Testing a new model of aphid abundance with sedentary and non-sedentary predators

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\textbf{Abstract}

Aphid population dynamics has been thoroughly investigated, especially in tree-dwelling aphids. Among the controls of the aphid rate of increase are the negative effects of antagonists, the positive effects of mutualists, the density-dependence of the aphid dynamics, and the non-stationary quality of plant tissues. Here we present a mechanistic model of aphid growth that considers most of these governing factors using a simple formulation. What is new in this model is that it considers two kinds of antagonists. The first kind is a guild of aphid predator specialists that includes ladybirds (Coleoptera: Coccinellidae), but also species of some families of Hemiptera, Diptera, and Neuroptera. The second kind of antagonists consists of omnivores or generalist predators and in this particular setting is exemplified by the European earwig \textit{Forficula auricularia} (Dermaptera: Forficulidae). The model developed here compared the effects of these two different kinds of aphid predators, the second one always at the site (sedentary predators) and the first one that arrives in important numbers only once the aphid population has already developed to some degree (non-sedentary predators). Multiple model parameter sets, representing different hypotheses about controls on aphid populations, were evaluated within the Generalised Likelihood Uncertainty Estimation (GLUE) methodology. The model correctly reproduced the experimental data obtained in an organic citrus grove showing the important effect that sedentary predators as earwigs can have on the aphid populations. Low densities of sedentary predators or even low predation rates can have a disproportionate effect on the final aphid density, as they prey on small populations, when the per capita effect on the aphid population is higher. During the main spring peak of aphids the role of non-sedentary predators is secondary, as they track the aphid density rather than control it. However, these non-sedentary predators are important within the proposed model to keep the second autumn peak of aphids at low values.

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1. Introduction

Aphids are one of the most important agricultural pests that feed on the phloem of many plants. Most of their damaging capacity to crops comes from their extraordinary capacity for population increase, mainly derived from the parthenogenetic and viviparous life history characteristics of the summer morphs. An almost universal characteristic of the dynamics of tree-dwelling aphids is the existence of an exponential increase in spring followed by a sudden total collapse of the population, called the mid-season or summer crash (Dixon, 1998; Karley et al., 2004). Frequently there is a secondary peak in the late summer, normally less important than the first peak.

Aphid population dynamics has been thoroughly investigated, especially in tree-dwelling aphids (Dixon, 1998, 2005) and even more in agricultural crops (Minks and Harrewijn, 1989; Blackman and Eastop, 2000). Among the controls on the aphid rate of increase are the negative effect of antagonists (predators and parasitoids; Kaneko, 2003; Snyder and Ives, 2003; Stadler, 2004), the positive effect of mutualists (Way, 1963; Buckley, 1987; Hölldobler and Wilson, 1990; Katayama and Suzuki, 2003), the density-dependence of the aphid dynamics (Dixon, 1998), the non-stationary quality of plant tissues (Dixon and Glen, 1971), and severe weather events (see some examples in Karley et al., 2004).

The most common aphid predators are ladybirds (Coleoptera: Coccinellidae), but Hemiptera (Anthocoridae, Nabidae and Miridae), Diptera (Syrphidae), Neuroptera (Chrysopidae, Hemerobiidae, and Coniopterygidae), and Dermaptera (Forficulidae) also feed on...
aphids (Sunderland, 1988; Solomon et al., 2000). Most of these predatory species, and especially Coccinellidae, only become abundant when the aphid density is already high (Solomon et al., 2000; Dixon, 1998). They are therefore unable to control the aphid population, at least during the spring peak. Parasitoids (Lysiphlebus for instance; Kaneko, 2003) are no better early controllers of aphid populations, as they need to parasitize the aphids before getting densities high enough to substantially affect aphid dynamics at subsequent dates.

The Forficulidae European earwig Forficula auricularia L. occupies a special position among the predators listed above as it is a sedentary and omnivorous species. It preys on several arthropod species and plant material. Its role as a controller of aphid populations in apple orchards in temperate regions has come to be regarded as important (Carroll and Hoyt, 1984; Solomon et al., 2000; Nicholas et al., 2005; Suckling et al., 2006). In a previous 5-year experimental study in a Mediterranean citrus grove we provided further evidence of the major role that earwigs can play as agents of aphids in cultivated trees (Pihøl et al., 2009). The experiment was primarily intended to evaluate a possible method of aphid control based on ant-exclusion from tree canopies. What we found, however, was that ant-free trees had more aphids than the control ones, the most likely explanation being the effect of the concurrent exclusion of earwigs alongside ants from the canopies. We also found a negative relationship between aphid and earwig densities in control trees, compatible with a top-down control of aphid by earwigs during the spring peak. In contrast, the abundance of Coccinellidae and predatory Hemiptera had a positive relationship with aphid density, suggesting in this case a bottom-up control of predators by aphids during the spring peak.

