_n(\mathbf{x}, t) = E_T \tau^{-1} (v_{n-1}(\mathbf{x}, 1) - q_n(\mathbf{x}, t)) p_n(\mathbf{x}, t), \end{cases} \quad (18)$$

373 where we have defined the diffusivity ratio $\delta = D_T/D_D$, the non-dimensional *T.*
 374 *sinensis* season length $\tau = T_T/(\eta T_D)$, and the effective egg number $E_T = \gamma N_T$.
 375 The initial conditions (17) become

$$\begin{cases} p_n(\mathbf{x}, 0) = q_{n-1}(\mathbf{x}, \eta\tau), \\ q_n(\mathbf{x}, 0) = 0. \end{cases} \quad (19)$$

376 By imposing no-flux boundary conditions on p_n , and looking for homogeneous
 377 solutions, the equations (18) together with the initial conditions, yield a set of
 378 ordinary differential equations whose solution is given in Appendix (5.2). By
 379 evaluating the solution at the time corresponding to the end of the *Torymus*
 380 season, that is at the non-dimensional time $t = \eta\tau$, we obtain the following
 381 map:

$$q_{n+1} = \begin{cases} \frac{E_T v_n q_n (1 - e^{\eta(E_T q_n - v_n)})}{v_n - E_T q_n e^{\eta(E_T q_n - v_n)}}, & E_T q_n \neq v_n \\ \frac{v_n^2}{v_n + \eta^{-1}}, & E_T q_n = v_n \end{cases} \quad (20)$$

382 where the egg densities q_{n+1} , q_n and v_n are evaluated at the end of their re-
 383 spective seasons. Albeit complicated-looking, the right-hand side of the map
 384 is a smooth function of its parameters, even for $E_T q_n = v_n$. In particular, it
 385 is a growing function of q_n , and, for realistic values of E_T and η , it rapidly
 386 approaches the horizontal asymptote $q_{n+1} \rightarrow v_n$. Therefore, the map (20), and
 387 thus the underlying equations (16), are a model that describes a contest compe-
 388 tition process among the individuals of *T. sinensis* (Brännström and Sumpter,
 389 2005).

390 2.3. The complete model

391 The equations for *T. sinensis*, discussed in the previous subsection, already
 392 depend on the density of *D. kuriphilus* eggs laid in the previous year. In order
 393 to have a fully coupled model, we only need to incorporate the parasitism of *T.*
 394 *sinensis* in the equations for *D. kuriphilus* discussed in sec 2.1. This is easily
 395 accomplished by observing that parasitized larvae of *D. kuriphilus* simply won't
 396 give rise to adults. Therefore we need to change the emergence rate (3) with

$$\text{emergence rate} = \frac{\eta V_{n-1}(\mathbf{x}, T_D) - Q_n(\mathbf{x}, T_T)}{T_D}. \quad (21)$$

397 The complete model, using the non-dimensional variables, then reads

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} p_n(\mathbf{x}, t) = \delta \nabla^2 p_n(\mathbf{x}, t) - \tau^{-1} (v_{n-1}(\mathbf{x}, 1) - q_n(\mathbf{x}, t)) p_n(\mathbf{x}, t) \\ \frac{\partial}{\partial t} q_n(\mathbf{x}, t) = E_T \tau^{-1} (v_{n-1}(\mathbf{x}, 1) - q_n(\mathbf{x}, t)) p_n(\mathbf{x}, t) \\ \frac{\partial}{\partial t} u_n(\mathbf{x}, t) = \nabla^2 u_n(\mathbf{x}, t) - \mu (2 - v_n(\mathbf{x}, t)) u_n(\mathbf{x}, t) + v_{n-1}(\mathbf{x}, 1) - q_n(\mathbf{x}, \eta \tau) \\ \frac{\partial}{\partial t} v_n(\mathbf{x}, t) = E_D \mu (1 - v_n(\mathbf{x}, t)) u_n(\mathbf{x}, t) \\ p_n(\mathbf{x}, 0) = q_{n-1}(\mathbf{x}, \eta \tau) \\ q_n(\mathbf{x}, 0) = 0 \\ u_n(\mathbf{x}, 0) = 0 \\ v_n(\mathbf{x}, 0) = 0. \end{array} \right. \quad (22)$$

398 In the case of space-independent solutions, the dynamic of this model is well
 399 approximated by the following map

$$\begin{cases} q_{n+1} = \begin{cases} \frac{E_T v_n q_n (1 - e^{\eta(E_T q_n - v_n)})}{v_n - E_T q_n e^{\eta(E_T q_n - v_n)}}, & E_T q_n \neq v_n \\ \frac{v_n^2}{v_n + \eta^{-1}}, & E_T q_n = v_n \end{cases} \\ v_{n+1} = 1 - e^{-k(v_n - q_{n+1})} \end{cases} \quad (23)$$

400 that describes the year-over-year change of the end-of-season density of *T.*
 401 *sinensis* and *D. kuriphilus* eggs. The second equation in (23) is found by looking
 402 for spatially constant solutions of the third and fourth equations in the complete
 403 model (22). Then one finds that in the system of ODEs (11) the source term
 404 $v_{n-1}(1)$ is replaced by $v_{n-1}(1) - q_n(\eta\tau)$. Following the derivation of Skellam's
 405 map of section 2.1 one finds the expression given in (23).

406 2.4. The value of the parameters

407 The mathematical model developed in this section depends on 11 free pa-
 408 rameters, listed in Table 1. Of these, one depends on the physiology and on the
 409 distribution of the chestnuts, namely the bud density β_{max} . Its numerical value
 410 and its significance will be discussed at the beginning of the next section.

411 The other 10 parameters are related to the physiology of either *D. kuriphilus*
 412 or to *T. sinensis*. The value of 6 of these, namely M , a , T_D , T_T , N_D , N_T , is
 413 fairly well-known; the value of η and γ is debatable, and it might be different
 414 in different regions of the world; the value of D_D and D_T is unknown, but
 415 the model links it to more readily measurable quantities. We shall now briefly
 416 discuss all of them in turn.

417 The maximum number M of eggs of *D. kuriphilus* per chestnut bud is only
 418 used in the definition of the non-dimensional densities (see Table 2) but it does
 419 not enter in the parameters that appear in the non-dimensional model (22).
 420 Thus, any uncertainty in its value would not affect the dynamics. Then there
 421 are three intervals of time: the life span a of adult individuals of *D. kuriphilus*;
 422 the number of days T_D during which the adults of *D. kuriphilus* are active (that
 423 is, the length of what we have called the “*Dryocosmus* season”); and the number

D_D	$0.77 \text{ km}^2 \text{ d}^{-1}$	Diffusion coefficient of <i>D. kuriphilus</i> .	See sec. 3.2.
a	2–10 days 2–3 days	Adult life span of <i>D. kuriphilus</i> .	EFSA (2010); Graziosi and Rieske (2014).
M	20–30 eggs bud ⁻¹	number of eggs of <i>D. kuriphilus</i> that can be laid on a bud.	EFSA (2010).
β_{max}	$2 \cdot 10^6$ buds ha ⁻¹	Maximum density of chestnut buds.	Bounous (2014).
η	0.5–0.98	Fraction of <i>D. kuriphilus</i> larvae surviving after overwintering.	Cooper and Rieske (2007); Quacchia et al. (2013).
T_D	30–50 days	Length of the egg deposition season for <i>D. kuriphilus</i> .	EPPO (2005).
N_D	100–300	Number of eggs per adult of <i>D. kuriphilus</i> .	Graziosi and Rieske (2014).
D_T	unknown	Diffusion coefficient of <i>T. sinensis</i> .	See sec. 3.3
T_T	37 days or more	Length of the egg deposition season for <i>T. sinensis</i> .	Piao and Moriya (1992).
N_T	71	Number of eggs per adult female of <i>T. sinensis</i> .	Piao and Moriya (1992).
γ	0.25–0.45	Fraction of <i>T. sinensis</i> larvae that are female and survive after overwintering.	Piao and Moriya (1992) Author's unpublished observations

Table 1: Parameters of the model and their likely value or value range.

$u_n = \frac{U_n}{\eta M \beta_{max}}$	Non-dimensional density of <i>D. kuriphilus</i> adults during the season n .
$v_n = \frac{V_n}{M \beta_{max}}$	Non-dimensional density of <i>D. kuriphilus</i> eggs laid during the season n .
$p_n = \frac{P_n}{\gamma \eta M \beta_{max}}$	Non-dimensional density of <i>T. sinensis</i> adult females during the season n .
$q_n = \frac{Q_n}{\eta M \beta_{max}}$	Non-dimensional density of <i>T. sinensis</i> eggs laid during the season n .
$\mu = \frac{T_D}{a}$	Non-dimensional length of the egg deposition season of <i>D. kuriphilus</i> .
$E_D = \eta N_D$	Number of larvae per adult of <i>D. kuriphilus</i> that survive the overwintering in optimal conditions.
$k = \begin{cases} k_+ = \frac{E_D}{\mu} (e^{-\mu} + \mu - 1) \\ k_- = \frac{E_D}{4\mu} (e^{-2\mu} + 2\mu - 1) \end{cases}$	Effective growth rate in the Skellam maps approximating from above ($k = k_+$) or from below ($k = k_-$) the year-over-year dynamics of <i>D. kuriphilus</i> ' egg density.
$\delta = \frac{D_T}{D_D}$	Diffusivity ratio.
$\tau = \frac{T_T}{\eta T_D}$	Non-dimensional length of the egg deposition season of <i>T. sinensis</i> .
$E_T = \gamma N_T$	Number of female larvae per adult female of <i>T. sinensis</i> that survive the overwintering in optimal conditions.

Table 2: Non-dimensional variables and parameters. Here the unit of time is T_D and the unit of space is $\sqrt{D_D T_D}$.

424 of days T_T during which the adults of *T. sinensis* are active (the “*Torymus*
425 season”). What matters for the model are the non-dimensional ratios T_D/a and
426 T_T/T_D . We take 10 as the reference value for the first, and 1 for the second.
427 We have verified that any discrepancy from these reference values, as long as it
428 is compatible with the observational uncertainties, makes little difference in the
429 end results. In particular, in the spatially homogeneous case, the calculations
430 of the previous section show that the map (23) does not depend on their ratio.
431 Finally we have N_D and N_T , respectively the average number of eggs carried
432 by *D. kuriphilus* and *T. sinensis* females. For the first we take the reference
433 value of 150 eggs per female, and for the second we take 70 eggs per female.
434 In the non-dimensional model (22) these parameters always appear multiplied,
435 respectively, by η and γ . Any uncertainty in the value of N_D and N_T is surely
436 swamped by the uncertainty in these two parameters.

437 In fact, the value of the two overwintering survival fractions η (of *D. ku-*
438 *riphilus*) and γ (of *T. sinensis*, which also includes the sex ratio) are debatable.
439 The works of Cooper and Rieske (2007) and of Piao and Moriya (1992) sug-
440 gest intermediate values for these parameters. However, our own observations
441 (published in Quacchia et al., 2013 for *D. kuriphilus* and yet unpublished for *T.*
442 *sinensis*) suggest much higher survival fractions. Whether these discrepancies
443 are due to regional variations (USA and Japan vs subalpine Europe) or to some
444 other cause is, at present, not known. Therefore, in the following, we devote
445 much attention to studying the dependence of the dynamics on the value of the
446 overwintering survival fractions.

447 The two diffusion coefficients D_D and D_T , respectively of *D. kuriphilus* and
448 *T. sinensis*, are completely unknown. In §3.2 we estimate the value of D_D on
449 the basis of the model results and of the observed speed with which a popula-
450 tion of *D. kuriphilus* is able to invade a chestnut forest. Not enough data are
451 available for attempting a similar deduction with D_T . The effect of changing
452 the diffusivity is studied in detail in §3.3.

