University of South Bohemia
Faculty of Science

Trends in insect biodiversity in a changing world

Ph.D. Thesis

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Annotation:

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In this thesis I investigated various factors that might affect species diversity and the relations between predator/parasitoid and host, using mainly insects as a model group. These factors were agricultural practices, landscape composition, climate change and invasive species.

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Declaration – Prohlášení

I hereby declare that I worked out this Ph.D. thesis on my own, or in collaboration with the co-authors of the presented papers and manuscript, and only using the cited literature.

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It is not the strongest of the species that survives, nor the most intelligent that survives.
But rather the one most adaptable to change.

Clarence Darrow

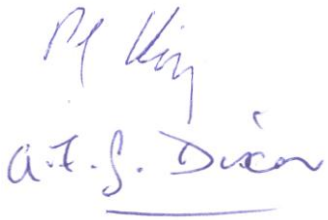
Author contribution statement

Olga M. C. C. Ameixa, author of this Ph.D. thesis, is the first author of tree papers (manuscripts) and two chapters in two books, the second and fourth author in two papers, respectively and has written a substantial part of these. Most of the raw data processing, as well as most of the statistical analyses were performed by her.

Pavel Kindlmann participated in all the papers and as supervisor helped with all necessary things. Anthony Dixon participated in "Ecological effects of invasive alien species on native communities, with particular emphasis on the interactions between aphids and ladybirds" (Paper II) and in "Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe" (Paper IV). Alois Honek and Zdenka Martinkova participated in "Position of *Harmonia axyridis* in aphidophagous guilds in the Czech Republic" (Paper III) and provided the raw data and advice regarding the ecology of ladybird species in "Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe" (Paper IV).

All co-authors hereby consent the publication of the papers in the PhD. thesis of Olga Ameixa and support it by their signatures:

Pavel Kindlmann

Anthony Dixon 

Alois Honek 

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TABLE OF CONTENTS

GENERAL INTRODUCTION

Extinction is a natural process, nowadays occurring at an unnaturally rapid rate as a consequence of human activities. We have already caused extinction of 5–20% of the species in many groups of organisms, and current rates of extinction are estimated to be 100–1,000 times greater than the pre-human rates (Lawton & May, 1995, Pimm et al., 1995). Some of the major threats to native biodiversity include agricultural intensification, habitat loss and introduction of exotic species (Wilcove et al., 1998).

Insects constitute a substantial proportion of terrestrial species richness and biomass, and play a significant role in ecosystem functioning (McGeogh, 1998). Although the number of described insect species is uncertain due to synonyms and lack of a global list, most authorities recognize 900000–1000000 named morpho-species, representing 56% of all species known on Earth (Groombridge, 1992, Anon, 2003). Sensible estimates of the number of insects yet to be discovered range from another 1 million to 30 million species (Erwin, 1982, 1991), although most of them predict around 2–8 million yet undiscovered species (May, 1990, Gaston, 1991, Stork, 1997, Ødegaard, 2000).

Biodiversity and agricultural practices

Agroecosystems include a large proportion of the world's biodiversity (Pimentel et al., 1992). For this reason, insects that inhabit agricultural land can be used as indicators of the disturbance associated with these environments.

Insects are frequently used as bioindicator species for monitoring and detecting changes in the environment. By using bioindicators it is possible to assess the impact of human activities on the biota, instead of examining the entire biota. Especially useful are species that provide early warning of change (Spellerberg, 1993).

Carabid beetles have been used as indicators in terms of how well they represent broader ecological responses to disturbances, since they are extremely sensitive to pH and humidity balance, as well as to toxic substances (agrochemicals). Changes in morphological characteristics of organisms have been used successfully as indicators of habitat quality and disturbance (Lagisz, 2008). This applies to carabids; their

characteristics are usually revealing their life strategies. Generally, small and winged carabids are present in more disturbed habitats, whereas large, apterous carabids are only present in non-disturbed areas. Environmental changes can cause changes in species numbers of indicator species, in abundance of individual species, or their physiological changes (Rainio & Niemelä, 2003). Increase or decrease of species number or abundance can be caused directly by changes in abiotic and/or biotic factors (Blake et al., 1996) or indirectly by changes of assemblages of other species (Haila et al., 1994).

