

1 **A modelling framework for pest population dynamics and management:**
2 **An application to the grape berry moth**

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29 **Abstract**

30
31 Physiologically based demographic models are important tools for the development of
32 sustainable pest management as they can realistically describe the spatio-temporal dynamics of
33 population abundance as function of environmental forcing variables, e.g. temperature, and
34 resource availability. The physiological based model presented here is based on a stochastic
35 demographic model for a stage-structured population that has application to a wide range of
36 species across different taxa. The species life-history strategies are described in terms of a set of
37 biodemographic rate functions dependent from the biological characteristics of the species and
38 their environmental driver variables. Model application required parameter estimation of the
39 biodemographic rate functions at two levels: assessing physiological responses at the per capita
40 level and/or using population time series data for rate functions estimation. To explore the
41 usefulness of the modelling framework in pest management, we consider the case study of the
42 grape berry moth *Lobesia botrana*, a major pest in European vineyard. Most of the model

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43 parameters were estimated from data in the literature. An unpublished dataset of population
44 dynamics collected in a vineyard in the Veneto region (Italy) over three years was used to estimate
45 the mortality function. Model validation was performed with a set of independent data.
46 Model simulations provided realistic trajectories of population dynamics obtained with a limited
47 dataset of initial conditions. The suitability of the model as a tool for decision support for grape
48 berry moth management is discussed.

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50

51 **Keywords:** population dynamics, stage-structured population, physiologically based
52 demographic model, *Lobesia botrana*, integrated pest management

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55 **1. Introduction**

56

57 Ecological disruption due to pest control, agronomic practices and climate change affects all
58 aspects of system sustainability, including farmer health and food safety, and ecologically based
59 pest management methods must be developed to manage these systems sustainably. Considerable
60 progress has accrued in the area of pesticide efficacy, application techniques, and related policy
61 (e.g., Directive 2009/128/EC on the sustainable use of pesticides in Europe). However, the crucial
62 unresolved issue remains of how to define sustainable pest management and how to implement
63 it in time and space. Key to correcting this lacuna at the local, regional and national level are
64 decision support tools based on pest population dynamics and trophic interaction models
65 describing the dynamics in the agro-ecosystems, the procedures for scenario assessment, and
66 knowledge-based decision making. Considerable progress has been made in this area, but the
67 discussion on the approaches and the technological solutions to be used for the development of
68 decision support tools requires further clarity.

69

70 Since the 1970s, multidisciplinary research involving biologists, ecologists, entomologists and
71 plant pathologists, mathematicians and meteorologists has developed useful tools to meet some
72 of these multiple objectives aided in the United States by the NSF/EPA/USDA funded IPM
73 projects (Norton and Holling, 1977, pp. 253-316). Getz and Gutierrez (1982) reviewed the origins
74 of systems analysis in crop protection and integrated pest management (CP/IPM) that integrated
75 developments in physiology (de Wit and Goudriaan, 1974), population dynamics (e.g., Gilbert
76 and Gutierrez, 1973; Gutierrez et al., 1977; Wang et al., 1977) and economics (Regev et al.,

77 1976), and that had later application to a wide range of crop systems (e.g., alfalfa, cotton, cassava,
78 olive, grape). Innovative elements of this work led to the development of an integrated approach
79 to support sustainable integrated pest management (IPM) programs, but despite wide application
80 the methods remain largely underutilized by the vast majority of agricultural researchers and
81 extension personnel, and in most cases decisions continue to be taken without the support of
82 quantitative tools.

83
84 Mechanistic approaches based on weather-driven ecological models were used to evaluate the
85 spatio-temporal dynamics of pest populations as forced by the crucial driving role on pest
86 population dynamics played by meteo-climatic features as well as other physical-biological
87 characteristics of the agricultural landscape (Gutierrez, 1996). Mechanistic models for population
88 dynamics based on physiological responses at individual level to environmental driving variables
89 have been proposed since the 1970's (Gutierrez, 1996; Gutierrez et al., 1975; McDonald et al.,
90 1989; Metz and Diekmann, 1986; Wang et al., 1977; de Wit and Goudriaan, 1974). These models
91 have been defined as physiologically based demographic models (PBDMs) (Gutierrez et al.,
92 2010) and offer several advantages for developing sustainable crop production systems (Gilioli
93 and Mariani, 2011). For example

94 (i) they account for the non-linear relationships between environmental forcing variables (e.g.,
95 temperature) and the biological processes enabling the population dynamics to be described
96 realistically;

97 (ii) they enable the evaluation of the effects of biological and ecological variability on population
98 dynamics, especially in complex systems over geographic space and time required for area-wide
99 pest management (Gutierrez et al., 2012);

100 (iii) they capture within the same modelling framework processes at different trophic levels and
101 the trophic interactions and their consequences in simple trophic web (Gutierrez and
102 Baumgaertner, 1984);

103 (iv) they allow fine-scale predictions of the phenology and population dynamics at different
104 spatial scales using ecologically meaningful state variables directly related to the pest impact on
105 plants density and biomass fundamental for decision making in pest control and management of
106 invasive species (Gutierrez and Ponti, 2013; Pasquali et al., 2015);

107 (v) they allow the exploration of complex scenarios in which no simple (i.e., linear) conclusions
108 can be drawn, for example evaluating the effects of management options based on different
109 techniques and tactic-strategy of implementation at different scales, or the large scale impact of

110 drivers of ecosystem change (Gilioli and Mariani, 2011; Gilioli et al., 2014; Gutierrez and Ponti,
111 2013;).

112
113 These characteristics make PBDMs particularly useful for the development of decision support
114 systems in IPM. In particular, PBDMs are suitable for management problems characterized by
115 heterogeneity and complexity related to the interaction among processes affecting the interactions
116 of systems components (e.g. plant, pest, as affected by the biotic and abiotic environment), at
117 different spatial scales (micro, meso, and macro-scales), requiring different information for
118 decision making at tactical, strategic and policy levels.