453 3. Results

454 3.1. Space-independent dynamics

455 The map (23), which describes the time evolution of spatially homogeneous
456 populations of *D. kuriphilus* parasitized by *T. sinensis*, predicts that, starting
457 from non-zero densities of both species, the subsequent dynamics will continue to
458 have non-zero densities at all later years, with upper bounds determined by the
459 availability of buds (for *D. kuriphilus*) and of galls (for *T. sinensis*; see sec. 5.3.1
460 for the mathematical proof). This property alone, however, does not guarantee
461 the survival of either species. If, at some point in time, the modeled egg density
462 of a species drops to sufficiently low values, then the model is predicting a local
463 extinction of that species. An order-of-magnitude estimate of the threshold
464 density that signals extinction may be obtained as follows: a full-grown chestnut
465 tree in spring produces about 10^4 buds; typical production orchards have a
466 density of 100 – 200 trees per hectare, while coppices may have up to 1000
467 stems per hectare, but with less buds per stem than in individual trees (Bounous,
468 2014). Thus we have $\beta_{max} \approx 2 \cdot 10^6$ buds ha^{-1} , and, allowing for uncertainties
469 in the above figures, it follows that V_{max} ranges between $10^7 - 10^8$ eggs ha^{-1} .
470 Therefore, non-dimensional densities v_n, q_n below $10^{-7} - 10^{-8}$ correspond to
471 less than one insect per hectare. For an isolated, hectare-wide orchard, this
472 would be the extinction threshold. For a chestnut woodland spanning several
473 square kilometers the threshold would be proportionally lower.

474 The map (23) depends on three parameters: η, E_T, k . The last two, in turn,
475 depend on other parameters, namely γ, N_T, η, N_D and μ (see Tables 1 and 2).
476 We shall discuss the dynamics of the map as a function of the overwintering
477 survival fractions η and γ (owing to the uncertainty of their value) and fix the
478 other parameters to the following values: $N_D = 150$ (eggs per *D. kuriphilus*
479 adult), $N_T = 70$ (eggs per *T. sinensis* female adult), $\mu = 10$ (ratio of lengths
480 of the season and individual life span for *D. kuriphilus*). Uncertainties in the
481 value of μ do not produce large changes: going from $\mu = 3$ to $\mu = 20$ gives
482 about 15% difference in the value of the constant k_- in (13). In Figures 2

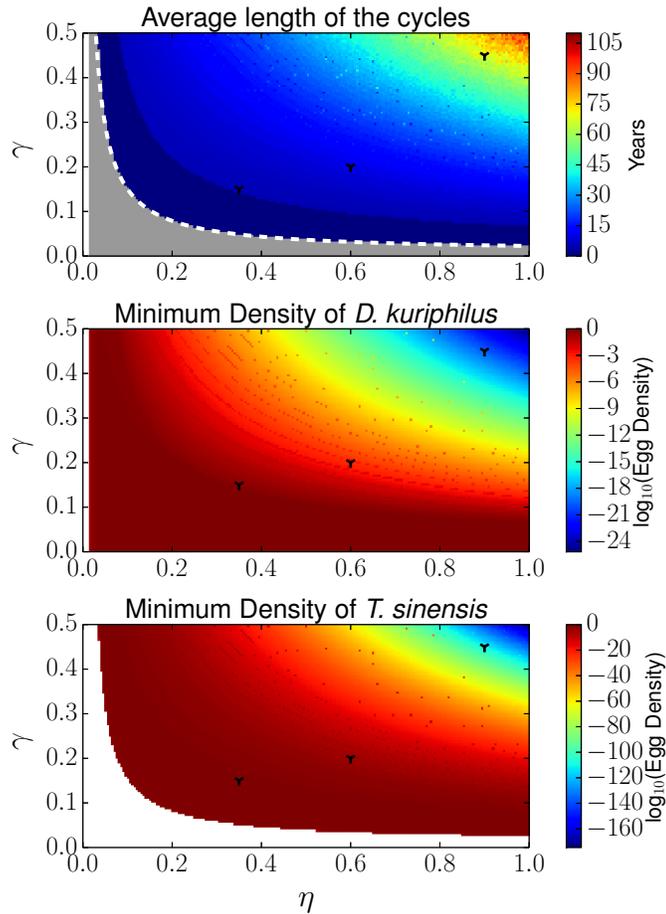


Figure 2: As a function of the overwintering survival fractions η and γ , top panel: average length of the predator–prey cycles; zero means that the coexistence fixed point is stable; the gray area that *T. sinensis* asymptotically becomes extinct; the white area that both species asymptotically become extinct; the white dashed line is the graph of (24). Middle panel: \log_{10} of the minimum density of *D. kuriphilus* eggs; the white region corresponds to asymptotic extinction. Lower panel: \log_{10} of the minimum density of *T. sinensis* eggs; the white region corresponds to asymptotic extinction. For each pair (η, γ) the statistics are computed over 3000 iterations of the map, after a 2000 iterations transient. The black markers show the parameters of Figures (3), (4), (5). Note that γ , the survival fraction of *T. sinensis*, also includes the sex ratio, and therefore may not be greater than 0.5.

483 to 5 we use $k = k_-$, because this choice gives a better approximation at low
 484 densities. Note that using $k = k_+$, is equivalent to using a larger value of E_D
 485 with $k = k_-$. The map (23) in some range of parameters, produces a dynamics
 486 in which the variables may swing by many orders of magnitude in a single year.
 487 This is the result of some subtle balances, (detailed in appendix 5.3.3) that are
 488 sensitive to numerical cancellation errors. Therefore, when using the map, all
 489 calculations have been carried out with 200 decimal significant digits, using an
 490 arbitrary precision numerical library Johansson et al. (2013). A more general
 491 and technical analysis of the map is given in Appendix 5.3.

492 Depending on the values of η and γ there are 4 possible dynamical outcomes
 493 qualitatively distinct: extinction of both species, extinction of the parasitoid,
 494 steady coexistence, and predator-prey cycles. The first 3 occur for unrealisti-
 495 cally low values of these parameters. If η is as low as to make $k < 1$ in (23), then
 496 the egg density of *D. kuriphilus* asymptotically goes to zero. As the gall wasp
 497 goes extinct, so does, in the model, *T. sinensis*, for lack of galls where to lay eggs
 498 (see section 4 for a discussion of this issue). This region of the parameter space
 499 is represented by the white vertical strip in Figure 2 (top panel). If η is such
 500 that $k > 1$ and γ is sufficiently low, then only *T. sinensis* becomes extinct, and
 501 *D. kuriphilus* reaches the non-zero fixed point of Skellam’s map (12). This is
 502 the gray region in Figure 2 (top panel). The exact threshold value of γ_{tr} cannot
 503 be expressed in simple terms, but a good approximation (the white dashed line
 504 in Figure 2, top panel) is

$$\gamma_{tr} \approx \frac{1}{N_T(1 - e^{-\eta})}. \quad (24)$$

505 The dark blue region above the threshold in Figure 2 (top panel) corresponds
 506 to the survival fractions at which both species survive and reach a stable fixed
 507 point. The shape of this region shows that, according to the model, a steady
 508 coexistence of both species may only occur if the overwintering survival fraction
 509 of at least one of the two species is unrealistically low.

510 When it exists, we find a unique coexistence fixed point. It can be visualized
 511 as the intersection between the set of points (v_n, q_n) such that $q_{n+1} = q_n$ (the

512 green lines in the right panel of Figures 3, 4, 5) and the set of points (v_n, q_{n+1})
 513 such that $v_{n+1} = v_n$ (the red lines in the right panel of Figures 3, 4, 5). We shall
 514 call these sets, respectively, q -nullcline and v -nullcline, and they intersect, at
 515 most, at a single point (see Appendix 5.3.2 for details). If the overwintering sur-
 516 vival fractions η and γ in Figure 2 (top panel) lie beyond the dark blue region of
 517 steady coexistence, a coexistence fixed point still exists, but is unstable, there-
 518 fore the insect egg densities fluctuate from year to year. When q_n is above the
 519 q -nullcline, then $q_{n+1} < q_n$, and if q_n is below, then $q_{n+1} > q_n$. Analogously,
 520 when v_n is above (below) the v -nullcline, then v_{n+1} is smaller (larger) than v_n .
 521 These drop or raise tendencies are depicted in the left panel of Figure 3, by the
 522 green vertical arrows for q_n , and by the red horizontal arrows for v_n . The arrows
 523 in the right panel of Figure 3 suggest that the sequence of states in a q_n vs v_n
 524 diagram rotates anticlockwise around the unstable fixed point, corresponding to
 525 cyclical increases and decreases of both species, in which maxima and minima
 526 of *T. sinensis* follow the maxima and minima of *D. kuriphilus*, yielding the kind
 527 of fluctuations that are ubiquitous in predator-prey dynamics (e.g. May and
 528 McLean, 2007, ch. 5). For generic values of η and γ these fluctuations are not
 529 periodic, nor asymptotically approach a periodic oscillation. However the cycles
 530 are characterized by a fairly well-defined time scale.

531 Figure 3 (left panel) shows 60 years of dynamics that one obtains by adopting
 532 for the overwintering survival fractions the very low values $\eta = 0.35$ and $\gamma =$
 533 0.15 , located just beyond the steady coexistence region. The initial state is
 534 designed to simulate the release of a tiny amount of *T. sinensis* in a large
 535 chestnut forest infested by *D. kuriphilus*. Thus we take $v_n = 1$ and $q_n =$
 536 10^{-9} . During the first two decades the population of *T. sinensis* grows steadily
 537 from the very low initial density, while the population of *D. kuriphilus* remains
 538 essentially unaffected by the presence of the parasitoid. When q_n approaches
 539 1, then v_n begins to decline. From then on, the densities of the two species
 540 oscillate in cycles that are about 5 years long. Omitting the initial transient,
 541 and plotting q_n vs v_n one finds that the succession of states describes the blue
 542 loop depicted in Figure 3 (right panel). With these low survival fractions the

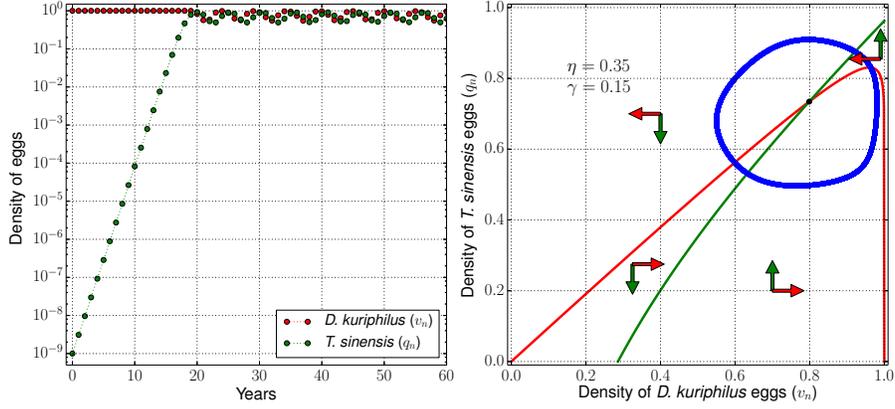


Figure 3: Left panel: time evolution of *D. kuriphilus* (red dots) and *T. sinensis* (green dots) egg density when the fraction of (female) larvae surviving the overwintering is, respectively $\eta = 0.35$ and $\gamma = 0.15$; see the text for the other parameters. Right panel: the red and the green curves are, respectively, the v -nullcline and the q -nullcline, which partition the plane in four regions; their intersection, marked by the black dot, is the unstable coexistence fixed point; the blue loops shows the states that the system occupies for asymptotically large times; the red horizontal arrows and the vertical green arrows show, for each of the four regions, whether the densities of the next state will be larger or smaller than those of a state in that region.

