

Scaling up population dynamic processes in a ladybird–aphid system

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Abstract Here, we study how scaling up to the metapopulation level affects predictions of a population dynamics model motivated by an aphidophagous predator–aphid system. The model incorporates optimization of egg distribution in predatory females, cannibalism among their offspring, and self-regulation of the prey population. These factors determine the within-year dynamics of the system and translate the numbers of prey and predator individuals at the beginning of the season into their numbers at the end of the season at the level of one patch—one suitable host plant or a group of these. At the end of each season, all populations of prey and all populations of predators are mixed (this simulates aphid host-alternation and ladybird migration to hibernation sites), and then redistributed at the beginning of the next season. Prey individuals are distributed at random among the patches as a “prey rain”, while adult predators that survived from the previous season optimize the distribution of their offspring, in that they prefer patches with sufficient amount of prey and absence of other predators. This redistribution followed by within-season dynamics is then iterated over many seasons. We look at whether small-scale trends in population dynamics predicted by this model are consistent with large-scale outcomes. Specifically, we show that even

on the metapopulation scale, the impact of predators on prey metapopulation is relatively low. We further show how the dates of predator arrival to and departure from the system affect the qualitative behaviour of the model predictions.

Keywords Aphids · Egg window · Ladybirds · Metapopulation · Model · Population dynamics

Introduction

A vexing problem in ecology is how to make predictions for population dynamics at large spatial scales based on the information gained at small spatial scales (Melbourne and Chesson 2005), because small-scale trends in population dynamics are often contradicted by large-scale outcomes (Chesson 1996; Englund and Cooper 2003). This becomes especially important when such metapopulation systems are considered, in which periods with prevailing local interactions alternate with interludes of massive redistributions of all individuals. Aphidophagous predators may serve as a good example. Here, we show how population dynamics of such systems on a large-scale is affected by the small-scale trends. We especially concentrate on whether the patterns of top-down regulation observed on a small-scale are conserved on the large, regional scale, as this is crucial for managerial decisions on biological control of aphids, serious pests on many crops.

It has been shown that top-down regulation fails in aphidophagous predator–aphid systems (Kindlmann and Dixon 2001). This can be explained as follows. Prey of aphidophagous predators occur in distinct patches (colonies) and adult predators are able to

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move easily between them. Therefore, food availability is unlikely to be the main limiting factor for adult predators (Kindlmann and Dixon 2001). On the other hand, juvenile mortality of aphidophagous predators is extremely high (up to 95–99%; Osawa 1993; Kindlmann et al. 2000) and has to be compensated by high adult fecundity. This means that life history strategies that minimize juvenile mortality are strongly selected for (Kindlmann and Dixon 2001). As adult aphidophagous predators visit a lot of patches of prey, they can opt for the most suitable patches at which to oviposit and therefore minimize juvenile mortality via optimization of their egg distribution.

The oviposition strategy of aphidophagous predators is determined by the bottlenecks in resources that occur during the period of the development of their offspring, and by cannibalism among the offspring (Kindlmann and Dixon 1999a). The generation time ratio (GTR, defined as the ratio of generation time of the predator to that of its prey; Kindlmann and Dixon 1999b) in the aphidophagous predator–aphid systems is large, so there is a pressure to choose colonies of prey, which are likely to persist for a long time. It means that only a short period early in existence of the colony—the “egg window” (Hemptinne et al. 1992)—is suitable for oviposition. The number of predatory juveniles surviving per prey patch is also strongly regulated and kept low by means of cannibalism among juveniles and by bottlenecks in prey abundance late in the existence of prey colony, when prey becomes scarce (Kindlmann and Dixon 1999a; Dixon 2000). Ladybirds, chrysopids, and syrphids have developed a simple mechanism that allows them to optimize their egg distribution in the above-mentioned sense: they avoid ovipositing in aphid colonies where larvae of other predatory species are already present (Hemptinne et al. 1993; Růžička 1994).

Thus, optimal oviposition strategies, rather than immediate availability of prey (as in classical population dynamics models), seem to determine population dynamics of aphidophagous predators. As a synergetic result of the short “egg window” plus the strong density-dependent cannibalism, the top-down regulation fails in aphidophagous predator–aphid systems, and the classical functional and numerical responses lack their influence on their population dynamics (Dixon 2000). A model has been developed that illustrates these considerations and shows how optimization of egg distribution in aphidophagous predator–aphid systems affects population dynamics of both predator and prey within one prey colony (Kindlmann and Dixon 2003). Its predictions are strongly supported by empirical data on the dynamics of a ladybird–aphid

system (Osawa 1993; Yasuda and Shinya 1997, 1999; Kindlmann et al. 2004).