Here we develop a mechanistic model of aphid dynamics that takes into account, among other factors, the existence of two different kinds of predators. One kind, exemplified by earwigs, are sedentary and omnivorous predators that do not rely necessarily on the presence of aphids to survive; they can start to consume aphids at the very beginning of the season, and thus have a disproportionate effect on further aphid densities. The other kind of predators, exemplified by ladybirds but also applicable to the most common aphid predators, only arrive at trees once the aphid population is already high. Despite consuming huge number of aphids, they normally do not control the first aphid outbreak, but possibly play a relevant role later in the season. In this paper we name these two types of aphid predators as sedentary and non-sedentary. There are already many published examples of models of aphid dynamics (Ro and Long, 1999; Gosselke et al., 2001; Karley et al., 2003), but only Ekboom et al. (1992) considered the effect of what we call here sedentary predators. Our model extends the Ekboom et al.’s model by considering the joint effect of sedentary and non-sedentary predators on aphid growth.

By evaluating which combinations of parameter values are consistent with the available observations, the model allows different hypotheses about the controls on aphid populations to be evaluated. In this study this is done within a framework that allows multiple models to be identified as potential hypotheses about system function (e.g. Beven, 2002, 2006, 2009). The main objective of this modelling exercise is to reproduce quantitatively the main characteristics of the aphid dynamics in the study of the citrus grove described above, but with some common characteristics to many other temperate agricultural ecosystems. The proposed model is intended to reproduce: (1) a much higher aphid density in the first than in the second aphid outbreak in the season; (2) a higher aphid density in the experimental (ant and earwig excluded) than in the control ones; (3) the inter-annual variability of aphid density, both in control and experimental trees.

2. Material and methods

2.1. Scope of the model

The processes included in the proposed model are those that we consider important to determine the total incidence of the aphid attack within a season. The observed variable that the model intends to fit is the cumulative aphid density, i.e., the area below the curve of aphid density vs. time. As there are normally two distinct peaks in the aphid curve separated by a mid-season crash, we calculated separately the cumulative densities of the first and second peaks (Fig. 1).

The model does not intend to reproduce the precise timing of the aphid outbreak and the maximum densities of aphids as other models of aphid dynamics do (Ro and Long, 1999). To be able to do so, additional processes, especially within-population structure and dynamics, would need to be further considered and more detailed field data would also be necessary (Parry et al., 2006). A further simplification of the model is that it does not consider multi-season dynamics, as it only intends to reproduce the outbreak and suppression of aphids within one growing season (Bonmarco et al., 2007).

Here we first present a description of our current understanding of the main determinants of aphid dynamics in the studied grove. This is what we call the perceptual model, which is also summarised in a diagrammatic form in Fig. 2. In the following section we translate the ideas outlined in the perceptual model into mathematical equations in what we call the conceptual model.

2.2. The perceptual model

Colonisation of citrus trees by migrant aphids does not occur until the first young shoots appear on the trees. This normally occurs in early April. Afterwards, aphid population increases exponentially. However, there is an upper limit in the number of aphids that can occupy a tree, and this carrying capacity can be considered proportional to the number of young shoots suitable for aphid colonies.
During most of this period of rapid increase in the aphid population, common aphid predators (non-sedentary predators) are normally at low densities. However, earwigs are already present in the canopies, albeit in low numbers, from the very beginning of the aphid exponential growth.

It is only when aphid density is already high that non-sedentary predators arrive. The most abundant predators in this grove are Coccinellidae. Once they arrive, they are more abundant in trees with more aphids.

Not long after the arrival of the predators, the density of aphids decreases very quickly, arriving normally to a value of zero by mid-June to mid-July (mid-season crash). In addition to the abundance of predators, a decrease in the number of suitable young shoots for aphids can also contribute to the crash of aphid population.

After the mid-season crash, in September and October of some years, aphid density increases again, but normally to a much lower value than in the first outbreak. During this period common aphid predators are fairly abundant in the tree canopies.

Aphid-tending ants are considered to play a positive role on the development of aphid populations (Tokunaga and Suzuki, 2008; Flatt and Weisser, 2000; but see Stadler and Dixon, 1998), but our experiment of ant-exclusion showed that this positive effect is dominated by the negative one of earwig predation.

Our current perceptual model of aphid dynamics in the studied citrus grove is summarised in Fig. 2. Aphid density is positively affected by ant presence and by young shoot abundance. Predators and aphid density itself negatively affect aphid growth. We considered two kinds of predators, sedentary and non-sedentary predators, with different temporal dynamics. Apart from all these biological interactions, at least one physical factor must be also taken into account, as it is well known that higher temperatures accelerate the development of insects.

The biological mechanisms that control the abundance of aphids in the first and second peaks are different. In the first one, earwigs are the almost the only available mechanism to counteract the exponential growth of aphids at the beginning of its growth period in spring. The actual level of aphid attack increases when earwigs are excluded (banded trees with entomological glue) or in years of low earwig abundance (see Section 3). After the summer crash, common predators are already abundant, so they can keep aphid density at low levels. Predation by earwigs continues, but as their numbers are much lower than other predators, they are proportionally less important than in the spring period.

2.3. Conceptual model

Aphid population growth follows a logistic equation and is consumed by predation by sedentary \( (P_E) \) and by non-sedentary predators \( (P_C) \). The subindexes E and C refer to earwigs and Coccinellidae, the most common representatives or sedentary and non-sedentary predators, respectively.

\[
\frac{dN_A}{dt} = rN_A \left( 1 - \frac{N_A}{K} \right) - P_E - P_C
\]

where \( N_A \) is the aphid density, \( t \) the time, \( r \) the intrinsic aphid growth rate and \( K \) the carrying capacity of aphids. \( K \) is the product of the number of young shoots \( (n_T) \) able to support an aphid colony and the maximum number of aphids that a single shoot can support \( (k) \).

