Aphid Biodiversity under Environmental Change

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Editors

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Patterns and Processes

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Preface

This book presents the results of recent research on aphid population dynamics and ecology relevant to current environmental changes resulting from global warming. It incorporates a selection of the contributions presented at the International Symposium on Aphids in Fremantle, Australia, in October 2005, plus some additional invited chapters. The objective was to incorporate the major issues in the field and simultaneously create a closely interrelated and integrated volume.

The first chapter sets the scene. Kindlmann and Dixon present a critical review of existing models of aphid population dynamics, examine the biological assumptions that are incorporated in the models and present one of the latest models of aphid metapopulation dynamics. They conclude that natural enemies are unlikely to affect aphid population dynamics late in a season, but in some years may have an effect very early in the season, when aphid colonies are still small and predators might be able to reduce the numbers of colonies.

The question, whether aphids will move to different locations, adapt to the change in conditions in their current habitat or go extinct is discussed by Ameixa. She concludes that the distributions of aphids are most likely to change, with the distribution of each species moving globally as their preferred habitat moves in response to changes in the climate, which may be more difficult than in the past because of habitat fragmentation and habitat loss.

The chapter by Harrington and Clark makes use of suction trap catches, the best available long-term data in the world on aphid dynamics. Acknowledging the difficulties of interpretation and prediction, they investigate whether there is any evidence that the start of the spring flight of aphids at particular locations is occurring earlier as winters get warmer, and whether this is more so for aphids that tend to be continuously parthenogenetic at that locality, and that the trend in the migration beginning earlier and ending later in more recent years is a consequence of an increase in average temperatures.

The paper by van Baaren et al. addresses the effects of climate on insect communities, focusing on aphids, aphid parasitoids, predators and hyperparasitoids. For each trophic level, the general effect of temperature change on insects is discussed, with emphasis on species belonging to aphid-based communities.

Michaud in his chapter claims that an increase in annual mean temperatures would have certain predictable consequences for cereal aphid populations via direct

effects on aphid biology, and indirectly through effects on plants and natural enemies. However, any sustained shift in prevailing wind patterns associated with atmospheric warming could generate an unpredictable cascade of ecological consequences for both agriculture and cereal aphids, mediated largely by changes in rainfall patterns and migration pathways, respectively.

Qureshi considers the impact of increasing temperature on the aphid species *Toxoptera citricida*, a cosmopolitan pest of citrus and a highly efficient vector of citrus tristeza virus. He concludes that the negative impact of rising temperatures on *T. citricida* populations may be more pronounced in the south than elsewhere due to the relatively higher temperatures there, with more beneficial effects evident in the north.

Clement et al. investigate the history of pea aphid outbreaks in the U.S. Pacific Northwest. Various abiotic and biotic factors and their possible controlling influence on changes in pea aphid densities, with emphasis on winter temperatures within the context of climate change, are presented and discussed.

Dixon and Hopkins study the mechanisms of coexistence of several aphid species on the same host plant. Using data on five species of aphids coexisting on the leaves of birch and indicate that the temporal patterns in their reproductive activity are associated with differences in their thermal tolerances.

Roy and Majerus deal with the role of ladybirds in the changing world. They conclude that it is difficult to assess the impact that anthropogenic factors will have on most species of coccinellid but logic suggests that the direct anthropogenic drivers of environmental change, both individually and in concert, will be highly deleterious to all but the most adaptable and eurytopic coccinellids.

Aphids have evolved a particular form of inducible anti-predator behaviour that involves the emission of alarm pheromone. Outreman et al. show that alarm signaling in aphids is associated with the ecological cost of attracting additional natural enemies and demonstrate that a full understanding of the evolution of inducible defenses has to consider a species' complete network of ecological interactions.

This book fills a significant gap in the recent literature: while there are several books on aphid biology and ecology and their importance as crop pests (Dixon 1998, 2005; Minks and Harrewijn 1987–1989; van Emden and Harrington 2007) there are none on the possible effects of environmental changes on aphid population dynamics and their biodiversity. This book will be a useful introduction to the subject for graduate students, researchers in crop science, crop protection, agricultural advisors and managers etc., but can also be used as a complementary text in any course on population dynamics and ecology of crop pests for undergraduates or graduates.