119
120 The modelling framework reported here is a particularization, for a suitable choice of the
121 biodemographic functions, of the most general mathematical framework presented in Buffoni
122 and Pasquali (2007) that allows to obtain the distribution of individuals in an age-stage structured
123 population in time and physiological age. Buffoni and Pasquali (2007) used Eulerian formalism
124 based on the Fokker-Planck (or forward Kolmogorov) equation (Gardiner, 1985, p.117) to
125 formulate a nonlinear stochastic model to describe the population dynamics of a species
126 characterized by either a continuous size structure or a discontinuous stage structure that includes
127 the dispersion effects of the individuals during the development. Numerical approximation and
128 analysis of existence and stability of equilibrium states of the stochastic Eulerian model were
129 discussed by Buffoni and Pasquali (2007). Properties and advantages of the forward Kolmogorov
130 model compared with other age structured models are illustrated in Buffoni et al. (1990, 1996)
131 and Di Cola et al. (1998, 1999). This modelling framework can be used to model a population
132 characterized by a discontinuous stage structure with continuous time- and age-structure within
133 a stage with the biodemographic functions dependent on time through temperature. Specifically,
134 the rate functions for fecundity and mortality are driven by biotic variables. The mathematical
135 and biological characteristics of this modelling framework fall under the ambit of the PBDM.

136
137 Here we develop a model to simulate the population dynamics of the grape berry moth (*Lobesia*
138 *botrana* Den. & Schiff.) (Lepidoptera Tortricidae), the most important pest of grape (*Vitis*
139 *vinifera* L.) in the Mediterranean basin (CABI, 2014). The pest attacks more than 27 families of
140 berry producing plants, but despite its wide host range, it causes economic damage only to
141 grapevine (CABI, 2014). The original geographical distribution follows a clear Palearctic pattern
142 and currently includes Southern and Middle Europe, Northern and Western Africa, Middle East,
143 West Asia (CABI, 2014; Maher and Thiéry, 2006; Thiéry and Moreau, 2005; Venette et al.,

144 2003), South America and localized in Northern California (Varela et al., 2010) before its
145 eradication. *L. botrana* is regarded as a potentially serious pest on a worldwide scale for all the
146 vine-growing areas that are presently unaffected (CABI, 2014).

147

148 Demographic modelling approaches for *L. botrana* aiming at tactical decision making have
149 lacked a fully mechanistic description of the demographic process (Schmidt et al., 2001, 2003).
150 Most prior models for *L. botrana* used to support IPM practices have been phenological models
151 (Baumgärtner and Baronio, 1988; Hardman, 2012) that predict the time of appearance of
152 developmental stages and are used to facilitate timing of sampling and control operations. Even
153 if temperature dependent development rate and stage-age structure are included in such
154 phenological models, they do not produce realistic projections of *L. botrana* population
155 dynamics, that are indispensable for pest control decision making based threshold levels of stage-
156 specific abundance (Hardman, 2012). Recently, analytical models for *L. botrana* population
157 dynamics have been developed but are ill suited for tactical decision making, but may provide
158 strategic evaluation of control measures (Ainseba et al., 2011; Picart and Milner, 2014). Only
159 Gutierrez et al. (2012) developed a fully mechanistic, physiologically based description of the
160 dynamics of grapevine and of *L. botrana* population dynamics. This model used a distributed
161 maturation time model (Vansickle, 1977) and was designed to simulate the dynamics and
162 potential geographic distribution and relative abundance of the moth in California, the continental
163 U.S.A and Mexico. It also served as the basis for a strategic analysis of the timing of mating
164 disruption pheromone for pest control.

165 In contrast to Gutierrez et al. (2012), the goal of our model development, parameterization and
166 model output is for use in field decision support for IPM practice implementation. Our modelling
167 framework focuses on tactical application of field-based PBDM applications that require field
168 calibration, validation before they are used. Estimation of the biodemographic functions using a
169 bottom-up approach are based on literature data on the life-history biology of *L. botrana*,
170 summarized in Gutierrez et al. (2012). The simplifying assumption of this and prior models is the
171 parameters of the biodemographic functions are time-invariant. In this paper we estimate the
172 mortality rate using unpublished field data on the dynamics of *L. botrana* life stages, collected at
173 Colognola ai Colli (Veneto region, Italy) during the years 2008, 2009, 2011. A top-down
174 approach is used to estimate the term of the mortality rate functions that depends on
175 environmental factors other than temperature, including plant resources shortfall and natural
176 enemies of the grape berry moth. The calibrated model was validated using an independent
177 dataset of *L. botrana* collected at the same location during two different years. The utility of the

178 calibrated and validated model for tactical field-based decision support of grape berry moth
 179 management is discussed.

180

181

182 2. Methods

183

184 2.1. Population dynamics model

185

186 The stochastic demographic model is based on a system of partial differential equations, that
 187 allows obtaining the temporal dynamics of the stage-structured population and their distribution
 188 on physiological age within each stage. Consider a stage-structured population composed of s
 189 stages, with stages 1 to $s - 1$ being immature stages, and s being the reproductive stage. In the
 190 model, t denotes chronological time while x represents the physiological age (i.e., the
 191 developmental index) indicating development over time (see, Buffoni and Pasquali, 2007, 2010
 192 and 2013, or Di Cola et al., 1999). Let

193

194 $\phi^i(t, x)dx$ = the number of individuals in stage i with age in $(x, x + dx)$, $i = 1, 2, \dots, s$.

195

196 A stochastic population dynamic model based on the forward Kolmogorov or Fokker-Planck
 197 equations (Gardiner, 1985, p.117), is used that simulates the variability of development rate
 198 among individuals (Buffoni and Pasquali, 2007)

199

$$200 \frac{\partial \phi^i}{\partial t} + \frac{\partial}{\partial x} \left[v^i(t) \phi^i - \sigma^i \frac{\partial \phi^i}{\partial x} \right] + m^i(t) \phi^i = 0, \quad t > t_0, \quad x \in (0,1), \quad (1)$$

$$201 \left[v^i(t) \phi^i(t, x) - \sigma^i \frac{\partial \phi^i}{\partial x} \right]_{x=0} = F^i(t), \quad (2)$$

$$202 \left[-\sigma^i \frac{\partial \phi^i}{\partial x} \right]_{x=1} = 0, \quad (3)$$

$$203 \phi^i(t_0, x) = \hat{\phi}^i(x), \quad (4)$$

204

205 where $i = 1, 2, \dots, s$, $v^i(t)$ and $m^i(t)$ are the stage specific development and mortality rates,
 206 respectively, that are assumed independent of age x , the $\hat{\phi}^i(x)$ are the initial distributions, while
 207 the σ^i are the diffusion coefficients, that are assumed time independent. The flux $F^i(t)$ in the
 208 boundary condition (2) are described as follows. $F^1(t)$ is the egg production flux and is given by

209

210 $F^1(t) = v^s(t) \int_0^1 \beta(t, x) \phi^s(t, x) dx$ (5)

211
 212 where $v^s(t)\beta(t, x)$ is the specific fertility rate at time t and age x . In particular, we consider

213
 214 $v^s(t)\beta(t, x) = b(t)f(x)$ eggs/adults with age in $(x, x + dx)$ /time unit (6)

215
 216 where $b(t)$ takes into account the effect of diet and temperature, and $f(x)$ is the maximum age
 217 specific fertility profile.