Biodiversity and global change

Climatic changes may also affect insect diversity and subsequently jeopardize the services provided by ecosystems, such as pollination of crops or pest control by predators. These changes affect not only the interactions between insects and plants, but also whole natural and agricultural ecosystems (Körner, 2000, Theurillat & Guisan, 2001). Even with some contrasting results, some studies indicate that current changes, especially the elevated concentrations of O_3 and CO_2 (IPCC, 2001), may affect the performance (e.g., growth and fecundity) and population dynamics of aphids (Holopainen, 2002, Percy et al., 2002 , Awmack et al., 2004).

Aphids are a good model for studying the effects of environmental change, since they have short life cycles, several generations per year and high fecundity (Dixon, 1985).

Biodiversity and invasive species

The introduction of a new organism into a new environment can have a significant effect on species conservation, since it is in itself a form of contamination (De Clercq et al., 2011, Elliott et al., 1996) and it is considered to be one of the major threats to native biodiversity (Wilcove et al., 1998). The introduction of exotic natural enemies with the purpose of reducing pest populations below levels at which they can cause economic injury to crops has gained a special place in crop management and has been one of the contributing factors for the establishment of exotic species. Recently, the ladybird, *Harmonia axyridis* (Pallas), has caused concern in some countries. It is native to Asia,

introduced several times into USA and more recently also to European countries, mainly for biological control of aphids (Koch, 2003, Roy & Wajnberg, 2008). It is currently the commonest invasive coccinellid in the US and Canada (Harmon et al., 2007).

However, the risks associated with invasive alien pests (e.g., widespread establishment or ecological effect) are difficult to quantify, as they involve interactions between factors operating across a range of spatial and temporal scales, such as the population dynamics of an invader, environmental conditions in the invaded region and the status of potential dispersal pathways (Barney & Whitlow, 2008).

Biodiversity and landscape changes

There is accumulating evidence that changes in land use, in combination with high agrochemical input in crop fields, are the primary causes for the rapid decrease of biodiversity in many of these landscapes (Robinson & Sutherland, 2002, Benton et al., 2003). Most imperilled species, however, face more than one threat, and it is difficult to disentangle proximate and ultimate causes of their decline or interactions between different threats and evaluate their relative importance (Gurevitch & Padilla, 2004). Land-use change is projected to have the largest global impact on biodiversity, followed by climate change, nitrogen deposition, species introductions and changing concentrations of atmospheric CO_2 (Sala et al., 2000).

Services provided by biodiversity – biological control

An important ecosystem function that has been associated with biodiversity is natural pest control (Ives et al., 2000, Wilby & Thomas, 2002). The suppression of pest populations in crops by natural enemies provides environmental and economic benefits, because it may reduce yield loss without causing any negative environmental consequences that normally result from using chemical pesticides (Naylor & Ehrlich, 1997 , Östman et al., 2003).

However, for a successful biological control, a good knowledge of the behaviour and ecology of natural enemies and pest species is necessary: sometimes the introduction of an exotic organism has worse consequences than the pest itself.

Parasitoids and predators of herbivores have evolved and function within a multitrophic context. Consequently, their physiology and behaviour are affected by elements from other trophic levels, such as their herbivore victim (second trophic level) and its plant food (first trophic level) (Price et al., 1980). Natural enemies base their foraging decisions on information from these different trophic levels, and chemical information plays an important role. While communicating intraspecifically through pheromones, herbivores are often much more conspicuous to their natural enemies that exploit these pheromones as kairomones in long-distance herbivore location (Haynes & Birch, 1985).

SCOPE OF THE THESIS

In this thesis I investigated various factors that might affect species diversity and the relations between predator/parasitoid and host, using mainly insects as a model group. These factors were agricultural practices, landscape composition, climate change and invasive species.

In **Paper I,** the effect of agricultural practices on biocontrol services provided by carabid diversity was determined by collecting data in 150 fields (30 farms, 5 fields per farm) distributed along the agricultural intensification gradient, based on the amount of fertilizers applied per hectare. The proportion of aphids glued on labels and exposed in the field, which were eaten by insect predators per unit time ("biocontrol potential") was the response variable and correlations between intensity of agricultural exploitation, predator abundance and biocontrol potential were calculated.