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Chapter 1
Modelling Population Dynamics of Aphids and Their Natural Enemies

Pavel Kindlmann and Anthony F.G. Dixon

Abstract Aphids are serious pests of many agricultural crops. Therefore, a good understanding of their population dynamics is vitally important for crop protection. There have been several attempts made to forecast the abundance of aphids and develop expert systems to help farmers optimize prophylactic measures and minimize their costs. The advisory systems, however, did not receive general acceptance and disappointingly few forecasting systems are in use. The failure of models to predict aphid population dynamics for practical purposes is due to the extremely wild oscillations in aphid numbers caused by intrinsic (size, fecundity, mortality, migration rate) and external factors (weather, especially temperature). As a consequence, the predictions are unlikely to be robust enough for reliable forecasting, mainly because they depend on the course of weather during the season, which cannot be predicted. Here we present a critical review of existing models of aphid population dynamics, examine biological assumptions that are incorporated in the models and present one of the latest models of aphid metapopulation dynamics. We conclude that natural enemies are unlikely to affect aphid population dynamics late in the season, but may have an effect very early in the season, when aphid colonies are still small and predators might be able to reduce the numbers of these colonies. Empirical verification of this is still very weak, however, and further experiments on this aspect of predator prey dynamics should be undertaken.

Keywords Aphids · Aphidophagous insects · Population dynamics · Predictive models · Trophic interactions

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1.1 Introduction

Aphids are serious pests of many agricultural crops. Therefore, a good under-standing of their population dynamics is vitally important for crop protection. Not surprisingly, the pest status of aphids and political concern over the prophylactic application of pesticides attracted the attention of modellers starting in the 1960s (Hughes 1963; Hughes and Gilbert 1968; Gilbert and Hughes 1971; Gosselke et al. 2001). Attempts were made to forecast the abundance of aphids and propose expert systems to help farmers optimize prophylactic measures and minimize their costs (Mann et al. 1986; Gonzalez-Andujara et al. 1993; Ro and Long 1999). These stud-ies usually concluded that forecasting is a better strategy than either no control or prophylaxis, where yields are average and above (Watt 1983; Watt et al. 1984). The advisory systems, however, did not receive general acceptance and disappointingly few forecasting systems are in use. Analysis of some of the existing models of aphid population dynamics reveals the reasons. For example, a model that describes the summer population dynamics of the grain aphid, *Sitobion avenae* (Carter et al. 1982; Carter 1985) was modified and extended to include the population dynamics of the aphidophagous predator *Coccinella septempunctata* (Skirvin et al. 1997a,1997b). It is claimed to give better predictions than the Carter et al. (1982) model, but there are few data against which it can be validated. The main weakness of the Skirvin et al. (1997a) model is that it gives the same prediction for identical initial conditions, which is contrary to what is observed in the field.

Early models of the population dynamics of the peach–potato aphid, *Myzus per-sicae* (Scopes 1969; Tamaki and Weeks 1972, 1973; Tamaki 1973, 1984; DeLoach 1974; Taylor 1977; Whalon and Smilowitz 1979; Tamaki et al. 1980, 1982; Mack and Smilowitz 1981, 1982; Smilowitz 1984; Ro and Long 1998) were recently improved by Ro and Long (1999). However, even this model is not validated against data that were not used to derive the parameters, which devalues the claim that it gives a good prediction. In addition, it also makes the unwarranted assumption that the decline in aphid abundance is caused by predators (see later in this chapter).

A simulation model developed to investigate the interrelationship of factors influ-encing the population dynamics of the bird cherry-oat aphid, *Rhopalosiphum padi*, in barley crops during autumn and winter (Morgan 2000) accurately predicts out-breaks and the peak aphid populations within 20% of that observed in all but one case. However, this model is not suitable for long-term predictions, as it requires the daily input of maximum and minimum temperatures, which invalidates its pre-dictive value, as these temperatures cannot be predicted with sufficient accuracy. Another model for this species was developed by Wiktelius and Pettersson (1985), but was not used for forecasting and therefore there is a need for further research on this topic.

A whole family of models of the cowpea aphid, *Aphis craccivora* (Gutierrez et al. 1974), and the pea aphid, *Acyrthosiphum pisum*, population dynamics (Gutierrez and Baumgärtner 1984a, 1984b; Gutierrez et al. 1984), and that of their natu-ral enemies (Gutierrez et al. 1980, 1981) were developed by Gutierrez and his group, but even these were not used for long-term predictions. Similarly, a com-puter simulation model developed to investigate spatial and population dynamics

of apterae of the Russian wheat aphid, *Diuraphis noxia* on preferred (wheat) and non-preferred (oat) hosts by Knudsen and Schotzko (1991) is only suitable for short-term (14 and 21 days) predictions. A transition matrix model developed to simulate the population dynamics of the green apple aphid, *Aphis pomi* (Woolhouse and Harmsen 1991) has also not been validated against an independent data set.