Predation \( (P_E \) and \( P_C) \), following Karley et al. (2003) is modelled as a Holling type III grazing function:

\[
P_E = N_E R_E \frac{N_A^2}{\sigma_E^2 + N_A^2}
\]

where \( N_E \) and \( N_C \) are, respectively, the number of sedentary and non-sedentary predators, \( R_E \) and \( R_C \) the maximum per capita consumption rate of aphids by sedentary and non-sedentary predators, and \( \sigma_E \) and \( \sigma_C \) the threshold parameters for sedentary and non-sedentary predators.

Density of earwigs \( (N_E) \) is considered to be constant during the year. It is assumed here that, being an omnivorous species that feeds on plant material and on many other species of insects, its density is controlled by processes beyond the scope of the present model. A different value of earwig density based on field observations was used for each year.

On the contrary, the abundance of non-sedentary predators is zero until a given aphid density is reached \( (\delta) \). Once \( \delta \) is reached, adult individuals of non-sedentary predators, such as ladybirds, start to lay eggs at a mean rate of \( e \) eggs per tree per day during \( p \) days. However, not all trees receive the same number of eggs, as those with more aphids will receive more eggs (Houdková and Kindlimann, 2006). Thus, the ith tree will receive \( e_i \) eggs following the rule:

\[
e_i = e \frac{N_i^v}{\sum_{i=1}^{n\text{trees}} N_i^v}
\]

The parameter \( v \) makes the relation between \( N_A \) and \( e_i \) follow a power law rather that a linear law. In the extremes, a value of \( v=1 \) produces a linear relationship between aphid and predator densities, and a value of \( v=0 \) results in all trees having the same number of predator eggs \( (e) \). All laid eggs become active feeding predators after a period \( r \) (measured in degree-days, see below).

The fact that in the model all eggs reach maturity will not have an important effect, as any proportional mortality of eggs could be compensated within the model, by a higher value of the parameter \( e \). A different value of \( e \) based on observations is used for each year.

In the absence of aphids \( N_C \) decreases at a rate \( \mu \). However, when aphids are present, their consumption reduces this mortality at a rate \( \gamma P_C \).

\[
\begin{cases}
\text{if}(\mu N_C > \gamma P_C) \Rightarrow \frac{dN_C}{dt} = (-\mu N_C) + (\gamma P_C) \\
\text{if}(\mu N_C \leq \gamma P_C) \Rightarrow \frac{dN_C}{dt} = 0
\end{cases}
\]

It is not allowed to have a positive rate of increase of \( N_C \), as it is assumed in the model that these predators are univoltine, as in other Iberian regions (Alvis et al., 2002; Soler et al., 2002). However, predation has a positive effect on \( N_C \) by reducing their mortality.

As aphids in the studied citrus trees belong to ant-tended species, and there are several aphid-tending ants in the orchard, a positive effect of ants has been included in the model as a modification of the intrinsic rate of growth of the aphids. So, in trees visited by ants (i.e., in control trees)

\[
r' = r(1 + a)
\]

where \( a \) is a positive number that summarises the beneficial effect of ants on aphid growth. In experimental trees \( r \) is not modified as they are not visited by ants \( (a = 0) \).

Finally, temperature is considered to affect aphid growth, predation rate and non-sedentary predator dynamics. The effect of temperature was implemented as an increase of those rates proportional to the accumulated heat measured in degree-days above a threshold. We considered different upper and lower thresholds for the degree-day calculations for aphids and predators. Aphid growth
at each time step was multiplied by the factor $f_A$,

$$f_A = \frac{dd_A}{dd^{\text{ref}}_A}$$

(7)

where $dd_A$ is the degree-days value of a given day and $dd^{\text{ref}}_A$ the degree-days of a reference day with constant 20°C temperature.

Similarly, the predation rates (Eqs. (2) and (3)) and the dynamics of non-sedentary predators (Eq. (5)) were multiplied by the equivalent factor $f_p$ for the predators:

$$f_p = \frac{dd_p}{dd^{\text{ref}}_p}$$

(8)

We implemented the equations of the conceptual model into a Java program. The differential Eqs. (1) and (5) were solved by the Euler method with a time step of 1 day. It was not necessary to use a shorter time step or a higher-order integration method (such as Runge–Kutta) to solve the equations for two reasons. First, there is not really a coupled predator–prey dynamics in the model, as $N_c$ cannot get bigger that the previous value; second, the values of $r$ used are low enough not to show any chaotic behaviour in the discrete logistic model. Running the model on a daily time step made the calibration of the model using Monte Carlo runs easier, as the execution time of an individual simulation was very low (2–3 ms per simulation on a personal computer).

2.4. Data set

The data used to test the proposed model is a 5-year experiment intended to study the effects of ant and earwig exclusion on the aphid abundance in an organic citrus grove (Piñol et al., 2009). What follows is a summary of the methodology and main results of that experiment.

The studied site is a plantation of citrus trees located at La Selva del Camp (Tarragona, NE, Spain; 41° 13’07”N, 1° 08’35”E). Climate is dry Mediterranean, normally with a rainy spring and autumn and a dry winter and summer. The grove was being converted from conventional to organic agriculture during the study period, and neither pesticides nor fungicides were applied during the entire period (2002–2006). From 2004 onwards the grove complied with all organic agriculture standards. Trees were watered when necessary.