In **Paper II,** a meta-analysis of published results was performed in order to determine, how intensification of agriculture and landscape composition affect diversity of four different taxa (birds, arthropods, mammals and plants).

Paper III addresses the question, how global warming is likely to affect aphid species population dynamics.

Paper IV presents an analysis of the degree of dominance of the invasive species named above, *Harmonia axyridis*, within aphidophagous guilds and of its association with particular habitats. The affinity of different ladybird species towards a number of habitats studied was assessed using the Canonical Correspondence Analysis.

Paper V concentrates on the ecological effects of invasive insect predators that feed on pest insects, since the former may potentially affect the biological control of the latter.

Paper VI presents a long-term study of coccinellid communities and an attempt to determine, whether recent changes in climate and agriculture have affected their composition. Coccinellids were sampled in cereal crops, on wild herbaceous plants and on deciduous trees.

Paper VII presents a contribution to our knowledge of rules governing one of the services provided by biodiversity – biological control. Here it was investigated, how

parasitoids locate their hosts, that is, the response of the aphid parasitoid, *Aphidius colemani*, to a mixture of odours of synthetic and plant-extracted nepetalactone (a component of aphid sex pheromone) and to (E)-*β*-farnesene (aphid alarm pheromone).

SUMMARY OF RESULTS AND DISCUSSION

No correlation was found between nitrogen input in the field and predator biocontrol potential, measured as the proportion of glued aphids remaining untouched after a fixed period of exposure in the field. Significant positive correlations were found between the numbers of glued aphids remaining and the height of the tillers, between the numbers of glued aphids remaining and weed abundance and between the numbers of glued aphids remaining and the average altitude of the farm. One of the most surprising results was the positive correlation between the numbers of glued aphids remaining and the number of carabids captured in the pitfall traps. Also in multiple linear regression, height of tillers and average altitude of the farm were significant as explanatory variables. For the diversity and density of ground-living predators, no significant correlations were found between the number of carabids and the number of tillers, between the number of carabids and the height of tillers, between the number of carabids and the number of aphids remaining and between the number of carabids and weed abundance. The average nitrogen input per farm over the last 4 years and the average input of nitrogen per wheat field were negatively, but also not significantly correlated with the average number of carabids captured. However, there was a significant increase of the number of carabids per field with increase in altitude. In the multiple linear regression, only the number of aphids remaining was the sole significant explanatory variable. Regarding the surrounding landscape, there were no significant differences between the average numbers of carabids caught in fields close to different types of habitats. The study of the relation between the surrounding landscape and the number of carabids caught revealed that there was a significant positive association between the presence of human settlements close to the field and the number of carabids caught, but not between the presence of a forest close to the field or a water surface and the number of carabids caught **(Paper I)**.

The results from the first study were not straightforward regarding the question, whether agricultural intensification reduces biodiversity in agricultural fields or not. For this reason, a meta-analysis was performed **(Paper II),** in which results obtained in different studies were compared using 4 different taxa (birds, invertebrates, mammals and plants). The results did not show a clear pattern for any of the taxa regarding the association with intensification of agriculture. However, there were significantly more

papers claiming a positive effect of landscape structure on biodiversity of invertebrates, compared with the other groups of organisms studied.

In **Paper III** a review of several published works on the effect of global change parameters and the performance of aphids was made. The results were contradictory, indicating positive, negative or no effects. However, it is known that in the past there were periods of climate instability, during which there were dramatic and fast climate changes. Therefore, paleontological data can provide a good idea of how insects have responded to previous climatic changes. There is some evidence that aphids are capable of adapting to climate change because fossil ones are often still extant, which indicates that extreme climatic events in the past did not always result in major evolutionary changes or extinction. The evidence indicates that aphids are most likely to move to different geographical locations in order to track more suitable conditions, which may be more difficult than in the past because of habitat fragmentation and habitat loss.