The problem is, however, that, between the seasons, both aphids and their predators redistribute themselves. In autumn, aphids migrate to produce a sexual generation, mate and produce eggs (often on plant species different from those where they have spent the spring and summer, as in host-alternating aphids), while aphid predators migrate to hibernating places, and both aphids and their predators move back in the spring. Massive migrations of both prey and predator mean that individuals originating from different colonies are mixed, and that new colonies, which will emerge the next year, will consist of individuals (or their descendants) that originated from different colonies in the previous year. The question of how to scale up from colony-scale interactions to regional-scale dynamics in aphidophagous predator–aphid systems (i.e., how the colony-scale interactions affect the population dynamics of a metapopulation consisting of all individuals that belong to any of the local colonies in a region) has, however, not yet been addressed. As long-term empirical data on regional-scale dynamics of aphidophagous predator–aphid systems are not available, mathematical models are the only means for predicting the outcome and deciding how to direct further field research.

In the model presented here, we extend the Kindlmann and Dixon (2003) model to regional-scale dynamics. We consider a number of patches (plants or clumps of plants). During the season, the local interactions in each of these patches are governed by the Kindlmann and Dixon (2003) model. Between the seasons, all prey individuals are mixed and redistributed at random to the patches, and all predator individuals are redistributed to the patches according to the optimal oviposition rules outlined above: eggs are laid only in patches, which contain aphids and no predatory larvae. The model predicts that, even on the metapopulation scale, the impact of predators on prey metapopulation is low. We further look at how other aspects, like the date of predator arrival to and departure from the system, affect the qualitative behaviour of the model.

The main difference between our model and previous metapopulation dynamic models concerning between-patch movement (e.g., Van Baalen and Sabelis 1993; Holyoak and Lawler 1996a, b; Holyoak 2000; Swihart et al. 2001; Bonsall et al. 2002; Neubert et al. 2002; and references therein) is in the approach to the within-patch dynamics. While in all other models trophic interactions between predator and prey are determining population changes, here it is optimization

of offspring distribution among patches by the predator and predator cannibalism within patches that drives most of the system dynamics.

The model

We consider a fixed number of patches, p . The patch may represent a single shoot, one plant, or a patch of these, depending on the mobility of the animals considered. The model has three components:

1. Egg-window dynamics: the period, when both prey and predators arrive and settle on the plants during spring.
2. Within-season dynamics: this component follows the previous one and simulates the system dynamics after the initial period of immigration and oviposition has ceased. During this phase, any additional immigration is considered as being small compared to intrinsic system dynamics and therefore neglected.
3. Between-season dynamics: this component is an iteration of the previous two components and mimics the system behaviour during the course of many years.

Egg-window dynamics

This component of the model simulates the growth of aphid colonies and the foraging and ovipositing behaviour of predators. We assume that the individuals of prey migrate into the patches only at the beginning of a season, but do not migrate between plants. The summer aphid populations are set up by parthenogenetic females immigrating from a winter host-plant, so there is no relationship between numbers of aphids this year and the last year on one particular plant. The fundatrices land on plants at random and start to reproduce with a constant growth rate, $R=0.4$. The target plant is chosen from a uniform distribution ($U(1, p)$).

The predators are introduced into the system with an initial amount of energy chosen from a normal distribution with $E_{\text{mean}}=20$, and standard deviation $E_{\text{SD}}=2$. In every step (one flight—we assume eight flights per day), all predators are distributed among the plants. The target plant is chosen randomly from the uniform distribution so it is possible to stay on the same plant or to meet other predators. The cost of flight is subtracted from the energy amount of each predator. If there are any aphids on the plant, the

predator feeds on them, but does not eat more than *lunch* (estimated variable) of aphids. Every eaten aphid represents one energy unit, which is added to the predator's energy reserve. If the predator reaches a *min* energy level (*min*, optional variable), it can lay a *batch* of eggs (e.g., 20, estimated variable). A necessary condition for laying eggs is the presence of aphids on the plant and the absence of conspecific larvae, which hatch 4 days after the oviposition (*hatch*, estimated variable). The energy used for oviposition is subtracted. The number of aphids eaten is subtracted from the colony. The plants without aphids or with either eggs or larvae are supposed to be unsuitable for oviposition. Once the proportion of unsuitable plants exceeds a critical value ($1-swPrey$, optional variable), the egg-window closes and the predators leave the system. The maximum length of the egg-window is 15 days. We do not consider any eggs laid later, because most of these larvae would die in consequence of a bottleneck in prey abundance. The final numbers of prey and predators at the end of the egg-window are used further in the within-season dynamics model.