Recently, spatio-temporal, or metapopulation models have been published (Weisser 2000; Winder et al. 2001). These are a promising development, but modellers employing this approach need to consider whether aphid migration, rather than predator-inflicted mortality, is the regulating factor. The question remains, whether predators drive aphid metapopulation dynamics, or as predicted by theory (Kindlmann and Dixon 1996, 1999) are responding to aphid abundance, which is self-regulated by migration.

In general, the failure of models to predict aphid population dynamics for practical purposes is due to the extremely wild oscillations in aphid numbers caused by intrinsic factors (size, fecundity, mortality, migration rate) and external factors (weather, especially temperature). As a consequence, the predictions are unlikely to be robust enough for reliable forecasting, mainly because they depend on the course of weather during the season, which cannot be predicted. In addition, most of the models tend to be very complex, which stems from the belief of their authors that complexity means better accuracy, which is not always the case (Stewart and Dixon 1988). This is because the measuring errors, associated with each of the large number of parameters, yield highly variable predictions. Thus, there is a serious gap in our knowledge, which needs to be filled in order to confirm or refute the understanding arrived at mainly by studying aphids living on woody plants. For a further discussion of forecasting, see Harrington et al. (2007).

1.2 Biological Background

1.2.1 Aphid Biology Relevant to Population Dynamics

Most aphid species can reproduce both asexually and sexually, with several parthenogenetic generations between each period of sexual reproduction. This is known as cyclical parthenogenesis and, in temperate regions, sexual reproduction occurs in autumn and results in the production of overwintering eggs, which hatch the following spring and initiate another cycle. Many pest aphids, however, do not overwinter as an egg but as nymphs or adults and others as both eggs and active stages (see Williams and Dixon 2007). For their size, the parthenogenetic individuals have very short developmental times and potentially prodigious rates of increase (de Réaumur 1737; Huxley 1858; Kindlmann and Dixon 1989; Dixon 1992). Thus, aphids show very complex and rapidly changing within-year dynamics, with each clone going through several generations during the vegetative season and being made up of many individuals, which can be widely scattered in space. The survival of the eggs and/or overwintering aphids determines the numbers of aphids present the following spring.

The study of the population dynamics of aphids living on herbaceous plants, including agricultural crops, is difficult because their host plants vary in abundance and distribution from year to year. Tree-living aphids, in addition to being very host-specific, live in a habitat that is both spatially and temporally relatively stable. Therefore, it is not surprising that most long-term population studies on aphids have been on such species (Dixon 1963, 1966, 1969, 1970, 1971, 1975, 1979, 1990; Dixon and Barlow 1979; Dixon and Mercer 1983; Dixon et al. 1993b; 1996; Barlow and Dixon 1980; Chambers et al. 1985; Wellings et al. 1985). However, some of the theoretical results obtained from these studies are quite general and can be applied to other aphid species.

