Atypical phenology of aphids (Aphidoidea) and their ladybird predators (Coccinellidae) arising from fluctuating spring temperatures

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KEY WORDS
Climate change, diet, habitat, specialization, weather

Entomologische Berichten 81 (6): 259-263

April and May 2019 were characterised by strongly fluctuating temperatures in the Dutch provinces of Noord-Brabant and Limburg, which led to changes in aphid populations and the phenology of the ladybirds feeding on them. Aphid species reached high abundances on some herbs and shrubs, but species on some trees were virtually absent. The immediate and reproductive effects on ladybird species were variable. Population sizes at the end of the year suggested that the total reproductive output of generalist ladybirds had been minimally affected, probably due to their broad dietary ranges. However, the fully arboreal *Adalia decempunctata* was much less abundant, likely due to scarcity of its tree-dwelling prey. In 2021, similar spring conditions again resulted in few aphids and ladybirds on trees, suggesting that some of the changes observed in 2019 might become more permanent.

Introduction

There are many field observations and studies showing that populations of aphids and their natural enemies are affected by the weather, especially by temperature (e.g. Dixon 1977, Majerus & Majerus 1996, Meisner *et al.* 2014). In the case of aphidophagous ladybirds, there have been a number of observations from the field linking population explosions to meteorological conditions, including via their effect on prey (Denemark & Losey 2010, Majerus & Majerus 1996, Nalepa *et al.* 1998). However, there are relatively few reports of prey-mediated effects of weather, including temperature, on the phenology of ladybirds. Such observations are generally useful in understanding climatic effects on the ladybird populations, and specifically now to provide insight into they could respond to climate change.

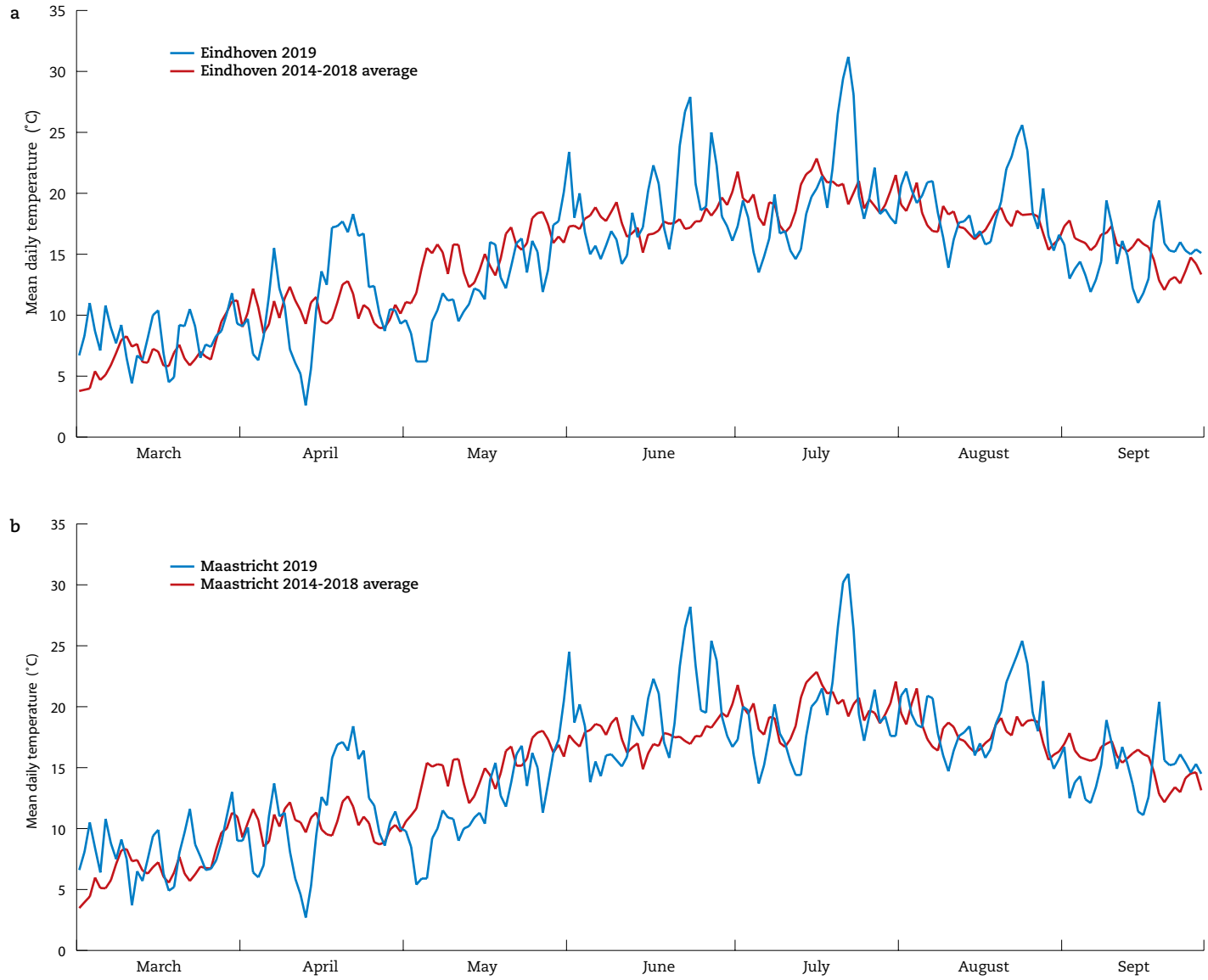
Since 2012, the author has been observing and collecting ladybirds at sites in Eindhoven (province of Noord-Brabant) and Maastricht (province of Limburg), both in the southeast of the Netherlands. The species I most regularly encounter – the natives *Coccinella septempunctata* Linnaeus and *Adalia bipunctata* (Linnaeus), and the invasive *Harmonia axyridis* (Pallas) – have been observed to each follow a similar yearly phenological pattern. *Coccinella septempunctata* reproduces early (April/May) on herbaceous plants, while *A. bipunctata* and *H. axyridis* reproduce in two phases: in later April/May on herbs and shrubs and in May/June on broadleaved trees. In 2019, I observed a notable deviation from the typical situation, most likely as a consequence of temperatures early in the reproductive season of these insects. In this paper I present observations made on these and other ladybird species and their aphid prey over the course of 2019. The observations were made at diverse sites that had been regularly visited over a number of years, but were largely incidental and non-systematic, although in the latter part of the season I carried out several surveys to confirm my observations on aphids and ladybirds on trees.