218
 219 $F^i(t)$, when $i > 1$, are the individual fluxes from stage $i - 1$ to stage i and are given by

220
 221 $F^i(t) = v^{i-1}(t)\phi^{i-1}(t, x), \quad i > 1.$ (7)

222
 223 The boundary condition at $x = 0$ assigns the input flux into stage i , while the boundary condition
 224 at $x = 1$ means that the output flux from stage i is due only to the advective component
 225 $v^i(t)\phi^i(t, 1)$ (Buffoni and Pasquali, 2007).

226
 227 The functions $\phi^i(t, x)$ allow to obtain the number of individuals in stage i at time t :

228
 229 $N^i(t) = \int_0^1 \phi^i(t, x) dx.$ (8)

230
 231

232 **2.2. The biodemographic functions**

233
 234 The PBDMs approach requires parameterization of basic bio-demographic rate functions, for
 235 development, fecundity and mortality. These functions are common to poikilotherm organisms
 236 across many different taxa, with the physiological responses to environmental forcing variables
 237 being basically the same (e.g., Gutierrez, 1996). Temperature is considered the most important
 238 driving variable in poikilotherm and is introduced in the dynamic models as an independent
 239 variable in the rate functions. The dependence of the rate functions on other environmental
 240 variables, including resources is straightforward (Gutierrez, 1996).

241
 242

243 ***Development rate function***

244

245 The development rate depends on environmental temperature. We use the development rate
246 Lactin function (Lactin et al., 1995)

247

$$248 \quad v^i(T(t)) = \delta^i \max \left\{ 0, e^{\alpha^i T} - e^{\alpha^i T_m - \frac{T_m - T}{\beta^i}} - \gamma^i \right\} \quad (9)$$

249

250 though other functional forms for the development rate function, similar to the Lactin function,
251 can be used (e.g., see Ainseba et al., 2011, and the review by Kontodimas et al., 2004).

252 In formula (9), $T = T(t)$ is the temperature at time t , T_m is the lethal maximum temperature, α^i
253 is the slope parameter describing the acceleration of the function from the low temperature
254 threshold to the optimal temperature, β^i is the width of the high temperature decline zone, γ^i is
255 the asymptote to which the function tends at low temperatures, and δ^i is a coefficient of
256 amplification of the curve.

257

258 ***Fecundity rate function***

259

260 Egg production is dependent on the physiological age of the adult, the phenological stage of the
261 plant, and the temperature. We refer to Gutierrez et al. (2012) for the functional form of the term
262 $f(x)$ in equation (6), but here we consider the physiological age as argument instead of the
263 chronological age

264

$$265 \quad f(x) = \max \left\{ \frac{\delta(\eta x - \xi)}{\theta(\eta x - \xi)}, 0 \right\}, \quad (10)$$

266

267 where $\delta, \eta, \xi, \theta$, are parameters to be estimated.

268 The term $b(t)$ in equation (6) depends on the phenological stage of the plant $P(t)$ (which is a
269 proxy for the plant resources) and on temperature, and is expressed as the product

270

$$271 \quad b(t) = b_0(P(t))a_0(\hat{T}(t)) \quad (11)$$

272

273 where $b_0(P(t))$ is a discrete function defined in the sequel, and the concave function

274

275 $a_0(\hat{T}) = 1 - \left[\frac{\hat{T} - \hat{T}_L - \hat{T}_0}{\hat{T}_0} \right]^2$ (12)

276

277 captures the effects of temperature with \hat{T}_L the minimum temperature of reproduction and \hat{T}_0 the
 278 half-width of the temperature interval of reproduction (Gutierrez et al., 2012).

279 In (11), $\hat{T}(t)$ is the average temperature over a time period $[t - \tau(P), t]$, where $\tau(P)$ is a suitable
 280 time interval, that depends on the phenological stage of the plant and is used to characterize the
 281 effect of the temperature on the fecundity of adult females.

282

283 ***Mortality rate function***

284

285 The mortality rate function is composed of intrinsic temperature-dependent (abiotic) mortality
 286 and a stage- and generation-dependent extrinsic mortality likely related to external natural control
 287 factors.

288 Following Briolini et al. (1997) the average stage proportional mortality as function of
 289 temperature is defined by

290

291
$$M^i(T) = \begin{cases} a^i \left(\frac{T - T_{M0}^i}{T_{M0}^i} \right) + \varepsilon & \text{for } T_{ML}^i \leq T \leq T_{MU}^i \\ 0.85 & \text{otherwise} \end{cases} \quad (13)$$

292

293 where ε and a^i are constants, and

294

295
$$T_{M0}^i = \frac{T_{ML}^i + T_{MU}^i}{2}, \quad a^i = (0.85 - \varepsilon) \left(\frac{T_{MU}^i}{T_{M0}^i} - 1 \right)^{-2}.$$

296

297 Then, from (13) and considering the stage-specific development rate function (9), we define the
 298 total stage-specific mortality rate $m^i(T)$ as

299

300
$$m^i(T) = \begin{cases} -v^i(T) \ln(1 - M^i(T)) + J^i(G(t)) & \text{for } T \in [T_{ML}^i, T_{MU}^i] \\ \left[-v^i(T_{ML}^i) \ln(1 - M^i(T)) + J^i(G(t)) \right] \left[(T_{ML}^i - T)^2 + 1 \right] & \text{for } T < T_{ML}^i \\ \left[-v^i(T_{MU}^i) \ln(1 - M^i(T)) + J^i(G(t)) \right] \left[(T - T_{MU}^i)^2 + 1 \right] & \text{for } T > T_{MU}^i \end{cases} \quad (14)$$

301

302 where $i = 1, 2, \dots, s$, and the values T_{ML}^i and T_{MU}^i depend on the interval of positivity of the
 303 development function. The term $-v^i(T)\ln(1 - M^i(T))$ is the temperature dependent intrinsic
 304 mortality (i.e., abiotic) and the term J^i is an extrinsic mortality term due to natural control factors
 305 and it depends on the stage and on the generation $G(t)$. Where no literature data are available to
 306 determine the values $J^i(G)$, they are estimated, for different stages and generations, following the
 307 procedure outlined in section 2.3.