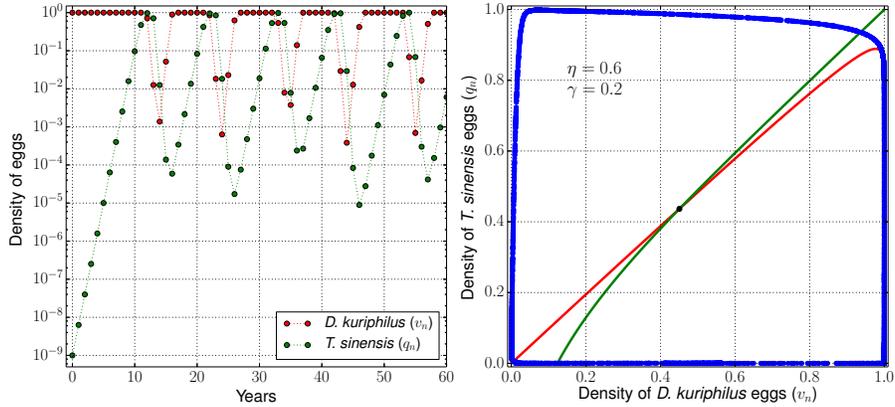


Figure 4: As Figure 3, but with $\eta = 0.6$ and $\gamma = 0.2$. These parameters might be representative of a situation in which *T. sinensis* suffers from hyperparasitism, as it is hypothesized for Japan.

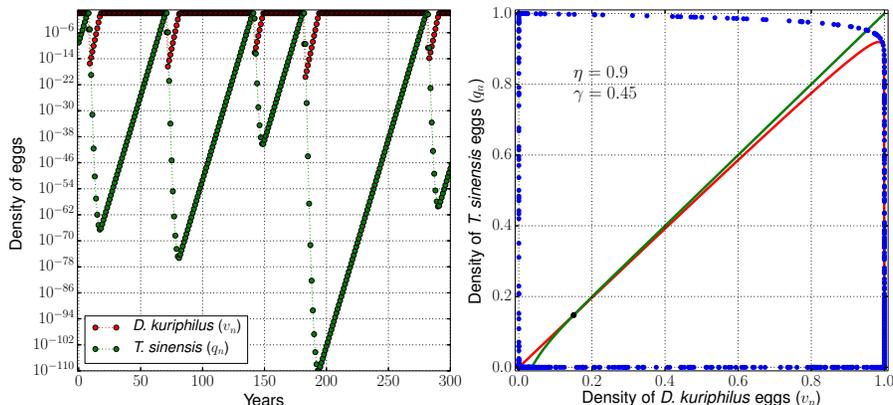


Figure 5: As Figure 3, but with $\eta = 0.9$ and $\gamma = 0.45$. These are parameters that we consider to be realistic for Europe. Note the extreme excursion of densities and the logarithmic density axis of the left panel.

543 loop winds relatively close to the unstable fixed point (the black dot at the
 544 intersection of the nullclines). Note that with these parameters the biological
 545 control is not achieved in a satisfactory way: the egg density of *D. kuriphilus*
 546 never drops below 50% of its initial value.

547 In Figure 4 we show the dynamics when the overwintering survival fractions
 548 are increased to $\eta = 0.6$ and $\gamma = 0.2$. Albeit still low, these values might rep-
 549 resent the case of Japan, where, according to Murakami and Gyoutoku (1991),
 550 a large amount of non-specialist parasitoid and hyperparasitoids species cause
 551 a high overwintering mortality both in *D. kuriphilus*, and, even more, in *T.*
 552 *sinensis*. These non-specialist parasitoids and hyperparasitoids are commonly
 553 associated to oak gall wasps, but are able to occasionally switch host plant and
 554 host species and can be a cause of overwintering mortality both for *D. kuriphilus*
 555 and for *T. sinensis*. The left panel of Figure 4 shows that the transient growth
 556 of *T. sinensis* is shortened to about a decade, after which it starts to dent the
 557 population of *D. kuriphilus*. The cycles after the transient have a length of 10-
 558 11 years, which is a time scale that roughly matches the observations in Japan
 559 (Moriya, personal communication). In the model, the egg concentration of *D.*
 560 *kuriphilus* remains almost constant, and very close to 1, for 6-7 years, while

561 the density of *T. sinensis* grows. Then, in the turn of 1–2 years *T. sinensis*
562 peaks and causes a sudden drop in the concentration of *D. kuriphilus*, and con-
563 sequently, also the population of *T. sinensis* drops in the following years. The
564 recovery of *D. kuriphilus* occurs in 1–2 years, starting from minimum densities
565 that may be smaller than 10^{-3} . The population of *T. sinensis* continues to
566 drop until the recovery of *D. kuriphilus* is almost complete, then it starts to
567 increase. By this time the density of *T. sinensis* may have reached densities
568 almost as low as 10^{-5} . The decline and the subsequent recovery of *T. sinensis*
569 span almost all the length of the cycle. High densities of *T. sinensis* occur only
570 for 2–3 years in each cycle. The right panel of Figure 4 shows the succession of
571 states (in blue, the initial transient was omitted) looping anticlockwise around
572 the unstable fixed point (the black dot). In this case the loop is pushed much
573 further away from the fixed point than in Figure 3, and the densities v_n, q_n
574 almost always assume either very low values or values close to 1. Even in this
575 case a satisfactory biological control is not achieved.

576 This kind of dynamics, in which *D. kuriphilus* remains most of the times at
577 densities close to 1, interrupted by brief bursts in the population of *T. sinensis*,
578 rather than performing mild oscillations at intermediate values, occurs every
579 time that the overwintering survival fractions are significantly removed from the
580 stability region of the fixed point. For example, if the overwintering survival
581 fractions are increased to values such as $\eta = 0.9$ and $\gamma = 0.45$, that we consider
582 compatible with the assessments of Aebi et al. (2007), and thus realistic for
583 the European setting, we observe the same stasis and burst dynamics as in
584 the previous case, but with much longer cycles, that may last several decades
585 (Figure 5). However, the really remarkable feature of this case is the extreme
586 depth of the drops in the population density of both species. The left panel in
587 Figure 5 shows that when the egg density of *T. sinensis* becomes close to 1, then
588 the egg density of *D. kuriphilus*, in a single season, drops to values that may be
589 smaller than 10^{-20} . The subsequent recovery of *D. kuriphilus* is not short, but
590 requires several years, during which the population of *T. sinensis*, for lack of
591 deposition sites, decreases to absurdly low values. As we argued at the beginning

592 of this section, cycles that reach minima this low are a mathematical fiction. In
 593 reality, the model is stating that *T. sinensis*, after the initial transient, wipes
 594 out the local population of *D. kuriphilus*, and then becomes extinct itself. We
 595 would like to stress that this is really a fifth dynamical regime, and it should
 596 not be confused with the extinction that takes places at the opposite end of
 597 the parameter space, when the overwintering survival fractions are very close to
 598 zero.

599 At very low densities, it would be more appropriate to switch to some form of
 600 stochastic model describing the probability of the presence of some individual
 601 insects in a given forest, rather than a density of the insects intended as a
 602 deterministic quantity. The map (23) may still give us some guidance in guessing
 603 what the stochastic dynamic could be. A Taylor expansion around $v_n = 0$,
 604 $q_n = 0$, shows that at very low densities, the map may be written at leading
 605 order as

$$\begin{cases} q_{n+1} &= \eta E_T q_n v_n + O(q_n^2 v_n, q_n v_n^2) \\ v_{n+1} &= k v_n - k q_{n+1} + O(q_{n+1}^2, v_n^2, q_{n+1} v_n) \end{cases} . \quad (25)$$

606 Note that q_{n+1} is smaller than v_n (in the complete map this holds for any value
 607 of q_n and v_n , see appendix 5.3.1, but it is evidently true when q_n is as small as
 608 to make $\eta E_T q_n < 1$). Therefore the following year, and as long as $\eta E_T v_n < 1$,
 609 the population of the pest will be growing, being to a very good approximation
 610 decoupled from the parasitoid, whose population, instead, will be shrinking. In
 611 this regime, if we interpret the densities as probabilities, we are led to believe
 612 that if pest attains very low densities, its chances of surviving would increase
 613 with time, but the parasitoid, at the same density, would have progressively
 614 lower chances of survival, until the host population had recovered to densities
 615 of order one. Thus the pest might survive, and the parasitoid become extinct.
 616 In less mathematical terms, if, by any chance, in a forest there were a handful
 617 of individuals of *D. kuriphilus* and of *T. sinensis*, the probability that the latter
 618 could find the galls of the former are very small, which puts the local survival of
 619 the parasitoid at serious risk in the absence of other hosts, while the pest would

620 have a very good chance of rebuilding its population.

621 The three panels of Figure 2 show, from top to bottom, the average length
622 of the cycles, and the minimum density attained during a cycle for *D. kuriphilus*
623 (middle panel) and *T. sinensis* (lower panel) as a function of η and γ . Note
624 that all reasonably high values of the survival fractions yield long cycle lengths
625 and extremely low densities at minimum, and thus explore the regime in which
626 the pest might survive the parasitoid as a result of stochastic fluctuations. Even
627 without invoking random effects, because the minima of *T. sinensis* are gen-
628 erally much lower than those of *D. kuriphilus*, there is the possibility that *T.*
629 *sinensis* reaches extinction-level densities before *D. kuriphilus*, which would
630 then remain completely unchecked. On the other hand, the map shows that
631 when *T. sinensis* attains densities very close to one, it is then able to bring
632 *D. kuriphilus* to extremely low densities in a single season (the mathematical
633 details are in appendix 5.3.3) which may be as low as to correspond to a local
634 extinction of the pest, even accounting for stochastic effects.

635 Finally, we mention that, for selected values of η and γ , the map (23) ap-
636 pears to be characterized by periodic cycles with amplitude and length smaller
637 than those found at different, but very close, values of the parameters (these
638 are the scattered dots of color slightly different than the surroundings visible in
639 Figure 2). These *regularity windows* are commonplace in discrete-time dynam-
640 ical systems such as the map (23) and are unlikely to persist if subject to the
641 random perturbations that are always present in a natural environment, but are
642 absent in this simple model. Thus their presence does not change the overall
643 qualitative description of the dynamics given above.

644 3.2. Space-dependent dynamics of *D. kuriphilus*

645 Before discussing the complete model (22) it is appropriate to analyze the
646 dynamics of *D. kuriphilus* alone, as it invades an idealized forest. We shall
647 consider a 1-dimensional spatial domain, that could be thought of as a very
648 long strip of trees whose width is negligible with respect to its length.

649 If *D. kuriphilus* is released at one end of the strip, in the absence of *T.*

650 *sinensis*, the equations (7), and their non-dimensional counterpart (8), describe
 651 the propagation of the population of the pest as it invades the domain. This is a
 652 traveling front joining the region in which the forest is fully infested by the pest
 653 to the region in which the pest is still absent, as illustrated in Figure 6A. Note
 654 that, owing to the large number of eggs that can be laid by a single individual,
 655 a relatively small density of adults is sufficient to saturate all of the available
 656 buds. Therefore, at the end of the season, the egg density front is offset with
 657 respect to the density front of the adult population. Numerical simulations (we
 658 used centered, second-order, finite-differences discretization for the diffusion
 659 term and Heun's method for timestepping) show a strong analogy with the
 660 propagation of a burning front, and the solutions are reminiscent of those of the
 661 well-known Kolmogorov-Fisher equation, which is the prototypical example for
 662 this kind of phenomena (see e.g. Murray, 2007, § 13.2). For the K-F equation
 663 a simple argument based on dimensional analysis shows that the speed and
 664 thickness of the front are directly proportional to the square root of the diffusion
 665 coefficient. The thickness is also directly proportional to the characteristic time
 666 of the chemical reactions, but the speed is inversely proportional to it.