Within-season dynamics

For simulation of the within-season dynamics we use the Kindlmann and Dixon (2003) model that consists of the following set of differential equations:

$$\frac{dh}{dt} = ax, \quad h(0) = 0, \quad (1)$$

(changes in the cumulative density of prey),

$$\frac{dx}{dt} = (r - h)x - \frac{vexy}{b + ex + y}, \quad x(0) = x_0, \quad (2)$$

(changes in prey density),

$$\frac{dy}{dt} = -\frac{vy^2}{b + ex + y}, \quad y(0) = y_0, \quad (3)$$

(decrease in predator density due to cannibalism), where $h(t)$ is the cumulative density of the prey at time t , $x(t)$ the density of prey at time t , a the scaling constant relating prey cumulative density to its own dynamics, r the maximum potential growth rate of the prey, $y(t)$ the density of predator at time t , v the predator voracity, b the parameter of the functional response of the predator, e the predator's preference for prey and T is the time when predator matures; coincides with the duration of a patch of prey, yielding final values $x(T)=x_{\text{aut}}$ and $y(T)=y_{\text{aut}}$ of the season.

The model has the following biological assumptions:

1. Insect herbivores, and aphids especially, have frequently been observed to first increase and then decline in abundance, even in the absence of natural enemies (Dixon 1997, 2000). Such declines are often caused by emigration from patches when the prey disperses to find new vacant patches. The prey individuals respond negatively to their cumulative density (Kindlmann et al. 2004). Thus, in our model, the regulatory term for prey, when alone, is its cumulative density, h , instead of some function of its instantaneous density. In contrast to the logistic or exponential growth models, our model allows prey to decline in abundance with increasing time even in the absence of natural enemies (Kindlmann et al. 2004).
2. The predator is supposed to be univoltine. Predators born in a patch rarely reproduce within the same patch (Dixon 2000), but after completing their development they fly off and reproduce elsewhere. Therefore, we assume that (1) the initial density of the predator in a patch is defined by the number of eggs laid there by adults that developed in other patches of prey, arrived at this patch, and reproduced there during the “egg window”, and (2) changes over time in the number of predators within a patch are due to larval cannibalism and not reproduction.
3. We assume that the predator is cannibalistic, but has a preference, e , for eating prey, as opposed to conspecifics. If they prefer prey, then $e > 1$, but e may also be less than one as, e.g., in the case when the larvae of a predator prefer to eat conspecific eggs, which cannot defend themselves. We have used $e = 1$, the predator shows no preference for either prey or conspecifics (the “meet and eat” hypothesis; Kindlmann and Dixon 2003).
4. The within-season simulation ends with the autumnal host-alternation. As only the alate individuals can reach a winter host-plant and reproduce there, the number of prey next year is derived

from the number of alates produced during the decline in the abundance. All eggs/individuals, which survive the winter, will appear in the system in the next season.

5. We consider only female individuals of predator supposing a 1:1 sex ratio. This does not affect the simulation outcome. The females conform to the optimal ovipositing behaviour outlined above. Larvae do not leave their patch of prey. The length of life of a female is given by its success in foraging and its ovipositing activity. Once the individual spends all its energy supply it dies (i.e., leaves the system). The number of predators next year is calculated from the autumn numbers by multiplying by winter mortality and only one-half of that is used as the number of females.

A typical trend in numbers in a patch predicted by model (1) is shown in Fig. 1. There is only one peak in the abundance of prey and the individuals respond negatively to their cumulative density resulting in the bottleneck in their abundance. There is no predator reproduction in the patch; therefore, predator numbers monotonously decline. As a consequence, if prey abundance (x) increases at the beginning (i.e., if y_0 is sufficiently small, so that $\lim_{t \rightarrow 0^+} \frac{dx}{dt} > 0$) then, as time proceeds, the dynamics of the prey is less and less influenced by the declining numbers of the predator. Because of the way the diet of the predator is defined [the terms containing v in (2) and (3)], the decline in predator numbers is more pronounced when there are few prey individuals relative to predator individuals; that is, when the ratio x/y is small at the beginning and when prey numbers have passed their peak and become small again due to the negative effect of cumulative density. Within the season, the predators have almost no influence on the prey dynamics in this system (Kindlmann and Dixon 1993). Not surprisingly, the number of predators that survive is positively influenced by the initial number of prey and negatively influenced by the initial number of predators (P. Kindlmann et al., unpublished data).