308

309 **2.3. Parameter estimation for *Lobesia botrana***

310

311 *L. botrana* has a stage structured population, with stages 1 to 3 being the immature stages (i.e.,
 312 egg, larva and pupa), while stage 4 is the reproductive stage (adult). Estimation of stage-specific
 313 biodemographic functions for development, fecundity and intrinsic mortality rates rely on
 314 bottom-up experimental data, while top-down field population data must be used to estimate
 315 mortality rates due to natural enemies. Development periods, including the adult life span, and
 316 fecundity rate were derived from laboratory experimental data and published in Baumgärtner and
 317 Baronio (1988), Brière and Pracros (1998), Briolini et al. (1997), Gabel (1981), Gutierrez et al.
 318 (2012), and Thiéry and Moreau (2005).

319

320 **Development rate function.** Parameters of the development rate function are estimated by means
 321 of a least square method using the dataset reported in Brière and Pracros (1998) and in
 322 Baumgärtner and Baronio (1988). The values of the parameters $\alpha^i, \beta^i, \gamma^i, \delta^i$, for all the stages,
 323 are given in Table 1. The development rate function for the adults is supposed to be equal to the
 324 one estimated for the pupae. In all the cases $T_m = 36$.

325

326

	α^i	β^i	γ^i	δ^i
$i = 1$	0.01	0.8051	1.0904	1
$i = 2$	0.003	0.662	1.0281	1
$i = 3$	0.0076	1.7099	1.0929	1.1
$i = 4$	0.0076	1.7099	1.0929	1.1

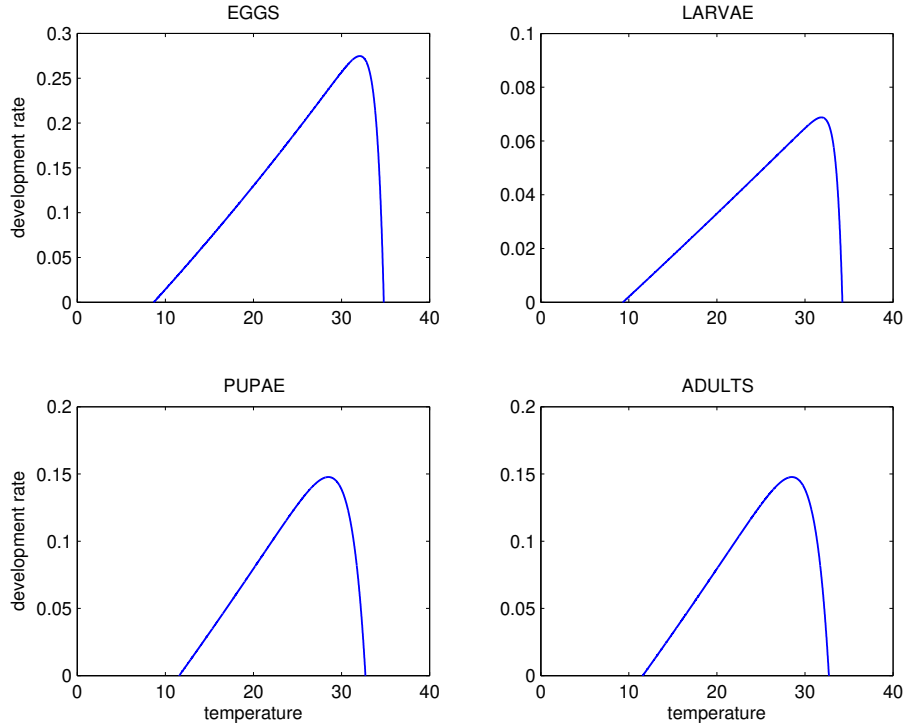
327

328 **Table 1.** Parameters of the stage-specific development rate function (8) for the four stages of *L.*
 329 *botrana*: eggs ($i = 1$), larvae ($i = 2$), pupae ($i = 3$), and adults ($i = 4$).

330

331 The estimated development rate functions (1/days) for the four stages as function of the
332 temperature ($^{\circ}\text{C}$) are represented in Figure 1.

333



334

335

336 **Figure 1.** Development rate (1/day) on temperature ($^{\circ}\text{C}$) for the four stages (eggs, larvae, pupae,
337 adults) of the grape berry moth *L. botrana*.

338

339

340 **Fecundity rate function.** As in Gutierrez et al. (2012), the fecundity rate is considered to be
341 dependent from the phenological stage of the plant, the temperature, and the physiological age of
342 the adult. The parameters appearing in function $f(x)$ in (10) are obtained fitting the
343 corresponding oviposition profile, in Gutierrez et al. (2012), duly converted as function of
344 physiological age (see also Baumgärtner and Baronio, 1988), and their values are

345

346 $\delta = 1.4175$, $\eta = 380$, $\xi = 16$, $\theta = 1.025$.

347

348 The values appearing in function $a_0(\hat{T})$ in (12) are (see Gutierrez et al., 2012)

349

350 $\hat{T}_L = 17$, $\hat{T}_0 = 7.5$.

351 Function $b_0(P)$ depends on the phenological age of the plant P expressed in terms of the BBCH-
 352 scale (Lorenz et al., 1994). The values for $b_0(P)$ are given in Gutierrez et al. (2012) and reported
 353 in Table 2. More precisely, $b_0(P)$ is a step function with steps at the BBCH stages indicated in
 354 Table 2.

355

Plant stage	P	$b_0(P)$ <i>eggs female⁻¹ day⁻¹</i>
Inflorescence	BBCH 53	0.31
Green berries	BBCH 71	0.48
Maturing fruits	BBCH 81	1