667 Equations (7) are more complicated. The change of variables that brings
 668 (7) into (8) also suggests a proportionality of speed and thickness of the gall
 669 wasp front to the square root of the diffusivity. However, there are three dis-
 670 tinct time scales that characterize the reaction-like terms of equations (7): the
 671 season length T_D , the individual life span a , and the reciprocal of the egg de-
 672 position rate, a/N_D . Thus, in the non-dimensional equations (8) there remain
 673 two independent parameters, namely E_D and μ . Figures 6B and 6C show the
 674 dependence of speed and thickness of the front on E_D and μ in a wide range
 675 of values. These data (represented by the solid lines) use the non-dimensional
 676 units of Table 2. In particular, the unit of length is $\sqrt{D_D T_D}$ and the unit of
 677 speed is $\sqrt{D_D/T_D}$. The speed of the front is evaluated as the speed of the point
 678 where the non-dimensional egg density v is equal to $1/2$. The thickness of the
 679 front is estimated as $(\partial v/\partial x)^{-1}$, where the derivative is evaluated at the same
 680 point. Both quantities are computed from the results of numerical solutions of

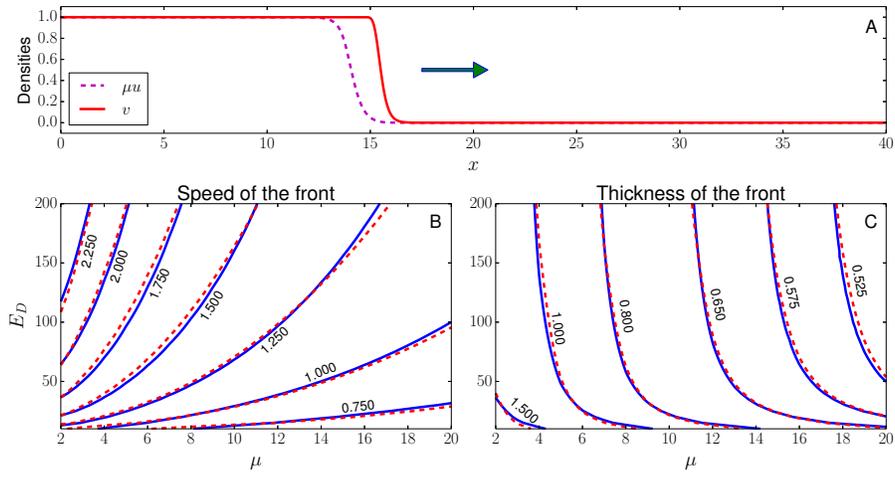


Figure 6: A) Density of eggs (continuous line) and of adults (dashed line) of *D. kuriphilus* at the end of the 10th season in a numerical solution of equations (8) with $\mu = 10$ and $E_D = 135$, where the pest is initially introduced at the left end of the one-dimensional domain. For clarity the density of adults is multiplied by μ . The arrow shows the direction of propagation of the front. B) Contour lines of the speed of the front as a function of the parameters μ and E_D . The solid lines are the numerical results, and the dashed lines are the fit $(1.95(E_D - 8)^{1/5})/(\mu + 2.75)^{1/2}$. C) Contour lines of the thickness of the egg density front as a function of the parameters μ and E_D . The solid lines are the numerical results, and the dashed lines are the fit $((2.26E_D + 7)/E_D)/(\mu + 0.1E_D^{1/2})^{1/2}$. All quantities in these figure use the non-dimensional units of Table 2.

681 the equations (8) subject to the conditions (9) and (10). The data may be fit-
682 ted reasonably well with simple analytic expressions (dashed lines, see the figure
683 captions for their expression in terms of E_D and μ). In terms of dimensional
684 variables, and of the parameters of Table 1, the fits for the speed S and the
685 thickness Δ of the front read

$$S = 1.95 (\eta N_D - 8)^{1/5} \sqrt{\frac{D_D}{T_D \left(\frac{T_D}{a} + 2.75\right)}}, \quad (26)$$

686

$$\Delta = \left(\frac{2.26\eta N_D + 7}{\eta N_D}\right) \sqrt{\frac{T_D D_D}{\frac{T_D}{a} + 0.1\sqrt{\eta N_D}}}. \quad (27)$$

687 These expressions are not formally deduced from the equations (we postpone
688 this issue to a future work), and thus should be considered to be reliable only
689 within the parameter range of Figures 6B and 6C. Nevertheless, they are fully
690 satisfactory for the problem of determining the magnitude of the diffusion coef-
691 ficient D_D on the basis of the observed propagation speed of the pest. Taking
692 into account that each year the gall wasp is active and mobile only during the
693 interval of time T_D , the speed of the front can also be expressed as $S = L/T_D$,
694 where L is the length traveled in one year by the infestation (as reported by
695 EFSA, 2010).

696 Taking $T_D = 40$ d, $a = 4$ d, $\eta = 0.9$, $N_D = 150$, from (26) we find

$$D_D \approx \frac{L^2}{83} \quad (28)$$

697 where the denominator is expressed in days. Using this in (27) we can link the
698 thickness of the front to the length it travels in a season, finding

$$\Delta \approx \frac{L}{2.1}. \quad (29)$$

699 For example, with $L = 8$ km, we have a thickness of the front $\Delta \approx 3.8$ km, and a
700 diffusion coefficient $D_D \approx 0.77$ km²d⁻¹. With a numerical value for the diffusion
701 coefficient we can explicitly convert our non-dimensional lengths in kilometers,
702 finding that, in this example, one unit of length is $\sqrt{D_D T_D} \approx 5.5$ km.

703 Assuming that the trajectories of individual insects approximate a Brownian
704 motion, Einstein's formula (see, e.g., Gardiner, 2004, §1.2) suggests that the

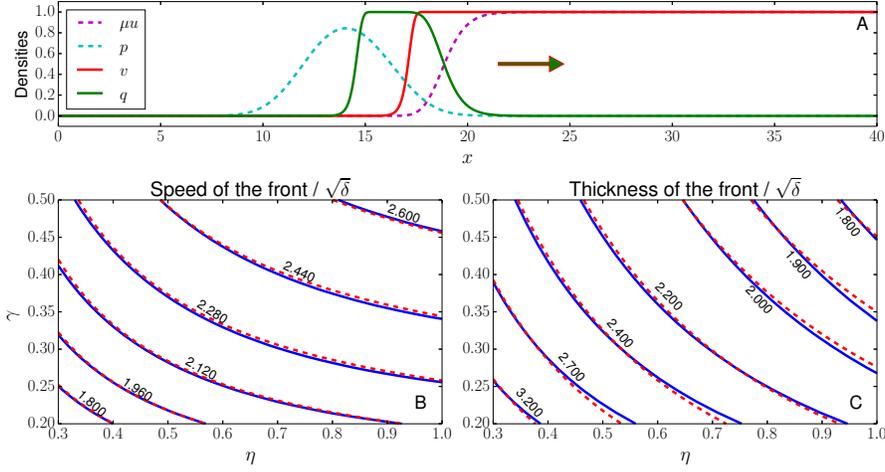


Figure 7: A) Density of eggs (red continuous line) and of adults (magenta dashed line) of *D. kuriphilus* density of eggs (green continuous line) and adults (cyan dashed line) at the end of the 7th season in a numerical solution of equations (22) with $\mu = 10$, $E_D = 135$, $E_T = 31.5$, $\gamma = 0.45$, $\eta = 0.9$, $\delta = 1$, $\tau = 1/\eta$, where the pest is initially homogeneously distributed throughout the one-dimensional domain, and the parasitoid is present only at its left end. For clarity the density of adults of *D. kuriphilus* is multiplied by μ . The arrow shows the direction of propagation of the front. B) Contour lines of the speed of the front as a function of the overwintering survival fractions η and γ . The solid lines are the numerical results, and the dashed lines are the fit $(\eta/(0.301\eta + 0.021))(\gamma - 0.05/(\eta + 0.12))^{1/5}$. C) Contour lines of the thickness of the egg density front as a function of the overwintering survival fractions η and γ . The solid lines are the numerical results, and the dashed lines are the fit $((0.88\eta + 1.55)/(0.6 + \eta))(\gamma - (1 - 0.6\eta)/(17\eta))^{-1/5}$. For values of δ different from 1, an excellent fit is obtained by multiplying these expressions by $\sqrt{\delta}$. All quantities in these figure use the non-dimensional units of Table 2.

705 typical displacement l of an adult after t days would be $l = \sqrt{2nD_D t}$, where
706 n is the dimensionality of the domain. Thus, in our idealized 1-dimensional
707 strip of trees the displacement over the entire adult life span (4 days) would be
708 $l \approx 2.5$ km, and in a 2-dimensional domain, such as a real wood, it would be
709 $l \approx 3.5$ km.

710 3.3. Space-dependent dynamics of the host-parasitoid system

711 If we start from an initial condition in which the idealized 1-dimensional
712 forest is fully infested by the pest, and the parasitoid is introduced at its left end,
713 then, in the course of years, the parasitoid population will propagate rightward,
714 as depicted in Figure 7A. As the parasitoid propagates rightward, it causes a
715 severe drop in the population density of the pest, which develops a left-facing

716 region of high gradient, connecting the part of the forest which has not yet been
717 reached by the parasitoid, and thus is still fully infested, to the part already
718 swept by the parasitoid, where the pest density has been severely reduced. The
719 reduction in the pest density is mirrored by a corresponding reduction of the
720 parasitoid density, which faces a drastic scarcity of its host in the region of
721 the forest that has already been swept. Therefore, the parasitoid population
722 propagates into an infested forest as a moving peak, rather than as a moving
723 kink.

724 The results of the numerical simulations show that the speed of propagation
725 of the parasitoid, and the thickness of the right-facing gradient region of its
726 egg density, are proportional to the square root of the diffusivity ratio $\sqrt{\delta}$ (see
727 Table 2), with excellent approximation, at least in the interval $\delta \in [0.1, 10]$. We
728 have also computed the dependence of speed and thickness on the overwintering
729 survival fractions η and γ . The results are reported in Figures 7B and 7C. These
730 results may be fitted by simple expressions, which, in terms of the parameters
731 of Table 1, read:

$$S_T = \frac{\eta}{0.301\eta + 0.021} \left(\gamma - \frac{0.05}{\eta + 0.12} \right)^{1/5} \sqrt{\frac{D_T}{D_D}}, \quad (30)$$

$$\Delta_T = \frac{0.88\eta + 1.55}{0.6 + \eta} \left(\gamma - \frac{1. - 0.6\eta}{17\eta} \right)^{-1/5} \sqrt{\frac{D_T}{D_D}} \quad (31)$$

733 These expressions are valid when the other parameters are $\mu = 10$, $E_D = 135$,
734 $E_T = 31.5$, $\tau = 1/\eta$, which should represent fairly well the relevant physiological
735 parameters of both the pest and of the parasitoid, as discussed in §2.4.

736 The density to which both the pest and the parasitoid drop on the left-
737 hand side of the right-moving peak, depends on the value of the overwintering
738 survival fractions η and γ , roughly in the same way as shown in Figure 2 for the
739 spatially homogeneous case discussed in §3.1. At low and intermediate survival
740 rates (such as those of Figures 3 and 4) the density drop spans at most a few
741 orders of magnitude, and it is thus insufficient to justify hopes of eradication of
742 the pest.