In **Paper IV,** the analysis of the degree of dominance of the invasive ladybird *Harmonia axyridis* within aphidophagous guilds and of its association with particular habitats in the year 2008 showed that *H. axyridis* became one of the most abundant species only three years after its establishment in the Czech Republic, especially in trees and shrubs.

In **Paper V,** the literature search shows that the colonization of patches of prey by invasive species may induce native predators to leave, but the evidence that invaders negatively affect the abundance of the native species was scarce and not persuasive. The reason may be that insect predators do not substantially affect the abundance of their prey, if the ratio of generation time of the predator to that of the prey is large, therefore the effect of invasion by long-lived alien predators on systems consisting of long-lived native predators and short-lived prey on the abundance of the prey is hard to detect.

Paper VI shows that over a period of 35 years, the compositions of the communities remained essentially similar. Only a few species, associated with particular types of vegetation, significantly differed in abundance in the first and second period. There was no obvious cause of this variation in abundance. The diversity of coccinellid communities was higher in the second period, although the number of individuals was lower. The arrival of the exotic *H. axyridis* (in 2006) has not yet resulted in any significant changes in communities of native coccinellids in Central Europe.

Paper VII shows that parasitoid females were significantly attracted by the semiochemicals, when their concentrations were high, in which case the females spent more time in squares with the semiochemicals. The majority of females preferred plant-extracted nepetalactone, when it was in high concentration, but they consistently did not respond to (E)-*β*-farnesene.

GENERAL CONCLUSIONS

Undoubtedly, biodiversity is declining at a global scale. However, the tendency to isolate the possible underlying factors that generate this decline may prevent us to see possible synergistic interactions between them.

It is clear that agro-chemicals and tillage can be very disturbing for life forms that use agricultural lands as habitats. However, at least in Europe, some lands have been cultivated for more than 2000 years, so organisms that inhabit these must be adapted to the constant changes and disturbances. Therefore, the lack of correlations between diversity and agricultural practices should be taken with caution.

In a fragmented landscape and with smaller suitable habitats, aphids will have a difficult task when facing global change. However not all species will respond in the same way. Finding suitable hosts may be easier for aphids, which are agricultural pests, because they are usually polyphagous, while non-pest aphid species usually only exploit one or two plant hosts. Also species with lower capacity of dispersion, like apterous ones, will have more difficulties in tracking suitable habitats.

Harmonia axyridis has been denominated as the most invasive ladybird species in the world, therefore it is not surprising that it has become one of the most abundant species only three years after its establishment in the Czech Republic. This species uses preferentially trees and shrubs as habitats. However, the impact of this species on the native communities requires more studies and careful analyses, since other factors, like changes in climate and agriculture practices may affect native ecosystems more strongly than the invasive species.

Biological control is one of the services provided by biodiversity that is fundamental for mankind. However, an effective biocontrol programme involves the knowledge of the basic behavioural responses of the agent used. In parasitoids, the location of a suitable host determines a successful control of the pest to be suppressed. The parasitoids responded more strongly to plant-extracted nepetalactone, when it was in high concentration, but they consistently did not respond to (E)-β-farnesene. The fact that (E)-β-farnesene, consistently did not cause a response from parasitoid females may be because this pheromone is a less specific cue, that is, it is also released by some plants when attacked by herbivorous insects. Therefore parasitoids can use the background of volatiles emitted by the plant host together with (E)-β-farnesene or the type of emission

(emission in pulses typical for attacked aphids rather than continuous emission typical for damaged plants) as cues when looking for a suitable host.

The value of biodiversity is unquestionable, and the ecological consequences of its decline should be minimized in order to preserve options for future solutions for the coming generations.

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ABSTRACTS OF THE PAPERS

Paper I

AMEIXA, O.M.C.C. AND KINDLMANN, P. (2008). Agricultural policy-induced landscape changes: effects on carabid abundance and their biocontrol potential. *European Journal of Entomology* 105: 467-476.