Eight control trees and eight experimental trees in which ants were excluded by applying a sticky barrier to the trunk were randomly chosen each year. A different group of 16 trees was used every year. Aphid populations were monitored every 1–2 weeks between April and October. Two circles of 0.25 m² were randomly selected on the canopy of each tree, and within each circle the number of young shoots capable of having aphid colonies were counted and assigned each shoot to one of the following density classes: no aphids, 1–5, 6–25, 26–100, and >100 individuals per shoot (each density class was considered to have 0, 2, 12, 50, and 250 individuals, respectively). Arthropods on the tree canopies were sampled once a month, using beating trays. Insects from groups having aphid predators were counted and identified to family (Coccinellidae, Neuroptera, Diptera), or species (Hemiptera, Dermaptera) level.

The seasonal course of the aphid population in each of the 5 years showed a peak in late spring/early summer followed by a crash that reduced the aphid population to zero. In the early autumn there was normally a small recovery of the aphid populations, but always of a much lower magnitude than the first peak. Contrary to expectations, the exclusion of ants from the tree canopies did not reduce aphid attack during the spring, but clearly increased it (experimental trees in Fig. 3A). The only likely explanation for this result is that, in this particular grove, the negative effect of earwig predation is more important that the positive one of ant-attendance on aphid growth.

The most abundant species of aphids were Aphis spiraecola Patch and A. gossypii Glover (77% and 15%, respectively, of the sampled individuals using beating trays). A few colonies of Toxoptera auranti (Boyer de Fonscolombe) and Myzus persicae (Sulzer) were also found every year. All four aphid species are ant-tended to some degree (Suay Cano et al., 2002; García Prieto et al., 2005). The most abundant species of ants were Lasius grandis Forel, Plogi-oleps pygmaea (Latreille), Formica rufibarbis Fabricius, F. subruwa Roger, and Pheidole pallidula (Nylander). Three of these species (L. grandis, F. rufibarbis, and F. subruwa) are known to tend aphid colonies. The most common non-sedentary aphid predators were, in order of abundance, Coccinellidae (Scymnus interruptus (Goeze) and Adalia decempunctata (L)), Hemiptera (the Anthocoridae Orius laevigatus (Fieber) and the Miridae Pilophorus perplexus Douglas and Scott), Neuropterans (of the families Chrysopidae, Hemerobiidae, and Coniopterygidae), and Syrphidae (Diptera).

2.5. Calibration of the model

The model was calibrated within the Generalised Likelihood Uncertainty Estimation (GLUE) framework (Beven and Binley, 1992; Beven and Freer, 2001; Beven, 2009). GLUE allows for the fact...
that there may be many different models and parameter sets that provide acceptable simulations of the available observations (the equilibrium thesis, see Beven, 2006, 2009). Calibration therefore consists of trying to identify a set of acceptable or “behavioural” models, by running a large number of simulations using randomly chosen parameter sets. Then, the model predictions are compared with the available observed data and a likelihood for each model realisation calculated, based on an appropriate measure of the goodness of fit. Non-behavioural models that do not provide acceptable simulations are given a likelihood of zero and are not considered further in analysis. If all models are considered to be hypotheses of how the system is working, then the behavioural models are those that are (conditionally) accepted, based on the observations available to date. Additional data can be used to constrain the behavioural models further and, in some cases, to reject all the models tried (e.g. Choi and Beven, 2007). The GLUE methodology has been previously applied to ecological models by, for example, Martínez-Vilalta et al. (2002) and Piñol et al. (2005, 2007).

In our case we used the median value (per year, per treatment and per season) of the observed cumulative aphid density (as depicted in Fig. 3A) as the reference data. This resulted in a total of 20 values (5 years × 2 treatments × 2 seasons) that the model is intended to simulate. As a measure of the goodness of fit we used the modelling efficiency (E) defined by Nash and Sutcliffe (1970) as a relative likelihood measure:

\[
L(\Theta_i|Y) \propto E = 1 - \frac{\sum_{j=1}^{n} (O_i - P_j)^2}{\sum_{j=1}^{n} (O_i - \bar{O})^2}
\]

(9)

where \( L(\Theta_i|Y) \) is the likelihood measure for the \( i \)th parameter set \( (\Theta_i) \) conditioned on the observations \( Y \). The right-hand-side of the equation is the model efficiency, which equals 1 for a perfect fit, with \( O_i \) and \( P_j \) being observed and predicted values of median cumulative aphid density, and \( \bar{O} \) the mean of the observed median density values. Models with \( E < 0 \) are no better than using the mean of the data as a model. Only parameter sets with an efficiency of higher than 0.60 were further considered for analysis.

Even a simple model such as the one described here has an elevated number of parameters, 17 in this case (Table 1), a value too high for an exhaustive Monte Carlo type calibration. In consequence, it was necessary to select a subset of these parameters to allow them to vary in the calibration and keep the rest of them fixed. We allowed only eight parameters to take random values with a uniform distribution (minimum and maximum values in Table 1) and kept constant the other nine parameters.