743 At higher survival rates the severity of the density drop is as large as to

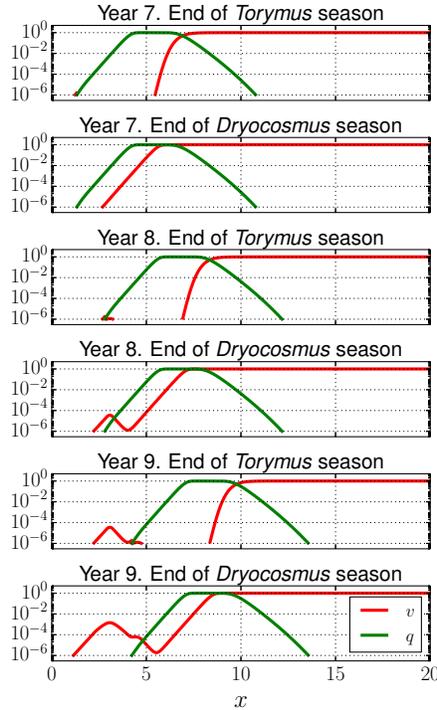


Figure 8: A time sequence showing the beginning of the recolonization of the forest by the pest after the passage of the parasitoid. The red line is the density of eggs or unparasitized larvae of the pest *D. kuriphilus*; the green line is the density of eggs or larvae of the parasitoid *T. sinensis*. Note the logarithmic scale. The ratio of the diffusivities (see Table 2) is $\delta = 0.3$, the other parameters are the same as in Figure 7A.

744 amply justify claims of local extinction: as the parasitoid sweeps the forest,
 745 virtually no host will be left unparasitized. Unfortunately, this effect alone does
 746 not guarantee a successful biological control. In fact, our model shows cases in
 747 which the pest is able to recolonize the empty forest left back by the passage of
 748 the parasitoid.

749 Figure 8 illustrates this phenomenon. In order to demonstrate that the model
 750 really allows for cases of recolonization, rather than failures of the parasitoid
 751 to attain a complete local eradication of the pest, in the run that produced
 752 Figure 8, at the end of the *Torymus* and of the *Dryocosmus* seasons, the egg
 753 density of both species was set to zero anywhere it was found to be below a
 754 threshold of local extinction equal to 10^{-6} non-dimensional units. The rationale

755 of identifying areas of very low density in the model as areas where no individual
756 insects are likely to be present was discussed at the beginning of §3.1. In this
757 run the initial conditions correspond to a release of a small amount of parasitoid
758 in a region spanning 1 non-dimensional units on the left end of the idealized
759 1-dimensional forest saturated by the pest. In a few years the population of the
760 parasitoid grows and spreads rightward into the forest, locally wiping out the
761 pest, and leaving a region devoid of both host and parasitoid behind its passage.

762 The time sequence of Figure 8 begins 7 years after the release of the para-
763 sitoid. At the end of the *Torymus* season, little or no *Dryocosmus* larvae remain
764 unparasitized in correspondence of the peak density of the parasitoid (Figure 8,
765 panel “Year 7 - End of *Torymus* season”). Then the surviving larvae of *Dryocos-*
766 *mus* emerge, and diffuse in the forest, looking for deposition sites. By the end
767 of the season, much of the ground lost to *Torymus* is recovered by *Dryocosmus*,
768 that arrives to lay some eggs even in the region on the left of the *Torymus* peak,
769 where the presence of the parasitoid is dwindling because of the scarcity of the
770 host. Thus, at the end of year 7, on the left of the *Torymus* peak, both host and
771 parasitoid are present, and, moving leftward, their density declines at a similar
772 rate (Figure 8, panel “Year 7 - End of *Dryocosmus* season”). The next year
773 *Torymus* once again wipes out all *Dryocosmus* larvae in the region where its
774 density is highest, and continues its march rightward. However, on the left end
775 of the *Torymus* peak, the density of the parasitoid is so low that it is unable to
776 control the pest. Therefore, the very small amount of *Dryocosmus* larvae origi-
777 nating from the eggs that were laid on the extreme left of the *Torymus* density
778 peak, are left virtually unaffected by the presence of the parasitoid (Figure 8,
779 panel “Year 8 - End of *Torymus* season”). Thus, they are able to develop into
780 *Dryocosmus* adults, that find, on their left, a forest devoid of the parasitoid and
781 ready to be recolonized (Figure 8, panel “Year 8 - End of *Dryocosmus* season”).
782 In the next year the recolonized patch widens to the left, and the density of the
783 pest increases (Figure 8, “Year 9” panels). In the following years (not pictured
784 in Figure 8), when the pest density has recovered to sufficiently high density
785 values, a second peak of the parasitoid population splits from the first, sweeping

786 leftward the recolonized forest. Subsequently, the pest passes back through this
787 second peak, just as it did with the first. With the choice of parameters of the
788 run in Figure 8, the long term dynamics is a never ending alternation of local
789 extinctions and recolonizations.

790 The inability of the parasitoid to control the pest at low densities of both
791 species derives from the very low probability of finding egg deposition sites when
792 both host and parasitoid are rare. This is a general characteristic of predator–
793 prey systems and the ultimate source of their cyclic behavior. In the case of the
794 present model, for spatially homogeneous solutions, the effect is well described
795 by the approximate map (25). For solutions that have a dependence on space,
796 local population flows caused by diffusion become important, and this means
797 that regions where the pest had been eradicated and thus the parasitoid has
798 dropped to densities at which it is unable to exert an effective control, may
799 come again within reach of the diffusing pest population, as we have illustrated
800 discussing the Figure 8. On the other hand, depending on the parameters,
801 the effect may also work the other way around: when the diffusivity of the
802 parasitoid is sufficiently high to avoid the recolonization of the areas behind
803 the peak, diffusion allows *Torymus* to maintain high concentrations even in
804 areas where *Dryocosmus* has already been brought below the local extinction
805 threshold. In this case the map (25) does not apply, and seems unlikely that
806 stochastic effects may offer a chance of survival to *Dryocosmus*.

807 In order to understand under which conditions the pest is able to cross the
808 parasitoid peaks and recolonize the forest, we have examined a large sample
809 of numerical solutions of the model equations, with different parameters. The
810 general pattern that emerges is the following: if the speed of propagation of
811 *Torymus* peaks (as given by eq. (30)) is appreciably larger than that of *Dry-*
812 *ocosmus* fronts (eq. (26)), then the pest will not be able to recolonize the forest.
813 Conversely, if the speed of *Dryocosmus* fronts is sufficiently larger than that of
814 *Torymus* peaks, then recolonization occurs. The precise boundary between the
815 two regimes is determined by the value of the threshold of local extinction.

816 The dynamics of traveling fronts of *Dryocosmus* and of sweeping peaks of

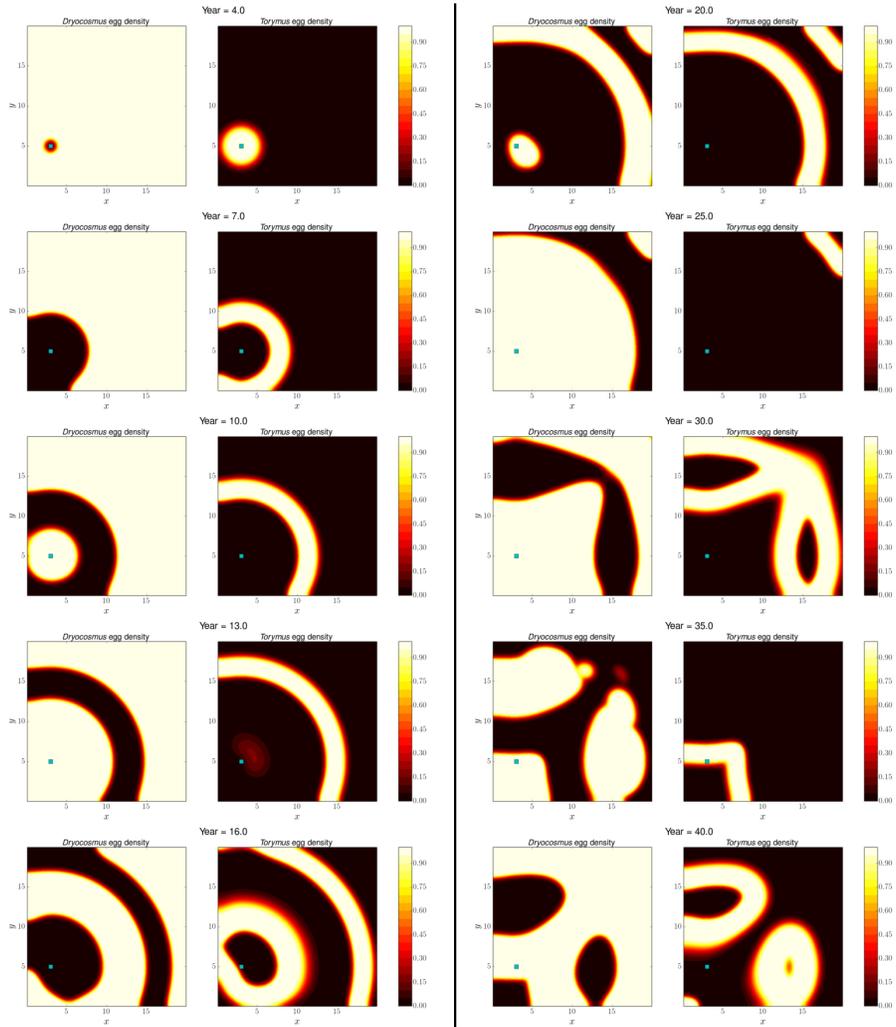


Figure 9: Time sequence of *D. kuriphilus* (left panels) and *T. sinensis* (right panels) egg densities in a numerical solution of the model equations with $\delta = 0.2$ and the other parameters as in Figure 8. The left column shows the earlier years after the release of a small amount of *T. sinensis* in a small patch of a square forest saturated by *D. kuriphilus*. The right column shows the dynamics on a longer time scale. The marker visible close to the lower left corner of all the panels is the release site of *T. sinensis*, and the place where the egg densities shown in Figure 10 are measured.

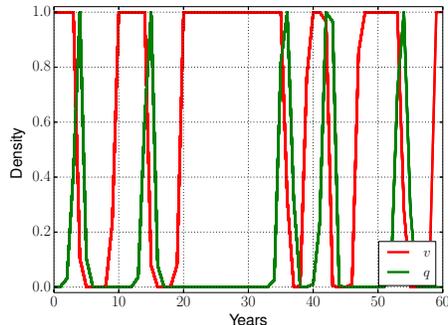


Figure 10: Densities of *D. kuriphilus* (v) and *T. sinensis* (q) eggs, at the end of each year, measured at the *T. sinensis* release site (shown in Figure 9) in the numerical solution of the model equations shown in Figure 9.

817 *Torymus* is present also when the spatial domain is two-dimensional. In this
818 case, peaks and fronts may be verbally described as waves propagating through
819 the forest, as illustrated in the time sequence of Figure 9. The *Torymus* is
820 initially released close to the lower-right corner of a square forest (the size
821 of 20×20 non-dimensional units corresponds in this numerical solution to a
822 physical size of approximately 110×110 km). It spreads radially, leaving a
823 roughly circular area of the forest free of both the pest and the parasitoid, which
824 is quickly recolonized by the pest. The parasitoid population then splits in two
825 parts: most of it continues to propagate through the forest in an expanding
826 arched wave, and a small part returns close to the release site, hunting the pest
827 that has recolonized the release area, giving rise to a second expanding arching
828 wave (left column of Figure 9). On longer time scales, because of the interaction
829 with the forest boundaries, these waves assume irregular shapes and form a
830 large variety of patterns (right column of Figure 9). The basic recolonization
831 mechanism, however, remains the same, and repeats endlessly.