Within a year, aphid dynamics are very complicated and, in looking for the mechanism of regulation, this needs to be taken into consideration. An initial dramatic increase in population size in spring is typically followed by a steep decline in abundance during summer and sometimes a further increase in autumn (Fig. 1.1). During spring and summer all the generations are parthenogenetic and short lived (1–4 weeks). In autumn, sexual forms develop, mate and give rise to the overwintering eggs from which fundatrices, the first parthenogenetic generation, hatch the following spring. The parthenogenetic generations overlap in time and the environmental conditions are rapidly changing. Therefore, an individual throughout its life, as well as individuals born at different, but close instants in time, can experience quite different conditions, which results in aphids evolving different and varying reproductive strategies.
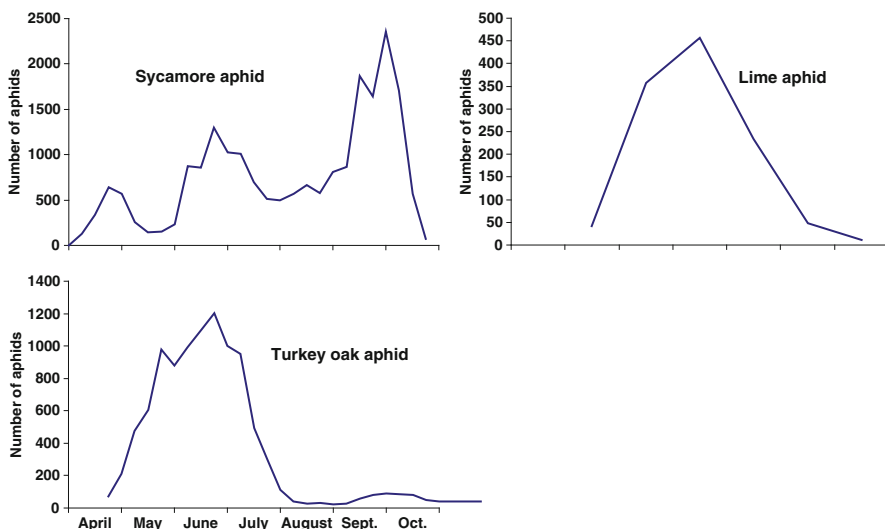
Fig. 1.1 Within season population dynamics of three tree-dwelling aphid species. Values based on direct counts of the number of individuals per 80 leaves, during the years 1960–1974 (Glasgow, UK, sycamore aphid), 1965–1972 (Glasgow, UK, lime aphid) and 1975–1995 (Norwich, UK, Turkey oak aphid). Data collected by A.F.G. Dixon and his students

The within-year dynamics of aphids are largely determined by seasonal changes in host quality. Aphids do best when amino acids are actively translocated in the phloem. In spring, the leaves grow and import amino acids via the phloem; in summer leaves are mature and export mainly sugars. In autumn, the leaves senesce and export amino acids and other nutrients. Thus on trees the leaves are most suitable for aphids in spring and autumn. The differences in within-year population dynamics of aphids are due to differences in the effect these seasonal fluctuations in host plant quality have on the per capita rate of increase and intraspecific competition in each species. This annual cycle, consisting of two short periods when the host plant is very favourable and a long intervening period when it is less favourable, is well documented for tree dwelling aphids. This has greatly facilitated the modelling of their population dynamics. In general the aphid carrying capacity of annual crop plants tends to increase with the season until the plants mature after which it tends to decrease very rapidly. Thus, the aphid carrying capacity of trees tends to be high in spring and autumn and low in summer, whereas that particularly of short-season annual crops tends to be low early in a year, peaking mid year and then declining.

A lot is known about the biology of the parthenogenetic generations of aphids, in particular the optimum behaviour for maximising the instantaneous population growth rate, r_m, under various environmental conditions (Kindlmann and Dixon 1989, 1992; Kindlmann et al. 1992) and the optimal strategies for migration (Dixon et al. 1993a). An individual-based model (Kindlmann and Dixon 1996), which incorporates the biology of tree-dwelling aphids, simulated most of the observed features of the population dynamics. It provided a theoretical background for the commonly observed phenomenon that the larger the numbers are at the beginning of a season, the larger and earlier the peak. Migration was shown to be the most important factor determining the summer decline in abundance, while changes in aphid size and food quality account for why the autumnal increase is less steep than in spring. Finally, the model suggests the possibility of a "see-saw effect" (a negative correlation between spring and autumn peak numbers) in some cases, a phenomenon observed in census data (Dixon 1970, 1971).

The regularity of the population fluctuations of the sycamore aphid from year to year: very regular 2-year cycles, as indicated by suction trap catches, has proved very attractive to modellers, who have applied time series analysis to the data (e.g., Turchin 1990; Turchin and Taylor 1992). The conspicuous cyclicity observed in yearly totals of the number of some species of aphid on trees, however, is mainly due to the cyclicity in the peak numbers in spring, which are closely correlated with the yearly totals. It is driven by the inverse relationship between the size of the spring peak and the autumnal rate of increase, the "see-saw effect" (Kindlmann and Dixon 1992). This effect is present in some (Dixon 1971), but not present or very weak in other (Dixon and Kindlmann 1998) empirical data. In *Drepanosiphum platanoidis* (sycamore aphid), where the total numbers on the host tree are relatively constant from year to year, there is a within year see-saw in abundance of aphids in spring and autumn. As most of the aphids that migrate over long distances, rather than between trees, do so in autumn, the result is the 2-year cycles observed in the suction trap catches (Dixon and Kindlmann 1998). Time series and correlation

analyses reveal that the spring and late autumn dynamics are often predictable, but not those observed in summer, as the size of the spring peak is not transferred into summer numbers of aphids (Kindlmann and Dixon 1992).