The four developmental thresholds for aphids and predators were fixed to reasonable values described in the literature (Wang and Tsai, 2000; Cividanes and Sakemi, 2002; Razmjou et al., 2006). The only use of these parameters in the model was to accelerate the rates of growth and predation as temperature grew warmer; no attempt was made to link cumulative heat accumulation values to developmental events (i.e., the arrival or departure of migrant aphids or predators).

The carrying capacity of aphids of individual shoots was fixed to 250 aphid shoot\(^{-1}\), the same value used in the evaluation of the population density of the shoots with the highest possible density class (>100 aphid shoot\(^{-1}\)).

The two threshold parameters of the type III functional response of predators (\( E_2 \) and \( E_3 \); \( E_2 \) for earwigs and \( \alpha_c \) for coccinellids and other predators) were also fixed. The chosen values \((\alpha_c > \alpha_E)\) reflect the fact that earwigs, being larger than all the other predators, are probably better at locating aphid colonies and, consequently, could reach high predation rates at a lower aphid density. In addition, the searching behaviour of Coccinellidae larvae is generally considered as inefficient (Solomon et al., 2000 and references therein).

The number of ovipositing days (\( p \)) of adult non-sedentary predators was also fixed, as a high value of this parameter would simply have the same effect as an increased maximum predation rate \( (\alpha_F) \), and, therefore, become redundant in the calibration process.

Finally, the delay between oviposition and eclosion of non-sedentary predators (\( \delta \)) was also kept constant for the same reason of the previous paragraph: a higher value of \( \delta \) could be compensated within the model by a later arrival of adult non-sedentary predators (\( \delta \)).

The mean number of eggs of non-sedentary predators \( (\varepsilon) \) and the population size of sedentary predators \( (N_s) \) were different each year, and the chosen values came from field observations. In the case of \( \varepsilon \) we used the median number of non-sedentary predators sampled in all trees (control and experimental) with beating trays in the month of June (Fig. 3B), because the maximum aphid density occurs around this sampling date. Sedentary predator density was taken as the mean value of earwigs present in tree canopies of control trees sampled with beating trays from April to October (Fig. 3C).

It is worth noting that aphid density and predator density are not strictly commensurate variables, as they were obtained using different sampling methods. The two 0.25 m circles used for counting aphids are not necessarily equivalent to the volume sampled with the beating trays. The earwig density is also incommensurable.

### Table 1

Parameters of the model. The last column indicates the values of each model used during the GLUE calibration of the model. When there is only one value in this column, that parameter was kept constant during all simulations; when there are two values, the parameter was randomly chosen from a uniform distribution with the indicated minimum and maximum values.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Units</th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( L_A )</td>
<td>°C</td>
<td>Lower developmental threshold of aphids</td>
<td>5</td>
</tr>
<tr>
<td>( U_A )</td>
<td>°C</td>
<td>Upper developmental threshold of aphids</td>
<td>30</td>
</tr>
<tr>
<td>( L_c )</td>
<td>°C</td>
<td>Lower developmental threshold of predators</td>
<td>10</td>
</tr>
<tr>
<td>( U_c )</td>
<td>°C</td>
<td>Upper developmental threshold of predators</td>
<td>30</td>
</tr>
<tr>
<td>( \tau )</td>
<td>day(^{-1})</td>
<td>Intrinsic rate of growth of aphids</td>
<td>0.15–0.40</td>
</tr>
<tr>
<td>( k_A )</td>
<td>aphid shoot(^{-1})</td>
<td>Carrying capacity of aphids of a young shoot</td>
<td>250</td>
</tr>
<tr>
<td>( R_c )</td>
<td>aphid day(^{-1}) pred(^{-1})</td>
<td>Maximum predation rate of non-sedentary predators</td>
<td>0–200</td>
</tr>
<tr>
<td>( \alpha_c )</td>
<td>aphid tree(^{-1})</td>
<td>Aphid density at half ( K_c )</td>
<td>200</td>
</tr>
<tr>
<td>( R_e )</td>
<td>aphid day(^{-1}) pred(^{-1})</td>
<td>Maximum predation rate of sedentary predators (earwigs)</td>
<td>0–400</td>
</tr>
<tr>
<td>( \alpha_e )</td>
<td>aphid tree(^{-1})</td>
<td>Aphid density at half ( K_e )</td>
<td>100</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>pred(^{-1}) aphid(^{-1})</td>
<td>Assimilation efficiency of non-sedentary predators</td>
<td>0.0–0.01</td>
</tr>
<tr>
<td>( \mu )</td>
<td>day(^{-1})</td>
<td>Mortality rate of non-sedentary predators in absence of aphids</td>
<td>0–0.15</td>
</tr>
<tr>
<td>( \theta )</td>
<td>adimensional</td>
<td>Positive effect of ant presence on the growth of aphids</td>
<td>0–1</td>
</tr>
<tr>
<td>( \delta )</td>
<td>adimensional</td>
<td>Threshold above which non-sedentary predators start to lay eggs</td>
<td>500–2500</td>
</tr>
<tr>
<td>( p )</td>
<td>day</td>
<td>Duration of the oviposition period for non-sedentary predators</td>
<td>10</td>
</tr>
<tr>
<td>( \tau )</td>
<td>°C day</td>
<td>Cumulative heat accumulation needed to eclosion an egg of a non-sedentary predator</td>
<td>50</td>
</tr>
<tr>
<td>( v )</td>
<td>adimensional</td>
<td>Power parameter for the partition of laid eggs among trees</td>
<td>0–1</td>
</tr>
</tbody>
</table>
Fig. 4. Comparison of the cumulative aphid density of the 100 best simulations (based on their efficiency) with the observed values. The upper two plots compare control and experimental (ant-excluded) trees and the lower two compare the spring peak with the autumn peak.