832 This means that the time scales of appearance and disappearance through
833 the years of both pest and parasitoid at any fixed place in the forest are de-
834 termined by the speed of propagation of the waves, and by the size and shape
835 of the forest itself. This is illustrated in Figure 10, showing the end-of-year
836 egg density of *Dryocosmus* and *Torymus* at the *Torymus* release site, in the

837 numerical solution of Figure 9. In this case we have tuned the diffusivity ratio
838 (namely, we used $\delta = 0.2$) explicitly to obtain cycles of pest and parasitoid on
839 a decadal time scale (roughly the same time scale as observed in Japan). Note
840 that, with these parameters, and neglecting the extinction threshold, homoge-
841 neous solutions would give the cycles shown in Figure 5, that have a much longer
842 time scale. The space-dependent solutions, instead, have the same time scale
843 of the homogeneous solutions of Figure 4, but with much higher overwintering
844 survival fractions.

845 4. Discussion and conclusions

846 In this paper we have developed a spatially explicit model that describes
847 the invasion of a chestnut forest by the gall wasp *Dryocosmus kuriphilus*, which
848 acts as pest of the chestnut outside its native China, as well as the effect of
849 the parasitoid *Torymus sinensis*, which is modeled as host-specific of the gall
850 wasp and perfectly synchronized to its life cycle. In the special case of a spa-
851 tially homogeneous distribution of both pest and parasitoid, the model can be
852 reduced to an iterated map. Otherwise it is a set of piecewise time-continuous
853 reaction-diffusion partial differential equations which describe the spread and
854 the competition for egg deposition sites of the adults of both species.

855 The primary aim of the model is that of elucidating the possibilities of ob-
856 taining a biological control of the gall wasp, and understanding possible causes of
857 failure in obtaining control. In this respect the crucial parameters are the over-
858 wintering survival fractions (the fraction of laid eggs that successfully emerge
859 the next year) and the diffusion coefficients of the two species.

860 If the overwintering survival fractions are sufficiently far from 100%, then
861 both the spatially explicit model and its spatially-independent counterpart show
862 persistent oscillations in the density of both species, reminiscent of the classic
863 predator-prey models, having an amplitude too small to be consistent with local
864 extinction. This is in agreement with the hypothesis of Murakami and Gyoutoku
865 (1991), that attributes the failure of achieving biological control in Japan to the

866 presence of non-specialist parasitoid and hyperparasitoids species, which would
867 cause a high overwintering mortality.

868 Our own observations strongly suggest that, in an European setting, the
869 overwintering survival fractions are, at least, 90%. In that case, in a spatially
870 homogeneous situation, the model exhibits drops of more than 15 orders of
871 magnitude in the density of the pest, followed by even larger drops in the density
872 of the parasitoid. In practical terms, drops of this magnitude can only be
873 interpreted as signaling the local extinction of the insect. Thus, in a spatially
874 homogeneous situation, and with parameters that we consider appropriate for
875 the European setting, the model predicts that the parasitoid would quickly
876 eradicate the pest.

877 However, ever since the seminal experiments of Huffaker (1958) on mites, it is
878 known that spatial inhomogeneities may delay or altogether avoid phenomena
879 of local extinction in predator-prey systems. In particular, spatially explicit
880 versions of the Nicholson-Bailey host-parasitoid model show that the dispersal
881 of the individuals spontaneously produces the formation of complicated, time-
882 varying, but persistent patterns. In these cases, forcing a spatially-homogeneous
883 environment (e.g. by reducing the size of the domain below the intrinsic scale
884 of the patterns) often results in a rapid local extinction of both the host and
885 the parasitoid (Hassel et al., 1991).

886 With our model we find a similar outcome. If the speed of propagation of the
887 host population is faster than that of the parasitoid population (those speeds are
888 strongly dependent on the diffusion coefficients of the two species) and the size
889 of the domain is sufficiently large, then the spatially explicit model never settles
890 into a spatially-homogeneous solution leading to extinction. Instead, the gall
891 wasp recolonizes the areas left empty after the passage of the parasitoid, in a
892 never ending sequence of crossing waves of population density, of which Figure 9
893 shows an example. We should note that the imperfect biological control achieved
894 in Japan should probably be explained in this way, because the attack rate of
895 indigenous parasitoids was later found to be no larger than 2% (EFSA, 2010),
896 thus making unlikely the hypothesis of low overwintering survival rates.

897 On the other hand, when the population of the parasitoid propagates suffi-
898 ciently faster than that of the pest, then a single density wave of the parasitoid
899 sweeps the forest, killing the host, and leaving neither species behind it. In this
900 case the end result of the spatially explicit and of the spatially homogeneous
901 models is the same, and they both suggest a complete eradication of the pest.

902 Quite remarkably, there is a very scant literature on the speed of propagation
903 of *T. sinensis* when it is released in a forest fully invaded by *D. kuriphilus*. In
904 the United States, after the release there has been a 30 years lapse with no
905 follow-up observations (Cooper and Rieske, 2007). Regarding Japan, Toda et
906 al. (2000) states that «*T. sinensis* had only dispersed 12 km from its release
907 point over a 6 year period» and quotes Moriya et al. (1989) as a source. However,
908 the quoted paper does not contain this information (and we shall assume that
909 it was a personal communication, instead). Other published data refer to insect
910 densities at the release site (Moriya et al., 1989; Murakami et al., 2001) but give
911 no information on the spatial patterns of the insect population densities and
912 their changes in time. A conference proceedings by Moriya et al. (2003) also
913 reports a speed of 12 km in the first 6 years after the release, but states that
914 in the following five years «a steady expansion has been observed at a constant
915 rate of ca 60 km per year». No explanation is offered concerning the cause of the
916 change in speed. For Europe we are not aware of published follow-up surveys
917 assessing the spatial distribution of *T. sinensis* in the years following a release.
918 Using equation (30) with the parameters used for Figure 5 and in section 3.2,
919 we find that the ratio of the diffusivities of *T. sinensis* and *D. kuriphilus* would
920 be $\delta \approx 0.02$ if the propagation speed were 2 km per season, and $\delta \approx 18$ if the
921 speed were 60 km per season. These numbers are at the opposite ends of the
922 realistic range of speed and diffusivities. We can report our direct experience
923 in following up releases in the Cuneo province (NW Italy): when *T. sinensis*
924 suddenly progressed by tens of kilometers in one year, or was found in sites where
925 no official release was ever performed, it was usually later found that releases
926 had been performed by private farmers. Because these unrecorded releases have
927 become commonplace (alive specimens of *T. sinensis* can be readily bought on

the market) a reliable quantitative assessment of the speed of propagation of *T. sinensis* may be extremely difficult to accomplish. If the population of *T. sinensis* could really expand at a speed of 60 km per year, that is at 7.5 times the speed of *D. kuriphilus*, then, according to our model, a single release would be sufficient to achieve a complete biological control, because the pest would be unable to recolonize the areas already swept by the parasitoid.

On the basis of qualitative personal observations, the authors suspect that *T. sinensis* actually spreads at a much lower rate than *D. kuriphilus*, and closer to what is reported by Toda et al. (2000). If this were confirmed, then, according to the model, we should expect that the release of *T. sinensis* at a single location within a large forest area would simply trigger a train of density waves of both the pest and the parasitoid, that would travel into the forest producing, at any fixed site, an alternating presence and absence of the insects on decadal time scales. A satisfactory control would then only be achieved by follow-up releases of the parasitoid, continuing for many years, at carefully chosen sites, in order to suppress any returning wave of *D. kuriphilus* that could recolonize the forest left empty by the previous sweep of *T. sinensis*. This strategy, obviously, calls for a campaign of accurate observations tracking the spatial distribution of both species in the course of several years.

It has been recently discovered that a very low fraction of *T. sinensis* larvae experience an extended diapause (Ferracini et al., 2015b), and that, on very rare occasions, *T. sinensis* may parasitize galls not belonging to *D. kuriphilus*, but to European gall-making species (Ferracini et al., 2015a). Both processes have been observed in controlled laboratory settings, and in amounts so small that we felt authorized to neglect them in the model. In addition, the scarcity of observed events makes it difficult to detect external causes (if any) that may trigger the extended diapause, or the success rate of attempts of parasitism of galls of indigenous species. Therefore, even if further research is ongoing, the current level of knowledge is still insufficient to develop a detailed quantitative model that includes those processes. However, both a prolonged diapause and the ability to parasitize other hosts would allow *T. sinensis* to survive in the absence

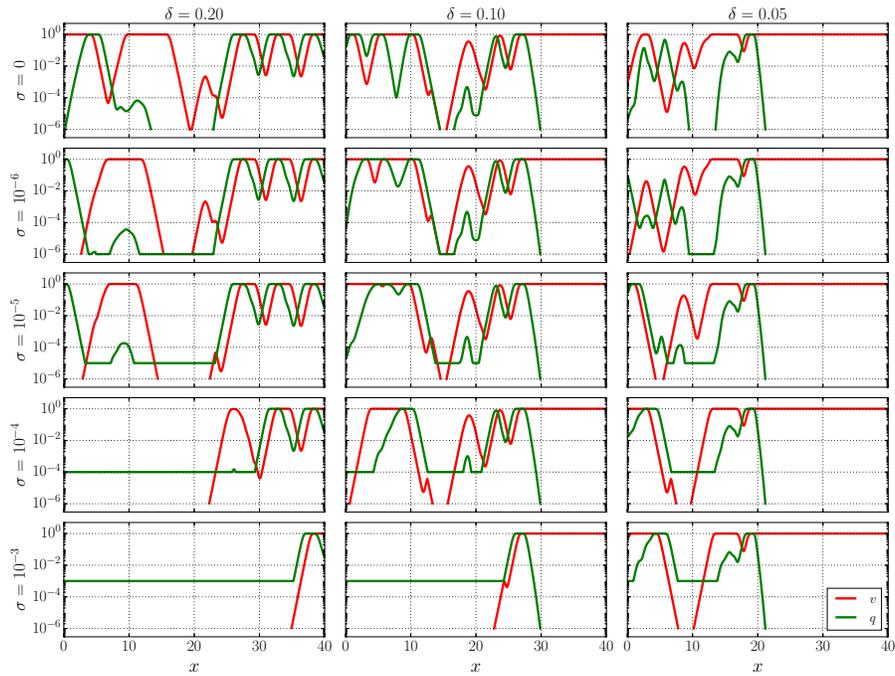


Figure 11: Egg density of *D. kuriphilus* (red) and *T. sinensis* (green) 35 years after the release of *T. sinensis* at the left end of the domain. The three columns, from left to right, refer to numerical solutions with diffusivity ratio $\delta = 0.2, 0.1, 0.05$ corresponding, respectively, to speeds of the *T. sinensis* front of about 6.4, 4.5 and 3.2 km per season. The rows, from top to bottom refer to: the unmodified model, and the model where *T. sinensis* in the areas already swept by the front, never drops below the threshold $\sigma = 10^{-6}, 10^{-5}, 10^{-4}, 10^{-3}$. All other parameters are as in Figure 8.

of *D. kuriphilus* (temporarily in the first case, on long time scales in the second).
Therefore, we have modified the model by imposing that in any place already
reached by the front of *T. sinensis*, at later times the density of the parasitoid
never drops below a threshold value σ , independently of the local density of *D.*
kuriphilus. This parameterization, albeit crude, is a simple and reliable way
to qualitatively assess the importance of any effects leading to the survival of
the parasitoid in the absence of the pest. The results are presented in Figure
11. The first row shows the egg density of pest (red) and parasitoid (green)
for $\sigma = 0$ (that is, for the unmodified model) 35 years after the release of the
parasitoid on the left end of an idealized one-dimensional forest, for diffusivity
ratios $\delta = 0.2, 0.1, 0.05$ (from left to right). In the rows below the first, the
threshold is set at $\sigma = 10^{-6}, 10^{-5}, 10^{-4}, 10^{-3}$. These values, translated to
dimensional quantities according to the estimates of section 3.1, range from one
T. sinensis individual every few trees to a few hundred *T. sinensis* individuals
per tree. When the threshold value is low the quantitative differences between
the modified and unmodified model are very small, even after 35 years. Only
when the threshold is high and the ratio of the densities is not too small the *T.*
sinensis surviving behind the front manages to avoid the recolonization by *D.*
kuriphilus. This result mathematically confirms what we expected: a very scant
population of *T. sinensis* surviving by parasitizing indigenous galls (or by any
other means) is unable to effectively find and parasitize galls of *D. kuriphilus*,
unless these are present in abundance. Therefore, when the pest recolonizes
the areas behind the *T. sinensis* front, first it rebuilds a sizable population,
and only then the surviving parasitoid can have a non-negligible effect. Of
course, a large population of *T. sinensis* surviving behind the front would be
effective at wiping out recolonization attempts. But such a large concentration
is completely incompatible with the observations.