356

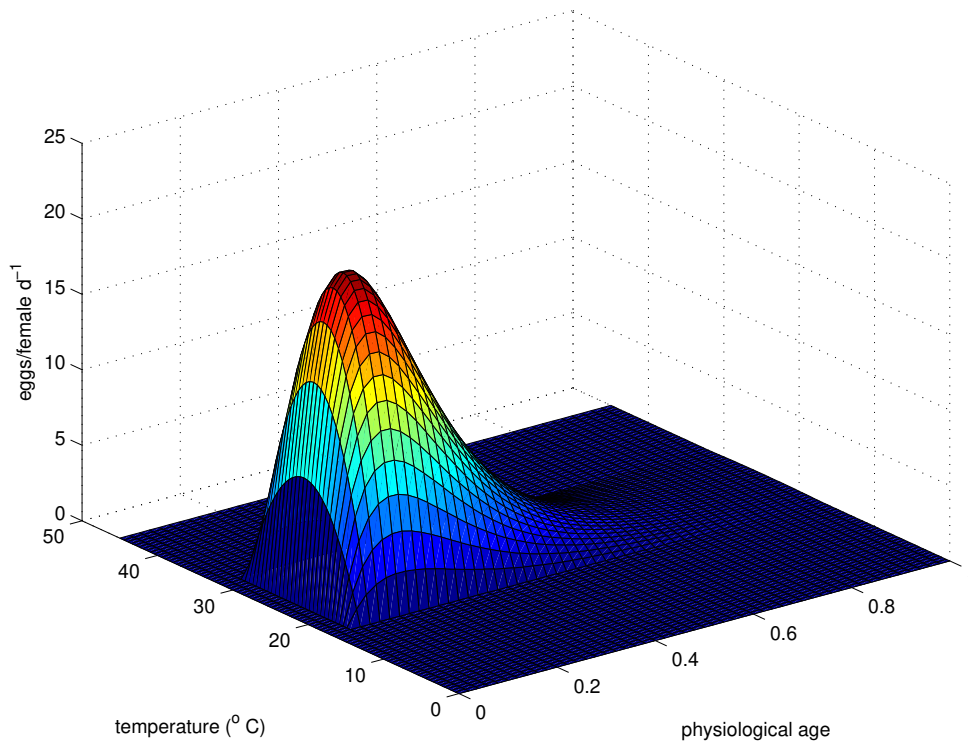
357 **Table 2.** Values of the step function $b_0(P)$, in equation (11), with steps in three plant
 358 phenological stages, following the BBCH-scale, for the grape berry moth *L. botrana*.

359

360

361 The function for fecundity $b(t)f(x)$, for $b_0(P) = 1$, is illustrated in Figure 2.

362



363

364

365 **Figure 2.** Fecundity rate function (eggs female⁻¹ day⁻¹) on temperature (°C) and physiological
 366 age (dimensionless) for adults of the grape berry moth *L. botrana*, for $b_0(P) = 1$.

367 **Intrinsic mortality rate function.** The mortality rate function was estimated using data in Briolini
 368 et al. (1997) and Gutierrez et al. (2012). Based on the development functions in Fig. 1, the values
 369 of the temperatures T_{ML}^i and T_{MU}^i appearing in formulae (13) and (14) are given in Table 3.
 370 Parameter $\varepsilon = 0.1$.

371

	$i = 1$	$i = 2$	$i = 3$	$i = 4$
T_{ML}^i	8.8	9.1	11.73	11.73
T_{MU}^i	34.79	34.27	32.67	32.67

372

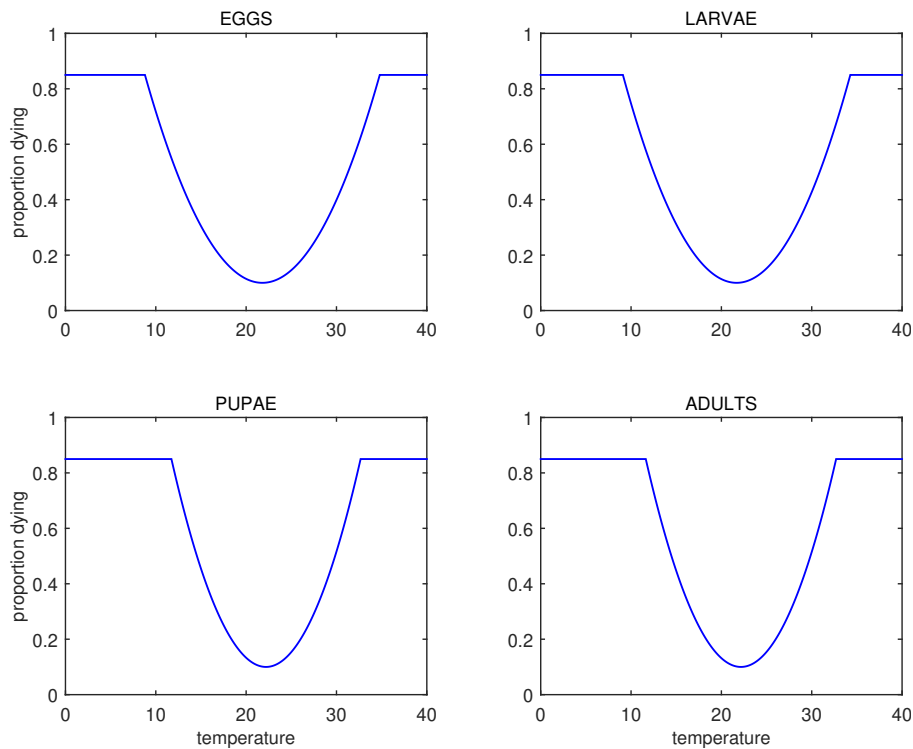
373 **Table 3.** Values of the temperatures T_{ML}^i and T_{MU}^i in equation (9) for the different stages of the
 374 grape berry moth *L. botrana*: eggs ($i = 1$), larvae ($i = 2$), pupae ($i = 3$), adults ($i = 4$).

375

376 The average stage-specific proportional mortality is represented in Figure 3 as function of
 377 temperature (see also Gutierrez et al., 2012). It is obtained from equation (13) considering as
 378 temperature limits the values indicated in Table 3.

379

380



381

382

383 **Figure 3.** Proportion of individuals dying as function of temperature (°C) for all the stages (eggs,
 384 larvae, pupae, adults) of the grape berry moth *L. botrana*.

385

386 **Extrinsic mortality rate function.** The extrinsic mortality component that account for the effect
387 of plant resource shortfalls and the action of natural enemies was estimated from field data using
388 the following procedure making the simplified assumption that the effects of these factors are
389 time and space independent. However, because of continuous reproduction and the overlapping
390 of generations of *L. botrana*, we cannot use cohort-based data for the estimation of the extrinsic
391 mortality, and hence the mortality rates must be estimated from the population dynamics data
392 using simulation modelling (Manly, 1989).

393 Generation $G(t)$, appearing in formula (13), can assume four values ($G(t) = 1,2,3,4$) because 4
394 generations may occur per year in vineyards in Southern Europe (Cozzi et al., 2006; Marchesini
395 and Dalla Montà, 2004; Pavan et al., 2010).