Fig. 1 Trends in time in prey (left) and predator (right) abundances predicted by the within-season model when $a=0.000005$, $r=0.3$, $v=0.1$, $b=0$, $e=1$, for $y(0)=0$ and $y(0)=60$ (left) and for $x(0)=10$ and $x(0)=50$ (right)—see insets for line codes

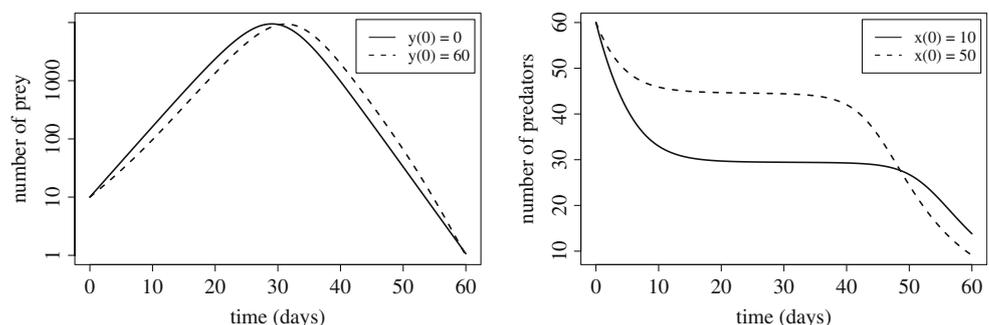
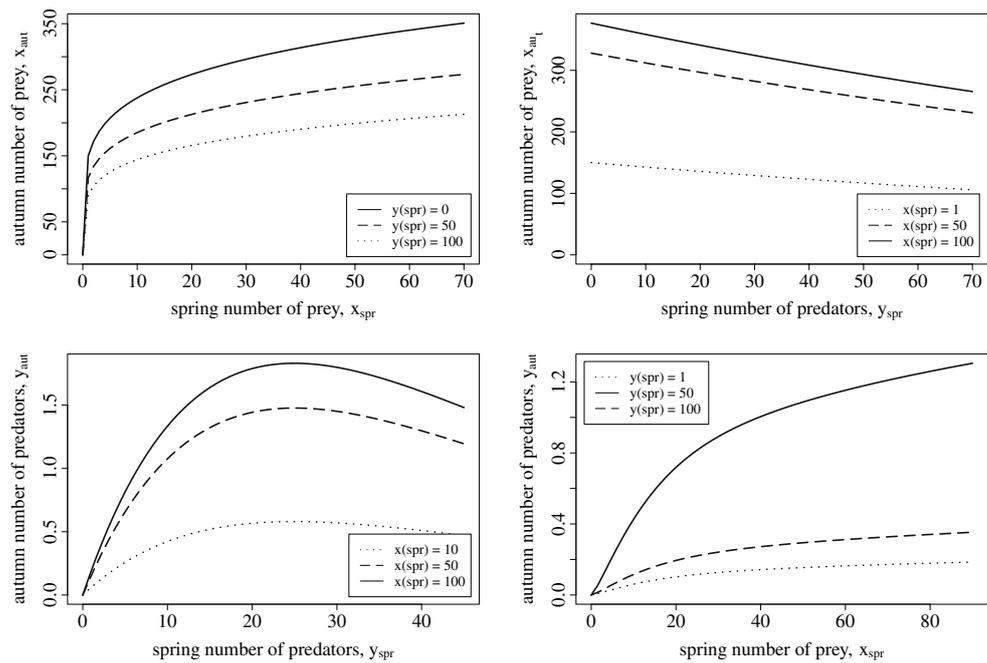


Fig. 2 Relationships between spring and autumn numbers of prey and predators, as predicted by model (1). Parameter values: $r=0.3$, $a=0.000005$, $v=0.1$, $b=0$, $e=1$



The predicted trends in abundance (Fig. 1) closely match those observed in nature in aphids (Dixon et al. 1996; Kindlmann and Dixon 1996, 1997; Dixon and Kindlmann 1998; Kindlmann et al. 2004) and ladybird beetles (Osawa 1993; Yasuda and Shinya 1997, 1999; Kindlmann et al. 2000).

Figure 2 shows the predicted final numbers of prey and predators (x_{aut} , y_{aut}) relative to their initial numbers (x_{spr} , y_{spr}) predicted by model (1) for different initial values of prey and predator numbers. We adapted the first relationship so that it shows the dependence of a cumulative number of alates on the spring number of prey (Fig. 2a). The dependence between the final number of prey and the initial number of predators is very weak, with the slope dependent on the initial numbers of prey (Fig. 2b). The dependence of the final number of predators on the initial number of prey (Fig. 2d) resembles a power function. There is a humped dependence of the final number of predators on their initial number (Fig. 2c).