Fig. 5. Comparison of the cumulative aphid density of control trees in the spring peak of the 100 best simulations (based on their efficiency) with the observed values for the 5 years of the study.
with the density of non-sedentary predators (both sampled using the same method), because earwigs are mostly nocturnal creatures (more than twice the number at night than during day hours in the studied grove, Espadaler and Piñol, personal observation). Consequently, the parameters that relate predator density to predation (\(R_C\) and \(R_E\)) cannot be directly compared, as they act within the model only as ‘effective’ parameters. The inter-annual variability of observed densities of sedentary and non-sedentary predators provide calibration data for the model (Fig. 3B and C).

The number of young shoots suitable for aphid colonisation was taken from measurements made at the same time as those of aphid density. The median value of all sampled trees was taken for each sampling date. The number of young shoots in non-sampling days was obtained by linear interpolation between the sampling dates.

Maximum and minimum temperatures were obtained from a meteorological station in Constanti, 9 km from study site. Degree-days for aphids and for predators were calculated using the double triangle method with horizontal cut-off (Roltsch et al., 1999).

3. Results

3.1. Model performance

The 600 million random parameter sets tested produced 19,500 simulations with efficiency larger than 0.6, the behavioural model threshold imposed to be further considered for analysis. The best 100 parameter sets produced a reasonable prediction of the observed cumulative aphid density (Fig. 4). As with the observations (Fig. 3A), simulated cumulative aphid density was lower in control trees than in ant-excluded trees, and it was much higher in the spring peak than in the autumn peak. The model was also able to reproduce the observed higher aphid density in control trees in years 2003 and 2004 than in the other 3 years (Fig. 5); however, the model was not able to reproduce the inter-annual variation of cumulative aphid density in experimental (ant-excluded) trees (Fig. 6).

3.2. Parameter space

Most of the eight parameters allowed to vary in the random calibration process showed some degree of sensitivity to the observed data (Fig. 7). In this kind of scatter diagrams non-sensitive parameters produce high efficiencies across the entire range of parameter values (i.e., the plot is relatively flat), whereas sensitive parameters have high efficiencies in a narrower range of parameter values. The most sensitive parameters were the intrinsic aphid growth rate \(r\) (with high \(E\) at values between 0.20 and 0.26 day\(^{-1}\), but with a secondary peak at ca. 0.30 day\(^{-1}\)), the maximum predation rate of earwigs \(R_E\), the intrinsic mortality rate of non-sedentary predators \(\mu\), the effect of ants on the aphids growth rate \(a\), the aphid density that triggers the arrival of non-sedentary predators \(\bar{i}\), and the parameter that controls the partition of non-sedentary predators among trees depending on their aphid density \(\bar{v}\). In contrast, the maximum predation rate of non-sedentary predators \(R_C\) and their assimilation efficiency \(\gamma\) were not so sensitive to the observed data.

It is however, incorrect to judge \(R_C\) and \(\gamma\) as unimportant, as they can interact with the other parameters of the model. Within the GLUE methodology the minimal unit to be considered is the parameter set, as individual parameter values do not often have an independent effect on model fit. For instance, Fig. 7 shows \(R_C\) to be rather insensitive, but not all values would render the same model efficiencies because of its clear link with parameter \(\delta\) (Fig. 8).

![Fig. 6.](image-url) Comparison of the cumulative aphid density of the experimental trees in the spring peak of the 100 best simulations (based on their efficiency) with the observed values for the 5 years of the study.
Fig. 7. Efficiency of all behavioural simulations vs. parameter values. The range in the x-axis is the same that it has been allowed to vary in the Monte Carlo simulations. Plot based on 600 million simulations of which 19,500 had an efficiency larger than 0.6.

Fig. 8. Two-way plot of all pair-wise combinations of parameter values. Each point represents one single behavioural simulation. To make the plot clear, only simulations with efficiency larger than 0.65 are shown. Units of the parameters are detailed in Table 1.
There were some other noticeable interactions among parameters (Fig. 8). The most conspicuous one was between parameters $R_E$ and $a$, suggesting that the observed aphid density could be obtained both with low (but not null) effect of earwigs ($R_E$) and ants ($a$) or with higher values of the same two parameters. Similarly, higher aphid growth rate $r$ could be compensated by a higher earwig predation rate ($R_E$). Also a late arrival of non-sedentary predators ($\delta$) was compensated by a major predation capacity ($R_C$).

### 3.3. Predation by sedentary and non-sedentary predators

In absolute terms, predation by non-sedentary predators was more important than predation by sedentary predators, both during the spring peak and during the autumn peak. However, it is necessary to remember that at the beginning of the growing period of aphids, non-sedentary predators have not yet arrived. The simulated relative importance of sedentary and non-sedentary predators is depicted in the 5 years of the study Fig. 9. At the beginning of the season (up to ca. day #150) all the predation was caused by earwigs. Afterwards, the relative importance of earwig predation decreased because non-sedentary predators arrived and started to feed on the aphid population. The importance of non-sedentary predators was much higher in 2003 and 2004 than in the other 3 years. After the summer crash, the relative importance of earwig predation started to increase again as consequence of the mortality of non-sedentary predators (earwig density is kept constant throughout the year in the model).