396 A least square estimation method, based on the demographic model presented above, was used
397 to estimate the mortality terms J^i , $i = 1, 2, 3, 4$ in (14) using data on the field abundance for the
398 stages. In particular, the sum of the square differences between simulated and observed
399 abundance data for all the four stages over all the years, was minimized to estimate the J^i .
400 Specifically, denoting by $\bar{N}^{i,y}(t_j)$ the number of individuals collected in stage i at time t_j , during
401 year y , we minimize the sum of squares

402

$$403 \sum_{y=1}^Y \sum_{i=1}^4 \sum_{j=1}^{m_y} [N^{i,y}(t_j) - \bar{N}^{i,y}(t_j)]^2 \quad (15)$$

404

405 with respect to the parameters $J^i(G)$, $i = 1, 2, 3, 4$, $G = 1, 2, 3, 4$, where m_y is the number of
406 observations in year y , and $N^{i,y}(t_j)$ is the simulated abundance of individuals in stage i at time
407 t_j , during year y , calculated using formula (8) duly discretized in time and space (Buffoni and
408 Pasquali, 2007) using a time step of one hour. Parameter Y denotes the number of years
409 considered for model calibration.

410 Because the dynamics of the different stages are linked through equations (1) - (4), it is not
411 necessary to collect data for all the stages to estimate stage specific parameters J^i , $i = 1, 2, 3, 4$.
412 If population data are not available for some stages, the procedure nevertheless applies. Once the
413 J^i have been estimated, they are introduced in the mortality function, and used to simulate the
414 dynamics for years different from those used for calibration phase. The comparison of model
415 predictions to the independent data is a measure of model validation success.

416

417

418 **2.4. Data on population dynamics**

419
420 Time series data on the population dynamics and abundance of all the biological stages of *L.*
421 *botrana* were not available in literature, and hence an unpublished time series data of population
422 dynamics of the grape berry moth collected in a vineyard located in Colognola ai Colli, a hilly
423 region in North-East of Italy during the period 2008-2012 of the late cultivar Garganega were
424 used. To keep the infestation level high and to minimize the impact on the moth population
425 dynamics, the experimental field was not treated with insecticides during the five years survey.
426 Adult males were sampled weekly using pheromone baited traps (Traptest Isagro) from the
427 beginning of April up to the end of the flights in November. Immature stages, eggs, larvae and
428 pupae, were counted on samples of 100 bunches using the same sampling interval over the same
429 period as for the adults. Only to estimate egg densities during the first generation was removal of
430 the plant material required for observation with a stereo-microscope. During the remaining part
431 of the survey, the counts were made in the field. Meteorological data are collected by a
432 meteorological station placed nearby the vineyard.

433

434

435 **3. Results**

436

437 Decision making in IPM is often based on thresholds of pest abundance based on field sampling
438 or in the tactical use of demographic model projection. The model includes estimates of intrinsic
439 sources of mortality based on laboratory data (see above), but to simulate the field dynamics of
440 *L. botrana* during the entire season, we must estimate the extrinsic mortality rate J^i due to the
441 action of natural enemies. We do this by minimizing the difference between the observed field
442 dynamics data and the predictions of the model.

443 To run the model, we must know population densities at the beginning of the season to drive the
444 simulation during the entire growing season, as no other information on the pest abundance is
445 provided. In our study the number of adult catches per trap per week recorded until the first larvae
446 of the first generation are observed were used as the initial condition for the model. To estimate
447 the J^i we used the field data collected at Colognola ai Colli for years 2008, 2009, and 2011
448 keeping all other model parameters fixed (i.e., model calibration). The data for 2010 and 2012
449 were used to test the model (validate).

450 Hourly temperature data are used as a driver environmental variable for model simulation.

451 Temperatures during the interval $\tau(P)$, considered equal to 10 days, appearing in the fecundity

452 function (section 2.2), was used to characterize the temperatures influencing the status of adult
 453 females, during all the plant phenological stages P . Taking the values of the diffusion coefficients
 454 in equations (1) - (3), $\sigma^i = 0.0001$, $i = 1, 2, 3, 4$, the least square minimization method outlined
 455 in section 2.3, for the years 2008, 2009, 2011, gave the estimates for the J^i reported in Table 4.
 456 The dynamics of all the immature stages, obtained for the estimated parameters, are represented
 457 in Figure 4 for the year 2008, 2009, and 2011.