By combining these dependences we found two equations approximating relations between the initial (spring) prey and predator numbers (x_{spr} , y_{spr}) and their final (autumn) numbers (x_{aut} , y_{aut}):

$$x_{aut} = a_1 x_{spr}^{b_1} \cdot e^{-c_1 y_{spr}},$$

$$y_{aut} = a_2 y_{spr} e^{-b_2 y_{spr}} \cdot x_{spr}^{d_2} (1 - e^{-c_2 x_{spr}}).$$

In this system, when predators are absent, the number of prey increases when the spring number of prey is low, but is strongly regulated by itself. Influence of the

predator on prey dynamics [the term $\exp(-c_1 y_{spr})$ is negative and dependent on the number of predators, y_{spr}]. The autumn number of predators is positively influenced by the spring number of prey [the term $x_{spr}^{d_2} (1 - e^{-c_2 x_{spr}})$]. The shape of the spring–autumn relationship in the number of predators is humped, indicating that predators do best at intermediate densities; when there are few predators, few of them survive and, because of cannibalism, few survive even when they are initially numerous.

The equations are used for each plant individually.

Between-season dynamics

The between-season dynamics is to a large extent determined by the within-season dynamics. The autumn numbers of prey and predators are multiplied by the probabilities of survival of winter P_x and P_y , respectively (optional variables). In case of prey, this simulates the autumnal production of sexual individuals, laying eggs, and overwintering. The final numbers of prey and predators are redistributed at the beginning of the next year-cycle similarly to their natural migration between host-plant species or to hibernation sites and back.

Parameters option

The optional variables in the “egg-window” simulation were estimated from the data in literature (Hukusima and Kamei 1970; Dixon 2000) or compared with our

Table 1 Parameters used in the “egg-window” dynamics simulation

Parameter	Value	Type
Number of plants	$p=10,000$	Fixed variable
Number of aphids	$x_{ini}=10,000$	Optional variable
Number of predators	$y_{ini}=100$	Optional variable
Start of predators activity	D	Optional variable
Energy - mean	$E_{mean}=20$	Fixed variable
Energy - standard deviation	$E_{SD}=2$	Fixed variable
Aphid growth rate	$R=0.4$	Variable estimated from data
Proportion of suitable plants	$swPrey$	Optional variable
Minimum for oviposition	$Min=30$	Optional variable
Number of eggs in batch	$Batch=20$	Variable estimated from data
Number of eaten aphids	$Lunch=5$	Variable estimated from data
Days before hatching	$Hatch=4$	Variable estimated from data
Energy for one batch	$E_{batch}=10$	Variable relative to E_{mean}
Energy for one flight	$E_{flight}=0.5$	Variable relative to E_{mean}

data. Table 1 shows parameters used in the first part of the simulation. The random choice of the target plant of the predator represents the major source of variability in the system. The food transformation efficiency was set so that the maximum amount of food per day is almost equal to the cost of a flight. The energy required for laying one batch of eggs was set so that the predator is likely to have enough energy to survive the egg-window. The model does not suppose that the female necessarily lays all her eggs during the egg-window. The energy required for one flight allows the predator to survive 4 days without nutrition.

The parameters used in the within-season dynamics are set so that the simulated relationships correspond with these described by Kindlmann and Dixon (2003) (Table 2).

The probabilities of survival of winter were set $P_x=0.015$ and $P_y=0.8$, so that the populations in optimal abundances did not go extinct.

Results

Figures 3 and 4 show the aphid and ladybird between-year population dynamics (total numbers of aphids and ladybirds on all plants in spring at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, for different times of predator arrival into the system and under the assumption that the predators leave the system when 30% of plants are still suitable (an aphid colony, but no predators are present on the plant). Aphid and lady-

bird dynamics are closely correlated and there are distinct 2–4 year oscillations. The later the predators arrive into the system, the smaller is the amplitude of the oscillations, which disappear completely when the predators arrive on day 5. The later the predators arrive into the system, the larger is the average density of both prey and predator. The equilibrium density of aphids in the absence of predators (not shown) is about 50,000 individuals, which is comparable with the case when predators arrive on day 10 in Fig. 3. When predators arrive earlier (days 1–3), the model predicts that they are able to reduce the average prey density only to about 30–50% of the predator-free value (about 20,000 when the predators arrive on days 1–3).