Recently, it emerged that some animals appear to move by performing so-called Lévy walks, that is, random trajectories approximated by sequences of straight segments, where the probability distribution of the lengths of each segment has long, algebraic tails, and the variance of the distribution diverges

990 (Viswanathan et al., 2008). If *D. kuriphilus* or *T. sinensis* adopted this strategy,
991 then the model would have to be corrected with the use of fractional diffusion
992 operators, rather than ordinary ones. However, it seems far-fetched to assume
993 that the individuals of *D. kuriphilus* or *T. sinensis* may be able to travel for
994 kilometers along a straight line, as required in order to perform a Lévy walk. In
995 addition, the results of (del-Castillo-Negrete et al., 2003) show that fractional
996 diffusion would generate traveling fronts that exponentially accelerate, rather
997 than maintain a constant speed. We are not aware of any report of a progressive
998 acceleration of a gall wasp invasion front.

999 Other dispersion processes, in addition to ordinary diffusion, may be present.
1000 The gall wasp spreading model of EFSA (EFSA, 2010) includes so-called long-
1001 distance dispersal (LDD) events. There are essentially two main causes for
1002 LDD events: transport due to antropic activities, and transport with the wind
1003 of individuals that ventured above the forest canopy (particularly on occasion
1004 of storms). Transport processes can easily produce patchiness (see, for example,
1005 the case of zebra mussels carried downstream a river: Mari et al., 2009). In our
1006 case, they are also completely random and unpredictable: while the outcome of
1007 each LDD event could be forecast by a model, after its occurrence, and provided
1008 the availability of sufficient observational data, the occurrence of the event itself
1009 can not be forecast. Because our model does not (yet) have the ambition of being
1010 an operational one, but it is meant to uncover and elucidate some ecological
1011 processes in the interaction between *D. kuriphilus* and *T. sinensis*, we have, for
1012 the moment, refrained from including LDDs into it.

1013 However, we do not expect LDDs to change the overall picture that has
1014 emerged about the likeliness of achieving biological control of *D. kuriphilus* with
1015 *T. sinensis*. In fact, a random LDD event involving *D. kuriphilus* may have a
1016 good chance of carrying the pest in a region where it is absent, thus creating a
1017 new hotspot of infestation. On the other hand, a random LDD event involving
1018 *T. sinensis* can only contribute to the effectiveness of biological control if the
1019 parasitoid lands in a region populated by the pest and devoid of the parasitoid.
1020 If it lands in an area where the pest is absent, the event has no effect. If it lands

1021 close to a parasitoid sweeping wave, that region would have been swept in any
1022 case, and thus the effect is also limited. Thus, it seems reasonable to assume
1023 that LDDs do not improve the chances of achieving control, and, if anything,
1024 they diminish them.

1025 An anonymous reviewer states that “researcher collecting oak gall wasp know
1026 that galls are easier to find on forest margins, along roads, that is in open areas”
1027 while acknowledging that “there is nothing published on the subject”. Of course
1028 we cannot rule out the possibility that the diffusion coefficients of the insects
1029 may be larger in proximity of the forest margins, or the presence of other similar
1030 edge effects. But we also cannot rule out that these anecdotal reports may be
1031 due, at least in part, to selection biases (galls being easier to see and collect along
1032 roads and forest margins, rather than in the thick). Unfortunately, lacking any
1033 published quantitative observation of any edge phenomena, we feel that the best
1034 course of action is to maintain the model as simple as possible, just as we did
1035 discussing about boundary conditions in section 2.1. The spatially extended
1036 pest–parasitoid dynamics illustrated in this paper is a robust property of the
1037 model equations and occurs in the bulk of the domain, and is not overly affected
1038 by what happens at the edges of the domain. We are thus confident that what
1039 we have discussed so far would remain qualitatively valid even if future studies
1040 (that we would consider as important and timely) recognized the objective and
1041 non-negligible presence of edge phenomena. At that point the model may be
1042 reconsidered and improved to incorporate the new findings.

1043 Even with all the caveats that we discussed in this section, the overall mes-
1044 sage remains the same: biological control of *D. kuriphilus* with *T. sinensis* may
1045 be an effective option, but success should be expected only if one is prepared to
1046 carefully track the distribution of both species and to suppress any new hotspots
1047 (or recolonization waves) with further releases of the parasitoid.

1048 **5. Appendix**

1049 *5.1. Approximations of the space-independent solution of the gall wasp equations*

1050 Let us define $y_n(t) = \log(1 - v_n(t))$. Substituting in (11) we obtain

$$\begin{cases} \dot{u}_n(t) = & -\mu(1 + e^{y_n(t)})u_n(t) + v_{n-1}(1) \\ \dot{y}_n(t) = & -E_D\mu u_n(t) \\ u_n(0) = & 0 \\ y_n(0) = & 0 \end{cases} \quad (32)$$

1051 Observe that in (32), because the egg density v_n obeys $0 \leq v_n < 1$, then
 1052 $-\infty < y \leq 0$, and thus it is $1 < 1 + e^{y_n(t)} \leq 2$. This implies that

$$\frac{v_{n-1}(1)}{\mu}(1 - e^{-\mu t}) > u_n(t) \geq \frac{v_{n-1}(1)}{2\mu}(1 - e^{-2\mu t}) \quad (33)$$

1053 Using these inequalities in the second of (32) and from $v_n(t) = 1 - e^{y_n(t)}$, follow
 1054 the inequalities

$$1 - e^{-\frac{E_D}{\mu}(e^{-\mu t} + \mu t - 1)v_{n-1}(1)} > v_n(t) > 1 - e^{-\frac{E_D}{4\mu}(e^{-2\mu t} + 2\mu t - 1)v_{n-1}(1)}. \quad (34)$$

1055 By evaluating the above expression at time $t = 1$ one finds that the year-over-
 1056 year evolution of the end of season egg density $v_n(1)$ may be approximated by
 1057 the map (12) with the constants (13).

1058 Note that the approximation from below, obtained by choosing k_- in (13),
 1059 is very accurate if the density of eggs laid in the previous year is low. In fact,
 1060 by taking $v_{n-1}(1)$ arbitrarily close to zero it is possible, from (33), to keep $u_n(t)$
 1061 as small as one wishes, for all $t \in [0, 1]$, and, from the second of (32) also $y_n(t)$
 1062 may be kept as close to zero as one wishes, for all $t \in [0, 1]$. Therefore, the
 1063 quantity $1 + e^{y_n(t)}$ may be kept arbitrarily close to 2, which is the value used
 1064 by the approximation from below. Conversely, if $v_{n-1}(1)$ is close to one, and
 1065 the product $E_D\mu$ is much larger than one, then $1 + e^{y_n(t)}$ will rapidly approach
 1066 the value 1. Therefore, we expect the approximation from above to be more
 1067 accurate at high densities of eggs laid in the previous year.

1068 5.2. *Exact space-independent solution of the equations for T. sinensis*

1069 By imposing no-flux boundary conditions on p_n , assuming that $\nabla v_{n-1} =$
 1070 $\nabla q_{n-1} = 0$, the equations (18) and the conditions (19) become

$$\begin{cases} \dot{p}_n(t) = -\tau^{-1} (v_{n-1}(1) - q_n(t)) p_n(t) \\ \dot{q}_n(t) = E_T \tau^{-1} (v_{n-1}(1) - q_n(t)) p_n(t) \\ p_n(0) = q_{n-1}(\eta\tau) \\ q_n(0) = 0 \end{cases}. \quad (35)$$

1071 Dividing the first by the second we have

$$\dot{p}_n = -\frac{1}{E_T} \dot{q}_n,$$

1072 and thus, by integration and using the initial conditions, we find

$$p_n(q_n(t)) = -\frac{q_n(t)}{E_T} + q_{n-1}(\eta\tau).$$

1073 Substituting this expression in the second of the equations (35) we obtain a
 1074 first-order, autonomous equation for q_n which yields the following solution

$$\begin{cases} \begin{cases} p_n(t) = \frac{\bar{q}_{n-1}(E_T \bar{q}_{n-1} - \bar{v}_{n-1}) \exp\left(\frac{t}{\tau}(E_T \bar{q}_{n-1} - \bar{v}_{n-1})\right)}{\bar{q}_{n-1} E_T \exp\left(\frac{t}{\tau}(E_T \bar{q}_{n-1} - \bar{v}_{n-1})\right) - v_{n-1}^*} \\ q_n(t) = \frac{\bar{v}_{n-1} \bar{q}_{n-1} E_T (1 - \exp\left(\frac{t}{\tau}(E_T \bar{q}_{n-1} - \bar{v}_{n-1})\right))}{\bar{v}_{n-1} - \bar{q}_{n-1} E_T \exp\left(\frac{t}{\tau}(E_T \bar{q}_{n-1} - \bar{v}_{n-1})\right)} \end{cases}, & E_T \bar{q}_{n-1} \neq \bar{v}_{n-1} \\ \begin{cases} p_n(t) = \frac{\bar{v}_{n-1} \tau}{E_T (\bar{v}_{n-1} t + \tau)} \\ q_n(t) = \frac{\bar{v}_{n-1}^2 t}{\bar{v}_{n-1} t + \tau} \end{cases}, & E_T \bar{q}_{n-1} = \bar{v}_{n-1} \end{cases}$$

1075 where, for brevity, we have defined the shorthands $\bar{q}_{n-1} = q_{n-1}(\eta\tau)$, $\bar{v}_{n-1} =$
 1076 $v_{n-1}(1)$. It can be verified, by expanding the exponentials in power series, that
 1077 the above solution is a smooth function of the quantity $E_T \bar{q}_{n-1} - \bar{v}_{n-1}$.

1078 5.3. *Mathematical properties of the space-independent map*

1079 5.3.1. *Boundedness of the global dynamics*

1080 The map (23), formally, does not allow for the extinction of either species.
 1081 Specifically, the map has the property that, if $E_T, \eta, k > 0$ and $0 < v_n, q_n$ then
 1082 $0 < v_{n+1}, q_{n+2} < 1$.

1083 This assert becomes apparent by rewriting the map in the following form

$$\begin{cases} q_{n+1} = \begin{cases} \left(\frac{1 - e^{\eta(E_T q_n - v_n)}}{\frac{v_n}{E_T q_n} - e^{\eta(E_T q_n - v_n)}} \right) v_n, & E_T q_n \neq v_n \\ \left(\frac{v_n}{\eta^{-1} + v_n} \right) v_n, & E_T q_n = v_n \end{cases} \\ v_{n+1} = 1 - e^{-k(v_n - q_{n+1})} \end{cases} \quad (36)$$

1084 It is straightforward to verify that

$$0 < [1 - \exp(\eta(E_T q_n - v_n))] [v_n E_T^{-1} q_n^{-1} - \exp(\eta(E_T q_n - v_n))]^{-1} < 1$$

1085 both if $E_T q_n < v_n$ and if $E_T q_n > v_n$. Obviously, it also

$$0 < v_n [\eta^{-1} + v_n]^{-1} < 1,$$

1086 which is relevant in the case $E_T q_n = v_n$. Therefore, from the equation for q_{n+1}
 1087 in (36) we have $0 < q_{n+1} < v_n$. Using this inequality in the equation for v_{n+1}
 1088 in (36) we have $0 < v_{n+1} < 1$, and, therefore $0 < q_{n+2} < v_{n+1} < 1$.