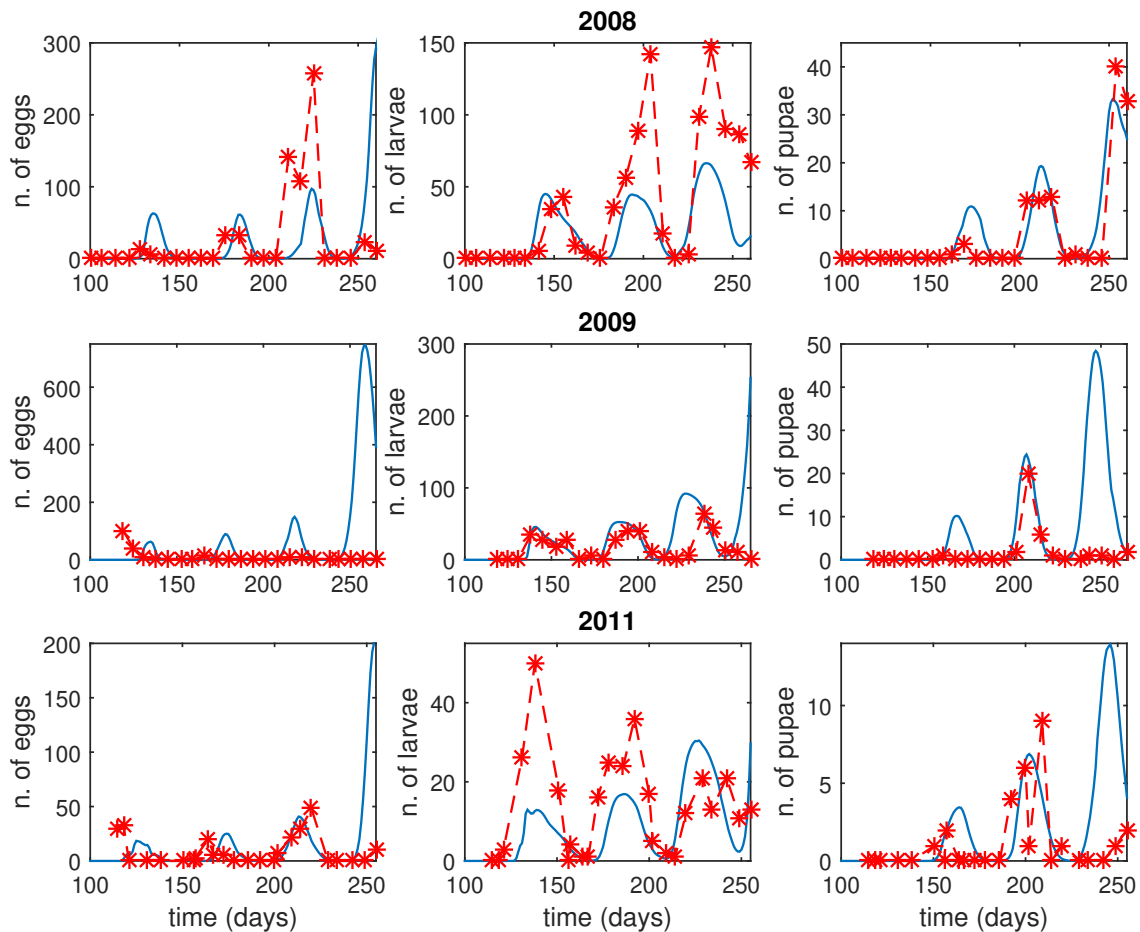
458

G	$J^1(G)$	$J^2(G)$	$J^3(G)$	$J^4(G)$
1	-	-	-	0
2	0	0.0489	0	0
3	0.198	0	0.0486	0.187
4	0.216	0	0	0.00753

459

460 **Table 4.** Values of the extrinsic mortality term J^i for different stages, eggs ($i = 1$), larvae ($i =$
 461 2), pupae ($i = 3$), adults ($i = 4$), and different generation G ($G = 1,2,3,4$) of *L. botrana*,
 462 estimated applying the method described in Section 2.3, for the years 2008, 2009 and 2011.

463



464

465
466 **Figure 4.** Sampled and simulated trajectories of population dynamics of *L. botrana* for the site
467 Colognola ai Colli obtained in model calibration in the years 2008 (first row), 2009 (second row)
468 and 2011 (third row). In the simulations the abundance of the different immature stages (number
469 of eggs, larvae, pupae per 100 grapes) is obtained substituting the values of the extrinsic mortality
470 term of Table 4 in the mortality rate function, and using the dataset of temperatures available.
471 Continuous line: simulated trajectory, dashed line: trajectory connecting sampled data (asterisks).
472

473 The simulated trajectories satisfactory fit the field data, despite an unknown sampling error that
474 could not be estimated. The simulated phenology of the pest accords well to the field data. In the
475 study site a partial fourth generation is predicted by the model as observed in the field data. This
476 phenology confirms that the grape berry moth has a fourth generation on grape as observed in
477 Northern Italy (Marchesini and Dalla Montà, 2004), and in the South of Spain (Del Tío et al.,
478 2001; Martín-Vertedor et al., 2010). Most larvae and all the pupae were in the grape bunches and
479 were removed by the harvest.

480 In some cases, the simulated population abundance approximates well the observed abundance,
481 in other cases the model overestimates the eggs and underestimates the larvae.

482 Model output can also be evaluated in terms of the information it provides for IPM decision
483 making. For example, using an action threshold for the second generation of 15 larvae per 100
484 berries bunches (CABI, 2014; Pavan and Sbrissa, 1997) the model suggests control intervention
485 in all three years, in line with the observed larval abundance.

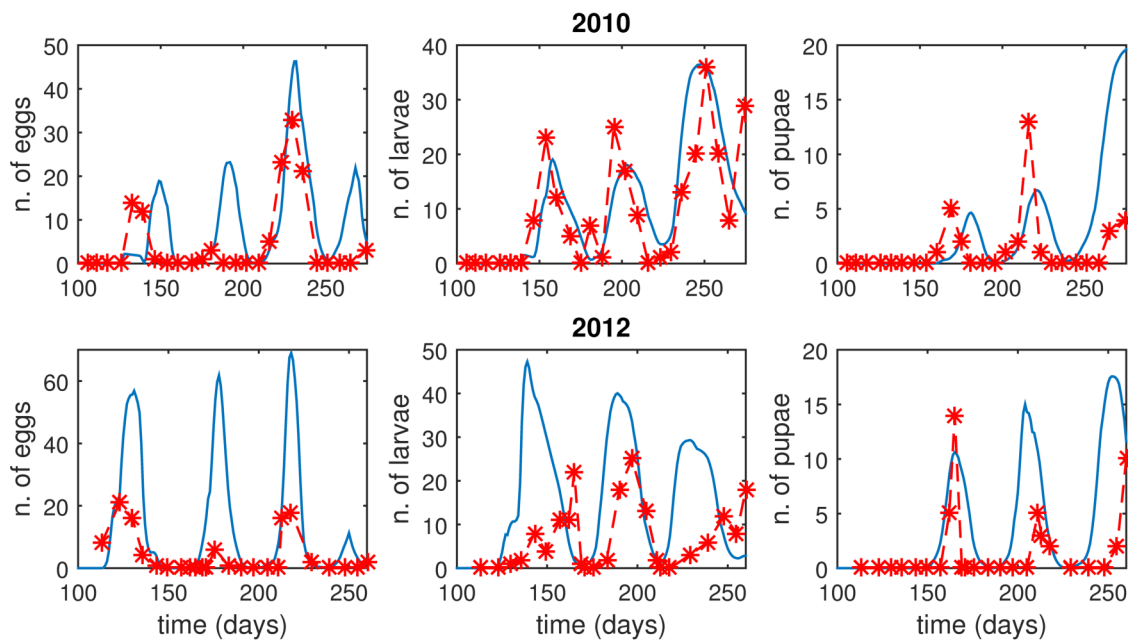
486
487 We note that all the immature stages were considered in parameter estimation with the model
488 attempting a best fit to all stages. It can be reasonably assumed that reliability in the sampled data
489 is different for the three stages, and this could explain in part the difference between simulated
490 and field dynamics. Possible effects of sampling errors are evident for example in 2008 (Figure
491 4) where inconsistencies between larval abundance and the recorded number of eggs can be
492 apparent, even when considering the different duration of the stages. A possibility to overcome
493 this problem is to consider only the abundance of one stage or few stages for the estimation
494 method presented in subsection 2.3, improving the fit of the selected stages. For example, the
495 most dangerous stages for the grapevine, the larvae, can be chosen.

496 To validate the model the estimated values for parameters J^i , $i = 1, 2, 3, 4$ (Table 4) are
497 substituted in the demographic model and used to simulate the dynamics of *L. botrana* for the
498 years 2010 and 2012. The trajectories obtained using the estimated parameters of Table 4 give a

499 good approximation of the behavior of field data (Figure 5), even if some problems of
500 inconsistency between the sampled number of eggs and larvae are also here evident. For example,
501 the number of eggs of the second generation is smaller than the number of larvae of the same
502 generation.

503 The quality of fit in both the calibration and validation phases are about the same, and suggests
504 that the estimated parameters J^i are valid for the whole sampling period 2008-2012, but the
505 assumption of constant parameters should be carefully investigated.