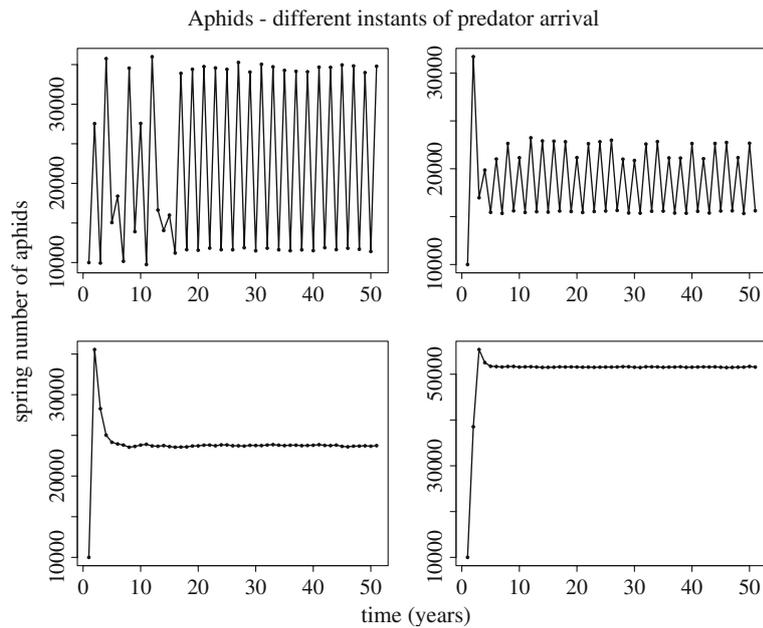
Figure 5 shows the same situation in the case when different predators arrive into the system at different times during the first 10 days of aphid colony existence and when the arrivals of the predators are uniformly distributed during this interval. A similar pattern as in Figs. 3 and 4 appears. Again, aphid and ladybird dynamics are closely correlated. Both the amplitude and the average population densities of both prey and predator are similar to the case when the predators arrive into the system on days 1–3 (compare with Figs. 3, 4). Thus, even in this scenario, the predators are able to reduce the average prey density to only to about 30–50% of the predator-free value.

Figures 6 and 7 show the aphid and ladybird between-year population dynamics (total numbers of aphids and ladybirds on all plants in spring, at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, for different times of predator departure from the system under the assumption that the predators arrive into the system on day 3. Again, aphid and ladybird dynamics are closely correlated and there are distinct 2–4 years oscillations. The earlier the predators leave the system, the smaller is the amplitude of the oscillations.

Table 2 Parameters used in the within-season dynamics model

Parameter 1	Parameter 2	Parameter 3	Parameter 4
$a_1=150$	$b_1=0.2$	$c_1=0.005$	
$a_2=0.05$	$b_2=0.04$	$c_2=0.1$	$d_2=0.3$

Fig. 3 Aphid between-year population dynamics (total numbers of aphids on all plants in spring, at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, for different times of predator arrival into the system, *D*: day 1 (*upper left*), day 3 (*upper right*), day 5 (*lower left*) and day 10 (*lower right*)



Discussion

Our simulations have shown the importance of scale in considering the dynamics of predator–prey systems with aphids as prey. In the small-scale model by Kindlmann and Dixon (2003), the population numbers at the end of the season were iterated and set equal to initial numbers at the beginning of the next season. Thus, seen from the biological point of view, the population dynamics on only one plant was considered there. The prey and predator have then shown 2-year cycles in abundance. In the simulations presented in this paper, where both

prey and predator redistributions at the end/beginning of each season among a large number of patches were considered, the qualitative behaviour of the model was similar: both prey and predator also oscillated with an approximately 2-year period when the predator was present. This qualitatively resembles the observed aphid population dynamics (Dixon et al. 1996). However, there are important differences between the small- and large-scale behavior of the model, which we will now describe and explain.

Interestingly, the later the predator arrived into our model system, the smaller was the amplitude of the

Fig. 4 Ladybird between-year population dynamics (total numbers of ladybirds on all plants in spring, at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, for different times of predator arrival into the system, *D*: day 1 (*upper left*), day 3 (*upper right*), day 5 (*lower left*) and day 10 (*lower right*)

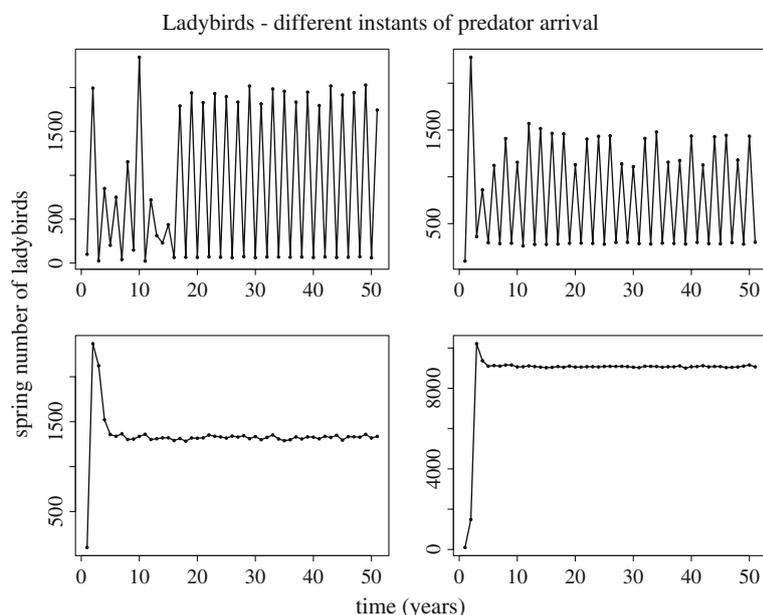


Fig. 5 Aphid (*top*) and ladybird (*bottom*) between-year population dynamics (total numbers of aphids and ladybirds on all plants in spring, at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, when predators arrive into the system at random during the first 10 days and leave when no more plants are suitable (*left*) and when 30% of plants are still suitable (*right*)