It is argued that aphid population density is regulated by density-dependent processes acting within years, which is reflected in the year-to-year changes in overall abundance (Sequeira and Dixon 1997). Some results suggest a curvilinear density dependence, with strong density-dependent regulation at low densities, and weak at high densities (Jarošík and Dixon 1999).

1.2.2 Biology of Natural Enemies Relevant to Aphid Population Dynamics

Aphidophagous predators, like ladybirds, hoverflies and lacewings commonly occur in agricultural crops, on herbaceous plants and trees. As many feed on aphid pests, their efficiency in controlling them is a widely discussed and controversial issue. Their aphid prey live in colonies, which are characterized by an initial rapid increase followed by an equally rapid decline in abundance resulting in extinction of the colony. The decline is not caused by aphid predators or parasites, even if they contribute to it. Instead, aphids cause the decline: they strongly react to their own density by switching to producing migrants, which disperse and search for another, more suitable host. Thus, when aphid density is high, most of the newborn leave immediately after they mature.

Aphid colonies are characterised by rapid increases and declines in abundance (Dixon 1998), which are not synchronized in time, as the aphids feed on different host plants with different phenologies (Galecka 1966, 1977). On a large spatial scale, at any instant, populations of aphids exist as patches of prey, associated with patches of good host plant quality (Kareiva 1990). That is, aphid predators exploit patches of prey that vary greatly in quality both spatially and temporally and therefore have evolved suitable strategies for effective exploiting this resource.

The adult aphid predator is winged, can easily move between patches of prey, and therefore can find suitable patches of prey. Its immature stages are confined to one patch and if this contains few prey items, the larvae starve and eat each other. Mortality of immature stages due to starvation, cannibalism or intraguild predation is enormous: 98–99% (Osawa 1993; Hironori and Katsuhiro 1997) and is mainly a consequence of low prey numbers that can occur at any time during larval development. Thus egg and larval cannibalism is adaptive, as by eating conspecifics larvae of predators increase their likelihood of survival (Agarwala and Dixon 1992, 1993).

From an evolutionary perspective, both predator and prey species strive to maximize their own reproductive potentials or, more strictly, their genetic fitness. However, whilst prey can exist perfectly well in the absence of predators, predators *require* prey. Therefore, it is in the predator's interest to practice *conservation*. The optimal strategy of the predator then involves the counteracting pressures to

maximize its own reproduction and survival, usually through the use of efficient hunting tactics, and yet conserve enough prey for its offspring (Berryman and Kindlmann 2008).

This is nicely exemplified by the case of long-lived insect predators feeding on short-lived prey. As most of these predators suffer an enormous egg and larval mortality due to cannibalism and intraguild predation, selection acts mainly on optimizing their oviposition strategies in terms of maximizing the likelihood that the offspring will survive until reproductive age. The oviposition strategy of a predator with a long larval developmental time relative to that of its prey depends on a longer projection of the future prey abundance in the patch, and therefore the possibility of experiencing more bottlenecks or a higher probability of a bottleneck in prey abundance than a predator with a short developmental time, and consequently must be more conservative in terms of preserving their prey (the "GTR hypothesis"). This "GTR hypothesis" seems to hold more generally and those interested in more details are referred to Kindlmann and Dixon (1999, 2001) and references therein.

Because of the immense egg and larval mortality, selection acts mainly on optimum oviposition strategies – those that insure the maximum likelihood of survival of the offspring – rather than maximization of the food eaten by the predator per unit time, as is assumed to be the case in most optimum foraging theories (Stephens and Krebs 1986). The optimum oviposition strategy of the adult is therefore determined mainly by expectations of future bottlenecks in prey abundance, as these will affect survival of its offspring, and not by the present amount of prey in the patch, as the adult is not limited by the amount of food in the patch as it can find another colony, if needed.

Aphid predators are a good example of the GTR hypothesis, as their developmental time often spans several aphid generations, during which the aphid numbers vary dramatically. Laying eggs in the presence of conspecific larvae is strongly selected against in these predators, because it results in these eggs being eaten by older conspecific larvae. In addition, laying eggs late in the development of an ephemeral patch of prey is maladaptive, as there is insufficient time for the larvae to complete their development. Thus, eggs laid by predators late in the existence of a patch of prey are at a disadvantage, as they are highly likely to be eaten by larvae of predators that hatch from the first eggs to be laid.