506



507

508

509 **Figure 5.** Sampled and simulated trajectories of population dynamics of *L. botrana* for the site
510 Colognola ai Colli obtained in model validation in the years 2010 (first row) and 2012 (second
511 row). In the simulations the abundance of the different immature stages (number of eggs, larvae,
512 pupae per 100 grapes) is obtained substituting the values of the extrinsic mortality term of Table
513 4 in the mortality rate function, and using the dataset of temperatures available. Continuous line:
514 simulated trajectory, dashed line: trajectory connecting sampled data (asterisks).

515

516

517 **4. Discussion and conclusions**

518

519 The modelling framework here presented is sufficiently general to model many pest species, both
520 in terms of stage structure and life history strategies. The model allows considering different stage
521 partitions of the population depending on the available information on the pest biology and

522 dynamics. In the application to *L. botrana* we considered four stages: eggs, larvae, pupae and
523 adults, but a more finer scale partition of the larval stages could be considered. In this case a
524 greater effort in data collection is required that may not yield a real marked improvement in model
525 performance.

526 High flexibility is also allowed in the characterization of the life history strategies. This allows
527 suitable definition of the biodemographic functions and their dependence on intrinsic (e.g.,
528 physiological age) and extrinsic (i.e., environmental) biotic and abiotic driving variables. As
529 applied to *L. botrana*, the development rate functions depend only on the temperature and the
530 biological stage. The fecundity rate function depends on the temperature, the physiological age
531 and the phenology of the host plant, that is a proxy for the type and amount of resource
532 availability. The mortality rate function has two components. The first is a stage-specific
533 mortality rate as a function of the development rate and the temperature. The second is a stage-
534 specific mortality component that estimates mortality due to the action of natural control agents.
535 Because is known that the activities of natural enemies (Marchesini and Dalla Montà, 1994 and
536 1998), as well as the availability of plant resources (Gutierrez, 2012) vary along the plant
537 vegetation period and the generation of the pest, the extrinsic mortality rate is also considered to
538 be dependent from the grape berry moth generation.

539 Estimation of life history components depending on extrinsic variables is critical for the
540 development of pest models, and for species like *L. botrana* that have continuous reproduction
541 and partially overlapping generations, simulation approaches are required to estimate them
542 (Manly, 1989). In the case of *L. botrana* the availability of a multi-annual dataset on population
543 dynamics allowed estimating the extrinsic mortality component via a least squares method that
544 minimized the difference between simulated and observed abundance. We note that the method
545 based on the use of model simulation and time series of population abundance can be extended
546 to the estimation of parameters of other biodemographic functions (e.g., fecundity) that are
547 known to be dependent on extrinsic variables not easily assessable in laboratory experiments
548 (Gilioli and Pasquali, 2007).

549 The initial conditions of the model for each year of the calibration and validation runs were given
550 by a limited dataset. Therefore, the modelling approach proposed here attempt to solves an
551 important issue of obtaining reliable projections of population dynamics limiting the sampling
552 costs using traps for adult moths. In the case study of *L. botrana*, once the mortality function is
553 estimated, the model predicts reliable phenology and reasonable dynamics of the abundance of
554 all the stages using environmental temperatures as drivers and the recorded abundance of adults
555 at the beginning of the flight period until the presence of the first larvae. This is similar to the

556 sampling effort required for phenological models with the added advantages of predicting the
557 density of damaging stages with the capacity to predict control intervention when economic
558 threshold levels have been reached. The biodemographic processes summarized in the model
559 functions allows mechanistic translation of adult flight data on the first generation of adult into a
560 realistic population dynamics, despite the fact that adult and pre-imaginal stage abundance do not
561 correlate.

562 The model simulated the phenology of the pest reliably despite the initial conditions of adult
563 flights had unknown sampling error and no information on the age structure of the population
564 was available. Because the simulated abundance of the damaging larval stage is of major interest
565 for IPM, the model approximates the observed abundance reasonably well, especially with
566 regards to action thresholds. This confirms the goodness of the parameter estimation despite the
567 unknown sampling error. The difference between simulated and observed abundance of eggs and
568 larvae could be partially attributed to environmental factors not accounted for in the model that
569 influenced survival, e.g. relative humidity (Schmidt et al., 2003). Furthermore, the model
570 simulates only local dynamics and the spatial movement of the pest on population abundance was
571 not considered.

572 At local-scale pest management (i.e., field-based), given that reliable temperature forecasts are
573 available, the model can accurately predict the temporal dynamics of the abundance of all the
574 stages of the pest including the ones relevant for control intervention. Such forecasting would
575 allow intervention before the pest causes irreversible or severe damages.

576 If the generality of model behavior is considered, many intervening factors could influence model
577 performance. For example, the presence of an early or late cultivar could greatly influence the
578 pest phenology and abundance. Also the composition and abundance of the community of natural
579 enemies could modify the pattern of population dynamics, both within and between the
580 vegetation periods. However, the model can potentially account for the effect of such extrinsic
581 factors if a fine tuning phase of model calibration is implemented.

582 Real-time simulation of pest population dynamics in agro-ecosystems with high spatial resolution
583 can support not only field-based IPM but also area-wide pest management (Elliot et al., 2008;
584 Faust, 2008; Gilioli et al., 2013). PBDMs like the one here proposed can be run on a grid with
585 reference to the set of nodes where the population samples are taken and temperature is measured.
586 In view of the fact that the availability of meteorological stations is a limiting factor for field-
587 based application of PBDMs, the interpolation of temperature data and the creation of field of
588 temperature accounting for the characteristic of the land and land use can improve model
589 performance in the perspective of area-wide pest management.

590 The ideal environment in which PBDMs are implemented for area-wide pest management are
591 geographic information systems able to manage different layers of information, such as field
592 temperatures, land physical characteristics and land use, as well as the model output. If data on
593 initial conditions are not available risk maps based on projected population trends due to short
594 and medium term weather forecasts can be derived (Gilioli et al., 2014). Under suitable scenario
595 assumptions on the initial conditions indexes of damage can be defined for comparatively
596 assessing the efficacy and the costs of different pest management strategies.

597 In a more strategic or policy-oriented perspective, simulation of scenarios at a large spatial and
598 temporal scale and based on indexes of risk defined in terms of pest abundance can be used to
599 assess the effects of drivers of ecosystem change (e.g., climate change) on the extant and the new
600 invasive species. This scenario analysis has important implications not only for IPM but also for
601 land management and stewardship.

602

603

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605

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615

616

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