One of the most important services provided by biodiversity is thought to be the biological control of pests in agricultural landscapes, including aphids on cereals. The food webs potentially contributing to biological control of aphids primarily consist of polyphagous predators, parasitoids and pathogens. The problems of aphid pests have increased greatly since the 1970-ies, possibly as an effect of agricultural intensification, which is thought to have reduced diversity and abundance of these predators and parasites and consequently their biocontrol potential. The main objective of this study was to test this by measuring this potential for biological control of aphids, and relate it to agricultural intensification and predator abundance. We selected 30 farms distributed along agricultural intensification gradients, based on the amount of fertilizers applied per hectare. Estimates of ground-living predator density were obtained using pitfall trapping over a one-week period. Traps were placed inside the cereal fields, 10 m from the margin, in 2 replicates per field. Predation risk due to ground-living predators (biocontrol potential) was estimated by monitoring removal of aphids glued to labels. This was done in the same fields, in the immediate vicinity of the traps, over a period of 2 days. The proportion of aphids eaten per unit time was the response variable. We present the correlations between intensity of agricultural exploitation, predator abundance and biocontrol potential. The outcomes are not straightforward in that intensification begets a reduction in predator density and biocontrol potential. We discuss the potential confounding issues that might have affected our results.

Key words: Agricultural intensification, biocontrol, density, diversity, species richness, food webs, predatory pressure

Paper II

AMEIXA, O.M.C.C. AND KINDLMANN, P. (2011). Biodiversity drifts in agricultural landscapes In: Gianfranco Venora, Oscar Grillo, J. López-Pujol, [eds.], *Biodiversity*, Intech, submitted

Since the publication of one of the most influential books of the twentieth century, "Silent Spring" by Rachel Carson, mankind has become aware of the potential dangers of the exposure to pesticides and destruction of wildlife through their widespread use. Pesticides are just the tip of the iceberg when we speak about agricultural intensification. Several studies and meta-analyses have been conducted since, with the sole purpose of finding a correspondence between the decline in biodiversity and agricultural intensification. They are, however, often inconclusive and contradictory: some data suggest a negative and other data no or even a positive relationship between agricultural practices and biodiversity. Here we analyze possible reasons for this discrepancy. We conclude that (1) the results strongly depend on the taxon studied, and (2) after years of intensive land use, it is not possible to expect a rapid response of biodiversity to environmentally-friendly changes in agricultural practices, even if these might lead to an increase in biodiversity in the long-run.

Key-words: Agroecosystems, biodiversity, agricultural intensification, organic farming, sustainable development

Paper III

AMEIXA, O.M.C.C. (2010). Aphids in Changing World, pp. 21-40. In P. Kindmann, A.F.G. Dixon and J.P. Michaud [eds.], *Aphid biodiversity under Environmental Change*. Springer, Dordrecht.

When in 1824 the French mathematician Jean Baptiste Joseph Fourier suggested that the Earth's temperature was slowly increasing it was not readily accepted. Some years later Svante Arrhenius (1896) and Guy Callendar (1938) sup- ported this hypothesis and added that the planet's temperature is increasing due to man's activities, in particular the production of CO2, which has a crucial role in this matter. Several authors question how global warming is going to affect the planet and life forms. This question is addressed here, in particular how it is likely to influence aphids. Will they move to different locations, adapt to the change in conditions in their current habitat or go extinct? An analysis of the literature on the reactions to the sort of changes aphids will be exposed to in global change scenarios revealed that the results are contradictory, indicating positive, negative or no effect. The consensus is that it is extremely difficult to do experiments that simulate future conditions, especially when more than one parameter is considered. Nevertheless, the paleontological data provide a good record of how insects have responded to previous climatic changes. The evidence indicates that aphids are most likely to move to different geographical locations in order to track more suitable conditions, which may be more difficult than in the past because of habitat fragmentation and habitat loss.

Key words: Aphids, Climate change, Adaptation, Behaviour, Host plant, Population dynamics, Extinction, Distribution, Trophic interactions.

Paper IV

AMEIXA, O.M.C.C., HONĚK, A., MARTINKOVA, Z. AND KINDLMANN, P. (2010). Position of *Harmonia axyridis* in aphidophagous guilds in the Czech Republic. *IOBC Bulletin* 58: 7-14.