The GTR hypothesis is strongly supported by recent empirical results: Mills (2006) and Mills and Latham (2009) show that generation time ratio is an important life history trait that could substantially improve the impact of natural enemies in biological control. They conclude that a small generation time ratio (coupled with a broad window of host attack) can facilitate the suppression of pest abundance by parasitoids, and is positively associated with success in biological control.

Empirical data also indicate that several different species of aphid predators have evolved mechanisms that enable them to oviposit preferentially in patches of prey that are in an early stage of development and avoid those that are already being attacked by larvae (Hemptinne et al. 1992, 1993, 2001). Females of these species strongly react to the larval tracks of their own species or of other aphid predators by immediately ceasing oviposition and flying away from the aphid colony. This

response strongly reduces the number of eggs laid per patch and in combination with density dependent cannibalism their effectiveness in regulating the numbers of their prey – aphids. Thus their optimum oviposition strategy, which maximizes the fitness of the individual, results in conserving their prey (or low impact on its numbers), exactly as stated above. Note that for evolution of this strategy no group selection is needed.

Thus oviposition commonly occurs only during a short "egg window", early in the existence of each patch of prey (Hemptinne et al. 1992). When predators are abundant and suitable patches of prey are rare, however, many eggs may nevertheless be laid in a patch during the "egg window". In such circumstances, strong density-dependent cannibalism (Mills 1982) greatly reduces the abundance of the predators relative to that of their prey. Therefore these predators have little impact on aphid population dynamics (Dixon 1992; Kindlmann and Dixon 1993, 1999; Dixon et al. 1995). However, they may nevertheless have short-term impact on local populations, valuable to farmers. The results of an international study of *M. persicae* populations on potato, carried out by 16 workers over 2 years in 10 countries (Mackauer and Way 1976), indicate that the aphid population increased regardless of predator presence, and the latter only affected reductions at times when the potential rate of increase of the aphids was low.

Hymenopterous parasitoids can mature on one aphid and would appear to be potentially more likely to regulate aphid abundance. However, their effectiveness is often reduced by: (1) their longer developmental time relative to their host, (2) the action of hyperparasitoids which, in many cases, are less specific than the primary parasitoids and (3) their vulnerability to attacks from aphid predators (Dixon and Russel 1972; Hamilton 1973, 1974; Holler et al. 1993; Mackauer and Völkl 1993). In addition, because of the risk of hyperparasitism, primary parasitoids are likely to cease ovipositing in a patch where many aphids are already parasitized, as high levels of primary parasitism make the patch attractive to hyperparasitoids. By continuing to oviposit in patches of aphids already attacked by conspecifics these natural enemies may reduce their potential fitness (Ayal and Green 1993; Kindlmann and Dixon 1993).

In the initial phase of aphid population increase on annual arable crops such as spring-sown cereals, there is often a slight dip or plateau followed by sudden acceleration. This is attributed to the activity of polyphagous predators (mainly carabid beetles, spiders and earwigs), and referred to as the "natural enemy ravine" by Southwood and Comins (1976). They suggested that the outcome of a spring invasion of aphids is often determined by the balance between the number of invaders and the size of the autochthonous population of polyphagous predators. Carter and Dixon (1981) offered an alternative explanation: the lack of population growth in the initial phase of the population dynamics was attributed to the intermittent nature of aphid immigration, which is amplified by the pre-reproductive period of the offspring of the immigrant aphids. However, it is more likely that the ravine in population dynamics is a consequence of not being able to detect population increase at low population density using small sample sizes (Jarošík et al. 2003). Small sample sizes were used in the studies cited by Southwood and Comins (1976) as evidence

for a natural enemy ravine. In the study of Smith and Hagen (1959) it was 200 alfalfa stems. In that of van Emden (1965) it was 90 mustard plants. Wratten (1975) used 30 stems of wheat. The study of Carter and Dixon (1981), in which an alternative explanation for the ravine was proposed, was also based on small sample sizes, with the maximum sample size of 600 tillers of winter wheat. Honěk and Jarošík (2000) and Honěk et al. (2003) also found no evidence that polyphagous predators affect cereal aphid population dynamics in the field. In the habitat they studied, carabid beetles were the dominant guild of polyphagous predators. However, these carabids are mainly seed predators (Honěk et al. 2003), and their activity was only loosely correlated with aphid density (Honěk and Jarošík 2000). In addition, aphids have a low nutritional value and are not a preferred food of carabids (Bilde and Toft 1999). However, in many crops other than cereals, there is a clear mid-season trough in aphid density between an early and a late peak similar to that which occurs on trees.