1089 5.3.2. Nullclines and the coexistence fixed point

1090 We defined v -nullcline as the set of pairs (v_n, q_{n+1}) such that $v_{n+1} = v_n$.
 1091 From the second equation in (23), we find that the v -nullcline has the following
 1092 explicit expression

$$q_{n+1}(v_n) = v_n + \frac{1}{k} \log(1 - v_n) \quad (37)$$

1093 whose graph is the red line in the right panel of Figures 3, 4, 5. A simple
 1094 calculation shows that if (v_n, q_{n+1}) is above the v -nullcline, then $v_{n+1} < v_n$,
 1095 and if it is below, then $v_{n+1} > v_n$. If $k > 1$ then the v -nullcline has a maximum
 1096 at

$$v_{mx} = \frac{k-1}{k}, \quad q_{mx} = \frac{k-1-\log(k)}{k}. \quad (38)$$

1097 It also has a zero at $v_n = 0$, and at a value larger than v_{mx} and smaller than
 1098 1, which does not have a simple explicit expression, and corresponds to the
 1099 non-zero fixed point of Skellam's map (12).

1100 Analogously we defined the q -nullcline as the set of pairs (v_n, q_n) such that
 1101 $q_{n+1} = q_n$. The q -nullcline has an obvious branch which is $q_n = 0$. From

1102 the first equation in (23), if $v_n, q_n \neq 0$ and $E_T q_n \neq v_n$, we have the following
 1103 implicit definition of the q -nullcline

$$\frac{v_n - q_n}{v_n} e^{\eta(E_T q_n - v_n)} = \frac{E_T - 1}{E_T}. \quad (39)$$

1104 In the case $E_T q_n = v_n > 0$, it is straightforward to verify from (23) that
 1105 only the point $(v_n, q_n) = (\eta^{-1}(E_T - 1)^{-1}, \eta^{-1}(E_T - 1)^{-1} E_T^{-1})$ belongs to the
 1106 q -nullcline, shown as the green curve in the right panel of Figures 3, 4, 5. If
 1107 $q_n \rightarrow 0$, the q -nullcline tends to the value

$$v_z = \frac{1}{\eta} \log \left(\frac{E_T}{E_T - 1} \right). \quad (40)$$

1108 Note that, if $E_T > 1$ then the right-hand side of (39) is larger than 0 and smaller
 1109 than 1. Thus, for fixed η and $v_n \neq v_z$, if $E_T \rightarrow \infty$ either there is no solution to
 1110 (39), or $q_n \rightarrow v_n$ from below. This observation suggests that for realistic values
 1111 of the parameters (that is η not much smaller than 1 and E_T quite larger than
 1112 10), taking $q_n \approx v_n$ for $v_n > v_z$ should give a reasonably good approximation
 1113 of the q -nullcline.

1114 With respect to the new variable $z = q_n/v_n$, the implicit expression (39)
 1115 may be made explicit, and one finds

$$v_n(z) = \frac{1}{\eta(E_T z - 1)} \log \left(\frac{E_T - 1}{E_T - E_T z} \right) \quad (41)$$

1116 Note that $0 < z < 1$ because $q_n = q_{n+1} < v_n$. It can be checked that this is a
 1117 strictly growing function of z , which is smooth even at $z = E_T^{-1}$. (In order to
 1118 verify the positive sign of the derivative the identity $\log(x) \leq x - 1$ can be useful.)
 1119 Thus the minimum of this function is attained in the limit $z \rightarrow 0$, where $v_n \rightarrow v_z$:
 1120 for $v_n < v_z$ the equation (39) has no solution. We also observe that, because
 1121 $v_n'(z) > 0$, to each value of z corresponds a unique value of $q_n(z) = z v_n(z)$.
 1122 Therefore, calling ζ the inverse function of (41), we have that the equation (39)
 1123 implicitly defines a unique continuous function $q_n(v_n) = v_n \zeta(v_n)$ of v_n , that
 1124 we shall call the non-zero branch of the q -nullcline, and that $q_n'(v_n) > 0$, as
 1125 depicted by the green line in the right panel of Figures 3, 4, 5.

1126 From the first equation in (43) below, (see also the surrounding discussion)
 1127 it is clear that, for states not belonging to the q -nullcline having arbitrarily

1128 small q_n , if $v_n < v_z$ then $q_{n+1} < q_n$, and if $v_n > v_z$ then $q_{n+1} > q_n$. Thus,
 1129 since the non-zero branch of the q -nullcline is unique, by the theorem of the
 1130 persistence of sign, if a state (v_n, q_n) lies on the left of the q -nullcline, then
 1131 $q_{n+1} < q_n$; if it lies on the right, then $q_{n+1} > q_n$.

1132 Fixed points are the intersection of the v -nullcline and of the q -nullcline.
 1133 There is always the fixed point $(v_n, q_n) = (0, 0)$. If $k > 1$ then there is also the
 1134 fixed point $(v_n, q_n) = (v^*, 0)$ where v^* is the non-zero fixed point of Skellam's
 1135 map (12).

1136 If $k > 1$ and $v_z < v^*$, then the non-zero branch of the q -nullcline (which is
 1137 a growing function of v_n) must cross at at least one point the v -nullcline (which
 1138 is positive and has a zero at $v_n = 0$ and a zero at $v_n = v^*$). We call this is a
 1139 *coexistence* fixed point, because both v_n and q_n are larger than 0. Note that,
 1140 except for unrealistically low values of k , the non-zero fixed point of Skellam's
 1141 map is very close to one. Thus, an approximate criterion for the existence of a
 1142 coexistence fixed point is $v_z < 1$. Using the expression (40) and the definition
 1143 of E_T (see Table 2), setting $v_z = 1$ one obtains the approximate threshold (24).

1144 We have ample numerical evidence, corroborated by asymptotic results, that
 1145 there is only one coexistence fixed point, although we cannot exclude that for
 1146 some finely-tuned value of the parameters more than one coexistence fixed point
 1147 could exist.

1148 In the realistic range of parameters, a very rough approximation of the po-
 1149 sition of the coexistence fixed point may be obtained by approximating the
 1150 v -nullcline as

$$q_{n+1}(v_n) \approx \left(1 - \frac{1}{k}\right) v_n$$

1151 and the q -nullcline as the straight line connecting the points

$$(v_n, q_n) = (\eta^{-1}(E_T - 1)^{-1}, \eta^{-1}(E_T - 1)^{-1} E_T^{-1}) \quad \text{and} \quad (v_n, q_n) = (1, 1).$$

1152 Looking for the intersection of these straight lines we find

$$\begin{cases} v_c = \frac{k(E_T - 1)}{E_T[\eta(E_T - 1) - 1] + k(E_T - 1)}, \\ q_c = \frac{(k-1)(E_T - 1)}{E_T[\eta(E_T - 1) - 1] + k(E_T - 1)}. \end{cases} \quad (42)$$

1153 More accurate approximations of the q -nullcline (and thus of the coexistence
 1154 fixed point) can be worked out by evaluating (41) at the values z_m such that

$$\frac{E_T - 1}{E_T - E_T z_m} = e^{\eta E_T / m}$$

1155 for distinct values of the arbitrary parameter m . This yields explicit expressions
 1156 of points $(v_n(z_m), q_n(z_m))$ lying on the q -nullcline among which it is possible
 1157 to interpolate with any standard method.

1158 5.3.3. Cycles around the fixed point

1159 The cyclic dynamics generated by the map (23) may be qualitatively under-
 1160 stood through the following argument. For small q_n , the map (23) becomes, at
 1161 leading order

$$\begin{cases} q_{n+1} = (1 - e^{-\eta v_n}) E_T q_n + O(q_n^2) \\ v_{n+1} = (1 - e^{-k v_n}) + O(q_n) \end{cases} \quad (43)$$

1162 Let us assume that initially v_n , albeit much larger than q_n , is small enough to
 1163 satisfy the inequality $(1 - e^{-\eta v_n}) < E_T^{-1}$, that is $v_n < v_z$ (see eq. 40). Thus
 1164 the egg density of *T. sinensis* decreases from one year to the next as long as
 1165 this remains true. In this regime *D. kuriphilus* is at leading order decoupled
 1166 from its parasitoid, and its egg density obeys Skellam's map (12). Therefore,
 1167 assuming $k > 1$, v_n will grow with n until it approaches the non-zero fixed point
 1168 of Skellam's map, which, for realistic values of k , has a numerical value very close
 1169 to 1. At this point the egg density of *T. sinensis* will be growing in time, but
 1170 it may require several years before reaching an $O(1)$ magnitude. Thus, starting
 1171 from very small values of v_n and even smaller values of q_n , we have that the
 1172 sequence of states, seen in a diagram q_n vs v_n , as in the right panel of Figure 5,
 1173 first moves horizontally (v_n growing, q_n very close to 0) and then vertically (v_n
 1174 very close to 1, q_n growing). When q_n reaches $O(1)$ the approximation (43) no
 1175 longer applies, and it is convenient to rewrite the map (23) as (36), and then

1176 (assuming $E_T q_n \neq v_n$) as

$$\begin{cases} q_{n+1} = \left(\frac{e^{-\eta(E_T q_n - v_n)} - 1}{\frac{v_n}{E_T q_n} e^{-\eta(E_T q_n - v_n)} - 1} \right) v_n \\ v_{n+1} = 1 - e^{-k(v_n - q_{n+1})} \end{cases} \quad (44)$$

1177 With $q_n = O(1)$ for large (realistic) values of E_T the parenthesis appearing in
1178 the first equation approaches 1 from below. Thus we have $q_{n+1} \approx v_n$, which
1179 leads to a cancellation in the exponent appearing in the second equation, causing
1180 a sharp drop in the value of v_{n+1} with respect to v_n . Thus the system jumps
1181 from a state ($v_n \approx 1$, $q_n = O(1)$) close to right edge of Figure 5 (right panel) to a
1182 state close to its upper edge ($v_{n+1} \approx O(1)$, $q_{n+1} \approx 1$) or, more often, depending
1183 on the exact value of q_n , to a state close to its upper-left corner ($v_{n+1} \ll 1$,
1184 $q_{n+1} \approx 1$). The next year, since $q_n \approx 1$ the value in the parenthesis becomes
1185 even closer to one, and the cancellation occurs again with greater violence. The
1186 ensuing further drop in the value of *D. kuriphilus*' egg density may be as large
1187 as ten orders of magnitude, with the parameters of Figure 5. Therefore, in
1188 the turn of just two years, *T. sinensis* wipes out almost all the population of
1189 *D. kuriphilus* and, consequently, its own, because of the constraint $q_{n+1} < v_n$.
1190 The dynamics then is well described by the approximate map (25) showing that
1191 the pest begins to rebuild its own population, while the parasitoid population
1192 declines. Thus the cycle starts again.

1193 Note that the cycles need not be exactly periodic. In fact, the intervals of
1194 exponential growth of q_n and the subsequent cancellation events could produce
1195 a quasi-periodic or maybe even a chaotic dynamics (however we did not inves-
1196 tigate this issue). More importantly, small differences in the value of q_n before
1197 the cancellation events can make a large difference in the number of orders of
1198 magnitude lost after the events, and thus in the number of years needed to
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