Temperature and initial phenology

Spring of 2019 was characterized by strong temperature fluctuations, with warmer weather than average punctuated by colder periods. From 10th to 14th April, average daily temperatures declined to less than 3 °C (figure 1) and minimum temperatures were below freezing. By 30th April, both plants and insects in Maastricht were observed to be phenologically about two weeks later compared to most earlier years, in an annual two-day entomology practical course. Temperatures were again considerably lower than average in early May (figure 1).

Aphids and ladybirds on herbs and shrubs

An effect of temperature was observable in aphids feeding on herbs and shrubs in April, but appeared to vary between species. *Aphis sambuci* Linnaeus, on its hostplant elder *Sambucus nigra* exhibited a reproductive delay, with colonies less well developed compared to previous years. By contrast, the rose aphid *Macrosiphum rosae* (Linnaeus) was, if anything, more abundant at the same sites than in previous years. It is possible that *M. rosae* began parthenogenetic reproduction earlier than *A. sambuci*, thus gaining from the early warm weather.



1. Mean daily temperatures from March to September in 2019 (blue line) compared to 2014-2018 means (red line) for (a) Eindhoven and (b) Maastricht. Data from the KNMI (http://projects.knmi.nl/klimatologie/daggegevens/selectie.cgi)
1. Gemiddelde dagtemperatuur van maart tot september in 2019 (blauwe lijn) vergeleken met 2014-2018 gemiddelden (rode lijn) voor (a) Eindhoven en (b) Maastricht. Data van het KNMI (http://projects.knmi.nl/klimatologie/daggegevens/selectie.cgi)

Furthermore, non-host alternating *M. rosae* persist on roses as parthenogenetic adults under milder winter conditions (Hille Ris Lambers 1939, Blackman & Eastop 2000), suggesting that this aphid might be less affected by colder spring conditions than many other aphid species.