1.2.3 Assessment of the Efficiency of Natural Enemies to Suppress the Abundance of Their Prey

Exclusion techniques, such as cages, are the most frequently used means of evaluating the efficiency of natural enemies to suppress the abundance of their prey (Luck et al. 1988). The growth rates and peak densities of aphid populations within cages that exclude natural enemies are usually larger than those in uncaged populations (e.g., Chambers et al. 1983; Elliott and Kieckhefer 2000; Michels et al. 2001; Basky 2003; Cardinale et al. 2003; Schmidt et al. 2003). However, cages change the microenvironment (Hand and Keaster 1967), especially temperature, which is thought to be important in determining the outcome of predator-prey interactions (Frazer and Gilbert 1976; Frazer et al. 1981). This by itself makes the results of cage experiments suspect.

Attempts to avoid the change in the microenvironment by using cages with a large (8 mm) mesh size (Schmidt et al. 2003) do not reduce predator densities within cages and are therefore completely useless for measuring the effect of predators on aphid populations as there are the same numbers of predators inside cages as in un-caged plots (Kindlmann 2010).

Even more importantly, cages prevent aphids from emigrating, which is their usual response to high density (Dixon 1998, 2005). Gardiner et al. (2009) show that after 14 days of caging there are an average of 20.7±1.4 alates per plant within exclusion cages but only 1.8±0.1 alates per plant in un-caged plots. Interestingly, when only polythene enclosures, 60 cm high, buried to a depth of 30 cm, and not cages, were used (Holland et al. 1996), which do not affect the microenvironment of the manipulated plots, allow aphids to emigrate, but exclude ground predators, there was no difference in the number of grain aphids in control plots and those where the number of ground predators were reduced.

Bearing in mind the above, it is therefore really surprising that despite this crystal clear evidence that cage exclusion experiments cannot be used for assessment of

predator effectiveness in reducing aphid population growth, they are still used for this purpose and such flawed results are presented as proof of their effectiveness. Other, objective methods of assessing the effectiveness of natural enemies in reducing the abundance of their prey, like removing the predators (Kindlmann et al. 2005) or direct observations like those in Costamagna and Landis (2007), are rare – most likely because they are much more time consuming.

1.3 Theory of Aphid Population Dynamics

1.3.1 Features of Aphid Population Dynamics that Should Be Incorporated in Models

If it is accepted that natural enemies do not regulate aphid populations, the modelling process is greatly simplified. The important features of any model are:

- Each year aphids show an initial dramatic increase in population size.
- This increase is typically followed by a steep decline in abundance.
- Sometimes there is a further increase in abundance.
- Migration is the most important factor determining the decline in abundance.
- Within season aphid dynamics often show a "see-saw effect" – a negative correlation between initial and final peak numbers.
- The greater the initial aphid numbers, the larger and earlier the peak.
- Very regular 2-year cycles are characteristic of aphid between-year population dynamics.
- Aphid population density is regulated by density-dependent processes acting within years, which can be potentially strong at low densities.
- Long term aphid dynamics appear to be little affected by the activity of insect natural enemies.

Here we present a recent metapopulation model of the dynamics of aphids and their predators that satisfies all the above assumptions, which was published by Houdková and Kindlmann (2006), extended by Houdková and Kindlmann (2010) and possibly represents the state-of-the-art in modelling population dynamics of aphids and their predators.

1.3.2 The Metapopulation 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. This 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.

1.3.2.1 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 individual prey arrive in the patches only at the beginning of a season and do not migrate between plants. The summer aphid populations are established by parthenogenetic females that emigrate from a winter host-plant, so there is no relationship between numbers of aphids this year and last year on one particular plant. The fundatrices land on plants at random and start to reproduce with a constant growth rate, R. 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 $Emean = 20$, and standard deviation $Esd = 2$. In every step (one flight – we assume several 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 and 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 a *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 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 deemed 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. Any eggs that may be laid later and any resultant larvae are unlikely to survive, for the reasons cited above, and are therefore not included in this simulation. The final numbers of prey and predators at the end of the egg-window are used in the within-season dynamics model.