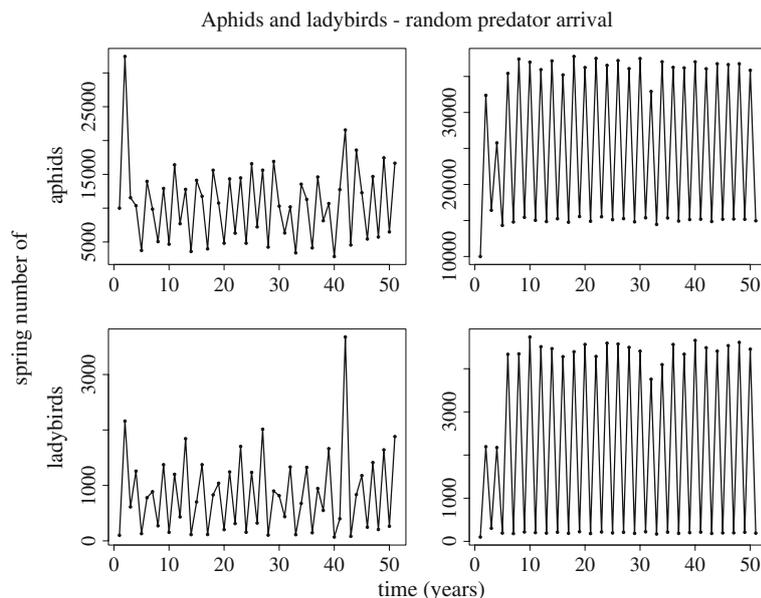
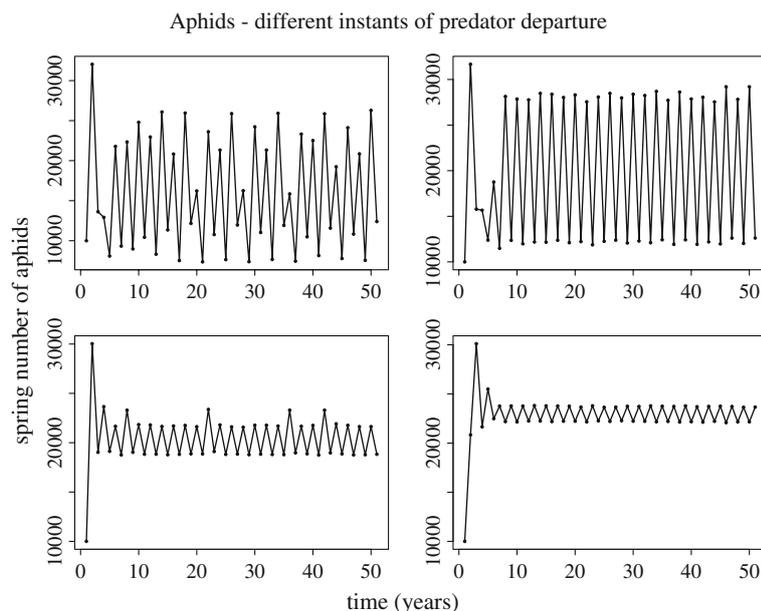


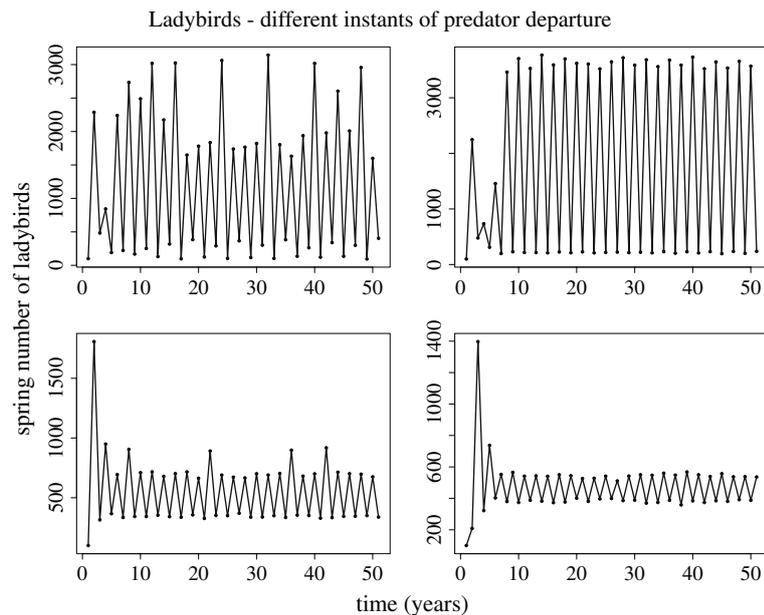
Fig. 6 Aphid between-year population dynamics (total numbers of aphids on all plants in spring, at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, for different times of predator departure from the system: when 10% of plants are still suitable (*upper left*), when 20% of plants are still suitable (*upper right*), when 40% of plants are still suitable (*lower left*), when 50% of plants are still suitable (*lower right*)