The effect of earwig density on the cumulative density of aphids in the spring peak was not linear, but had a clear threshold, above which the density of aphids was almost zero. As an example to illustrate this behaviour we calculated the density of aphids in control trees in the spring of 2002 for different values of earwig densities $N_E$ (Fig. 10). It can be observed that between earwig densities of $0–0.3$ ind. tree$^{-1}$ the decrease in aphid density is, more or less, linear. However, a value of $0.4$ ind. tree$^{-1}$ reduced the aphid density to almost zero. This particular value of the threshold was probably selected in the calibration process as a value that made years 2003 and 2004 to be below the threshold (and consequently have high aphid densities) and the other 3 years above (with very low aphid densities).

4. Discussion

#### 4.1. Model performance

The model was able to reproduce the observed higher aphid density in experimental (ant and earwig excluded) trees compared to control ones during the spring (Fig. 4). The main factor in the model that contributed most to the difference between control and experimental trees was the absence of sedentary predators in experimental trees. These experimental trees had no ants in their canopies, but the negative effect of predation by earwigs was more important than the positive one of ants on the aphid growth. Nevertheless, we saw (Fig. 8) that the effects of the maximum earwig predation parameter ($R_E$) and the positive effect of ants on aphid growth ($a$) were related one to another and that either high or low values of both parameters were necessary to produce behavioural simulations. Since the two variables (ant and earwig presence) are inextricably linked in the experimental design, it was impossible to separate the two effects. An experimental design that allowed ants to visit tree canopies but not earwigs would be necessary to make a more complete study of the effects of the two groups of animals.

The importance of sedentary predators was reinforced by the fact that the 2 years with high aphid densities in control trees (2003 and 2004; Fig. 3A) were those with lower measured earwig densities (Fig. 3C), an observation also reproduced by the model (Fig. 5). The lower density of aphids in the control trees occurred despite having, within the model, less non-sedentary predators than in the experimental trees. The non-sedentary predators were distributed among trees in proportion to the aphid density of the tree (Eq. (4)) and in a given year, were higher in the experimental than in the control trees. This feature of the model tries to mimic the preference of coccinellids and other aphid predators to lay eggs in places more likely to have high aphid densities (Kindlmann and Dixon, 2001). We also observed this positive relationship between non-sedentary predators (coccinellids and predatory Hemiptera in our case) and aphid density during the spring peak in the studied grove (Piñol et al., 2009).

The observed high inter-annual variability of the aphid attack in control trees could alternatively be attributed to other factors, such as a variable meteorology, or different number of migrant aphids landing on control trees. We believe that this is not the case because the inter-annual variability was lower in the experimental than in the control trees. The potential in 2002, 2005, and 2006 to have a...
high aphid density existed, and it was observed in the experimental trees (Fig. 3A). Thus, the difference must be due to some factor occurring in the control trees and not in the experimental ones. As we stressed before, we believe that this factor is a higher density of earwigs in 2002, 2005, and 2006, compared to the lower values in 2003 and 2004. As we have seen (Fig. 10), sedentary predators behaved as a threshold variable, dividing the possible outcomes into one with high aphid density (when the density of earwigs was low) and one with low aphid density (when the density of earwigs was high).

However, the model was not that good at reproducing the inter-annual variability of spring aphid density in the experimental trees between the different years (Fig. 6). In particular, the model fails to reproduce the extremely high aphid density in experimental trees during the spring of 2004 (Figs. 3 and 6). The model was able to reproduce the observed much higher density of aphids during the spring peak than during the autumn peak (Fig. 4), an observation fairly common in many other studies (Stadler, 2004). Neither sedentary predators nor ants have anything to do with these results, as the densities of these organisms were kept constant throughout the year in the model. The main characteristic of the model responsible for this result is the late arrival of non-sedentary predators (Stadler, 2004). However, some of these predators remain in the tree in autumn and impede the second aphid peak from becoming large. A higher number of young shoots in the spring than in autumn also contributes to the difference between the spring and autumn peaks (results not shown), but the difference in the aphid density was more than one order of magnitude higher than the difference in the number of young shoots.

4.2. Mid-season crash and predation

There is some controversy about the cause of the almost universal mid-season crash in aphid populations (Dixon, 2005). Karley et al. (2004) list severe weather events, natural enemy attack, and changes in plant suitability as the main ecological factors causing the mid-season crash of aphid population. They also list enhanced migration, reduced birth rate and elevated mortality by predation as the population processes underlying the crash. Previously, in an experimental and modelling study of potato aphids (Karley et al., 2003) they estimated, approximately, that reduced fecundity of aphids (1/3) and enhanced predation rate (2/3) were the factors behind the mid-season crash in their study. Other authors (Kindlmann and Dixon, 1996) consider that migration is the most important process that explains the summer crash rather than predation.