Harmonia axyridis was first recorded in the Czech Republic in 2006. Here we present an analysis of its degree of dominance within aphidophagous guilds and of its association with particular habitats in 2008. The dominance affinity of different ladybird species towards the habitats where they were found was studied using Canonical Correspondence Analysis (CCA). The biplot shows a clear invasive pattern in the year studied. In the present study, *H. axyridis* was one of the most abundant ladybirds, especially in trees and shrubs. Although it is too early to make firm conclusions about the role that this ladybird has on the native communities, it is worrying that it became one of the most abundant species only three years after its establishment in the Czech Republic.

Key words: *Harmonia axyridis*, diversity, abundance, habitat affinity, generation time

Paper V

KINDMANN P., AMEIXA, O.M.C.C. AND DIXON, A.F.G. (2011). Ecological effects of invasive alien species on native communities, with particular emphasis on the interactions between aphids and ladybirds. *Biocontrol* (In Press)

The ecological effects of introduced species on native organisms can sometimes, but not always be significant. The risks associated with invasive alien pests are difficult to quantify. This paper concentrates on the ecological effects of invasive insect predators that feed on pest insects, because the former may potentially affect the biological control of the latter. The literature indicates that invasive predatory insects generally are resistant to changes in environmental conditions, long-lived and voracious with a high reproductive rate, high dispersal ability, able to spread very rapidly across landscapes and exhibit phenotypic plasticity. Their colonization of patches of prey may induce native predators to leave, but the evidence that invaders negatively affect the abundance of the native species is scarce and not persuasive. Insect predators do not substantially affect the abundance of their prey, if the ratio of generation time of the predator to that of the prey is large (the generation time ratio hypothesis), therefore the effect of an invasion by long-lived alien predators on systems consisting of long-lived native predators and short-lived prey on the abundance of the prey is hard to detect.

Key words: invasive alien species, predators, insect pests, ecological effects, intraguild predation

Paper VI

HONEK, A., MARTINKOVA, Z., KINDLMANN, P., AMEIXA, O.M.C.C. AND DIXON, A.F.G. (2011). Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe. submitted to *Environmental Entomology*

In northern temperate zones, aphidophagous coccinellids (Coleoptera: Coccinellidae) are important components of the fauna. They are well studied because they are abundant, easy to sample and identify. Here the results of a long-term study of coccinellid communities and an attempt to determine whether recent changes in climate and agriculture have affected their composition are reported. Coccinellids were sampled in cereal crops, on wild herbaceous plants and deciduous trees during two periods (1976-1983 and 2002-2010). There are similar species-rich communities of coccinellids on trees and wild herbaceous plants and a poorer community on cereals. Over the 35 years of this study, the compositions of the communities remained essentially similar. Only a few species, associated with particular types of vegetation, significantly differed in their absolute abundance in the first and second period. There was no obvious cause of this variation in abundance. Diversity of coccinellid communities was higher in the second period, although the number of individuals was lower. The arrival of the exotic Harmonia axyridis (in 2006) has not yet resulted in any significant changes in communities of native coccinellids in Central Europe.

Key words: Coccinelids, communities, aphidophagous, biotope, abundance, diversity, *Harmonia axyridis*.

Paper VII

AMEIXA, O. M. C. C. AND KINDLMANN, P. (2011). Effect of synthetic and plant-extracted aphid pheromones on the behavior of *Aphidius colemani*. *Journal of Applied Entomology*, DOI: 10.1111/j.1439-0418.2011.01638.x

Parasitoid females use several chemical cues to locate hosts. A better knowledge of how they respond to a complex of these cues in a small range may help us to understand how to manipulate the parasitoids in the field. Here, the response of the aphid parasitoid *Aphidius colemani* to a mixture of odours of synthetic and plant-extracted nepetalactone (a component of aphid sex pheromone) and to (E)-*β*-farnesene (aphid alarm pheromone) was investigated. The behavioural responses of A. colemani to three semiochemical groups with different concentrations were studied in a square arena. Parasitoid females were significantly attracted by the semiochemicals, when their concentrations were high, in which case the females spent more time in squares with semiochemicals. The majority of females preferred plant-extracted nepetalactone, when it was in high concentration, but they consistently did not respond to (E)-*β*-farnesene.

Key words: (E)-*β*-farnesene, *Aphidius colemani*, *Nepeta cataria* oil, synthetic nepetalactone