oscillations and the higher were the long-term (across many years) average densities of both predator and prey. This can be explained as follows. In the “within-season dynamics” component of the model, the predators affected the prey population dynamics only very weakly. In biological terms this means that at any instant, the abundance of aphids within a particular colony, once established, was only weakly influenced by the abundance of the predators. Thus the only critical phase of the season, when predators may be able to affect prey metapopulation dynamics, can be *before* the establishment of the colonies, during early spring—during the “egg-window dynamics”

component of our model. During this period, when aphid colonies are still small, a predator may—at least in theory—destroy a whole aphid colony at which it arrives. The total aphid metapopulation size in autumn is equal to the product of the expected number of aphid migrants produced per colony (determined by the “within-season dynamics” component of the model) times the number of established colonies. While the former is—according to our model—relatively unaffected by the predators, the latter (and therefore the whole product) may be. Thus early arriving predators may be able to affect population dynamics of their prey more effectively than latecomers

Fig. 7 Ladybird between-year population dynamics (total numbers of ladybirds on all plants in spring, at the time when the egg-window has just been opened) during 50 years of simulations, as predicted by the model, for different times of predator departure from the system: when 10% of plants are still suitable (*upper left*), when 20% of plants are still suitable (*upper right*), when 40% of plants are still suitable (*lower left*), when 50% of plants are still suitable (*lower right*)



by reducing the *number* of established colonies rather than their *size* and/or *number of autumn migrants*. Our simulations predict, however, that the main effect of predators even in this case is on the *amplitude* of the prey oscillations, rather than on their *average value*, which is a non-intuitive and important result. In other words, if predators arrive early, the model predicts that they slightly decrease the average prey density (calculated across many years), but—more importantly—they contribute to the increase of the amplitude of the 2-year oscillations in prey (and also their own) abundance. This prediction clearly invites an empirical verification, which will, however, need years of targeted observations.

Two practical results arise from these considerations: (1) the top-down regulation fails in aphidophagous predator–aphid systems even on a metapopulation scale; the impact of predators on aphid average density (across many years) is relatively small, no matter when they arrive; and (2) if predators were able to “come to an agreement” and all of them arrived later, each of them would profit in terms of achieving a higher average population density. This is, of course, counter-selected, as selection acts on an individual basis and early comers have a selective advantage at the expense of the common profit (the famous “tragedy of commons”).

It is difficult to find appropriate data to verify our predictions, as population dynamics is only very rarely monitored at a large number of patches simultaneously. Suction trap data, collected in France, England, and other countries, although containing only indirect counts (i.e., numbers of migrants in the air), might serve as some indicator of the qualitative trends

in aphid dynamics at large scales. However, preliminary autocorrelation and partial autocorrelation analyses (unpublished) indicate that there is only rarely a detectable periodicity in the aphid dynamics. If there is one, it is weak and has a period two. Then a question arises, whether it is not only a statistical artefact, stemming from performing multiple statistical tests: it is well-known that if the likelihood of type I error in one test is p , then the likelihood of at least one type I error in n tests is $1-(1-p)^n \gg p$. Thus, when multiple tests are performed, the likelihood that at least one test will lead us to believe that the null hypothesis is false, even if it is true (i.e., no oscillations in our case), is strongly increasing. On the contrary, within one patch, there is a strong evidence for the see-saw effect, i.e., 2-year oscillations (Dixon 1997). The worst problem is, however, with reliable data on ladybird population dynamics, which seem to be non-existent.

In summary, it seems that aphids are strongly self-regulated within a patch, but this regulation is weaker when a large scale is considered, as then other factors, like randomness due to large-scale redistributions (as in our simulations), but probably also weather, may play a stronger role and sometimes cause the regular 2-year cycles to disappear. This may be a reason why all attempts to develop good predictive models for long-term aphid population dynamics have failed. The effect of predators on aphids within a patch was shown to be almost negligible (Kindlmann and Dixon 2001, 2003) for the reasons described in the Introduction. Our simulations indicate that this can be extended to large-scale population dynamics. The

critical point for verification of our predictions is the availability of reliable large-scale data on predator between-year population dynamics. The future research should be directed towards their obtaining.

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