Being so simple, our model was unable to distinguish among the population processes indicated above. In fact, the predation simulated by Eqs. (2) and (3) must be seen as an ‘apparent’ predation. Of course some aphids are consumed by predators, but other can escape by emigration or simply by dropping to the ground. Dropping behaviour seems to be an important population process among aphids; once on the ground most of these individuals face further predation risk by ground predators (Roitberg et al., 1979; Loughridge and Luff, 1983; Bryan and Wratten, 1984; Winder, 1990) or mortality from desiccation (Roitberg and Myers, 1978, 1979; Dill et al., 1990). Losey and Denno (1998) reported drops to the ground of 7% of aphids with no predators present, 14% in presence of predatory Hemiptera, and 60% in the presence of the ladybird Coccinella septempunctata L. In our model the cause of the summer crash of aphids is the interaction between aphids and predators (especially with non-resident predators when aphid density is high; Fig. 9) and the population process behind the mid-season crash is the rather ill-defined ‘apparent’ predation, that includes predation, migration and dropping behaviour.

Parasitic wasps were not included in the model, despite reports that they can reduce aphid growth and interact with predators and ants (Kaneko, 2007). The main reason for not doing so was that the parasitic Hymenoptera in the studied field have not been identified, and consequently we cannot distinguish those that are aphid parasites from those that are not. However, we suspect that they are not important during the spring peak of aphids as the proportion of mumified aphid individuals found was very low (only 4.5 ± 0.5% during the period March–July of years 2002–2005) and there were no differences between control and ant-excluded trees (Piñol et al., 2009). However, parasitoids can be important in the autumn peak of aphids. If this was the case, the role of parasitoids would not be conceptually different to the effect attributed to non-sedentary predators in the model, and they could be considered together as late-arrival antagonists that do not limit the density of aphids during the spring, but that contribute to keep them at low densities during autumn.

4.3. Equifinality and uncertainty issues

In contrast to some other environmental models that have been applied using the GLUE methodology (Martinez-Vilalta et al., 2002; Beven, 2009), the one presented here showed a relatively high sensitivity of most parameters to the conditioning data, and most parameters had well defined regions where maximum efficiencies were obtained (Fig. 7). However, if the same figure is plotted considering only the best 100 parameter sets, the picture that emerges is different (Fig. 11). These 100 simulations have similar efficiencies (0.661–0.688) and therefore produced very similar results (see the narrow range of predictions of Figs. 4–6). In fact, all these 100 parameter sets produced reasonable (behavioural) explanations of the observed data. Despite this, some of the parameters of these models had a very wide range of possible values; two of them over the entire simulated range (Rc and γ), four over half of the range (Rg, μ, a, and ν), and in only two (r and d) were the behavioural models restricted to a relatively narrow region of the parameter space.

The above observation is the rule rather than the exception in environmental modelling and reinforces the idea of the equifinality of the models as hypotheses about how the system functions. If several parameter sets produce models with very similar performances against the conditioning data, it would be misleading to summarise the results by showing only the parameter set with the highest performance. Remember that in this study, as the running time of each simulation was very low, we conducted a very high number of simulations (6 × 108) in the eight parameter space. It is therefore unlikely that a clearly better parameter set would have been found.

4.4. Applicability of the model to other ecological and agricultural systems

The model presented in this study was developed having a particular citrus grove in mind. However, the applicability of the model goes beyond that particular site. Earwigs have proved to be able to control populations of aphids in apple orchards of temperate areas in Europe (Solomon et al., 2000), the United States (Carroll and Hoyt, 1984), Australia (Nicholas et al., 2005), and New Zealand (Suckling et al., 2006).

In addition to earwigs, there are other arthropods that have a diet wide enough and that are already present in the plant when the aphid population starts to increase which could be considered under the label of sedentary predators that we used here. Van der Berg et al. (1997) lists in this category lycosid spiders, some predatory ants and gryllids in soybean fields in Indonesia. Other spiders and carabids could also be considered in this category, and our model potentially applied to these systems. Ekborg et al. (1992)
also showed in a simulation study that two polyphagous carabid species could control the population of the cereal aphid *Rhopalosiphum padi* if they were present at the very beginning of the aphid season.

Here we showed that an omnivorous predator, such as the European earwig, was able to keep aphid population at low levels, whereas a more specialized guild of aphid predators (Coccinellidae, Hemiptera, Neoptera and Syrphidae) was unable to so, at least during the first peak of aphids in spring. It can be argued that these predators are not specialists like some other organisms such as parasitoid wasps (*Snyder and Ives, 2003*), but certainly earwigs have a wider diet than ladybirds and the other aphid predators. Since softer agricultural practices, such as integrated pest management (IPM) and organic agriculture, are currently expanding rapidly, the role of earwigs and of other sedentary and generalist predators in the control of pests merits additional attention.

5. Concluding remarks

The model developed here has compared the effects of two different kinds of aphid predators, one kind always present in the citrus trees (sedentary predators) and another kind that arrives in important numbers to the grove once the aphid population has already developed to some degree (non-sedentary predators). The model correctly reproduced the experimental data showing the important effect of sedentary predators such as earwigs had on the aphid populations. Low densities of sedentary predators or even low predation rates can have a disproportionate effect on the final aphid density, as they prey on small populations, when the per capita effect on the aphid population is higher. During the main spring peak of aphids the role of non-sedentary predators is secondary, as they track the aphid density rather than control it. However, these non-sedentary predators are important within the proposed model to keep the second autumn peak of aphids at low values. Potentially, the proposed model could also be applied to some situations where earwigs or other non-sedentary predators are important and previous models were not useful.

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