Ladybird species also exhibited a variable response. In late April in Maastricht, fourth instar *C. septempunctata* larvae were already observed in a large ornamental rose bed (120 m^2) heavily infested with *M. rosae*, while *H. axyridis* and smaller numbers of *A. bipunctata* had only recently begun to mate and oviposit. It is known that *H. axyridis* reproduces later than *C. septempunctata* in the same aphid-bearing patches (e.g. Jansen & Hautier 2008), but the marked difference suggests that while *C. septempunctata* had reproduced during the warm conditions of early April, the reproduction of *H. axyridis* and *A. bipunctata*, had been further delayed due to the subsequent cold period in mid-April. In turn, it seems probable that this delay might in part explain the excessively high abundance of *M. rosae*, as it would have experienced lower predator pressure than usual early on. The effect on *H. axyridis* was probably more severe than just delayed reproduction, since population sizes of this ladybird appeared to be lower than previous years. This may be explained by higher than usual mortality as a consequence of the April cold period occurring when the ladybirds were already active: cold is known to be life-threatening for active *H. axyridis* (Watanabe 2002).

Initial reductions in predator pressure also could have favoured later-reproducing aphids on herbaceous plants and shrubs, as the effects described for roses appeared to be more widely spread. This was the case for nettle aphids *Microlophium carnosum* (Buckton) specifically: this aphid species reached higher abundances than observed in previous years. At a site in the south of Maastricht, where common nettle *Urtica dioica* grew with other ruderal plants alongside a ditch and adjacent paths, *M. carnosum* was increasing on 30th April, reaching very high abundances by 25th May. The ladybirds *C. septempunctata*, *H. axyridis* (figure 2) and *A. bipunctata* were ultimately attracted to these aphids in considerable numbers and all these species reproduced there. The numbers of *A. bipunctata* were higher than observed in previous years and matched those of *H. axyridis*, which were similar to before. In addition to the high abundance of aphids observed, the absence of aphids occurring

2. *Harmonia axyridis* ovipositing on nettles infested with the aphid *Microlophium carnosum*, in Maastricht (province of Limburg), 21.v.2019. Photo: John Sloggett
2. *Harmonia axyridis* legt eieren op brandnetels geïnfecteerd met bladluis *Microlophium carnosum* in Maastricht (Limburg), 21.v.2019.

on some trees (see below) could have acted to concentrate the partially arboreal *A. bipunctata* and *H. axyridis* on nettles, and other herbs and shrubs. This would explain the higher than usual numbers of *A. bipunctata* on nettles; however, as *H. axyridis* were generally low in number in early 2019 (see above), when concentrated on nettles they only reached similar numbers to earlier years at the same site. By 11th June, aphids and adult ladybirds were declining at the site, though pupae of *H. axyridis* and *A. bipunctata* were present.

Aphids and ladybirds on trees

The most marked effect of spring temperatures appears to have been on aphids and ladybirds on trees, most notably on lime *Tilia* and tulip tree *Liriodendron*. Both are often heavily infested with aphids (*Eucallipterus tiliae* (Linnaeus) and *Illinoia liriodendri* (Monell) respectively) and thus can harbour large numbers of ladybirds, most notably *H. axyridis*, but also *A. bipunctata*. However, in 2019 there were very limited numbers of aphids on both types of tree, most likely due to the low temperatures in early May, limiting aphid population growth (cf. Dixon 1971). On 18th June, a search for ladybirds on lime trees in Maastricht found very few aphids and virtually no ladybirds where both are usually common. Around the same time, a search on tulip trees in central Eindhoven showed that some trees were infested with isolated aphid colonies, but far fewer than usual; there were a few ladybirds and egg clutches present on the trees, but ladybird oviposition petered out much earlier. On 17th July, a single tulip tree in central Maastricht was found to be heavily infested with *I. liriodendri* and to have many *H. axyridis* pupal skins and young adults on it, but this was at least two weeks later than normal. Additional surveys of limes and tulip trees were carried out in July and August, looking for signs of prior aphid infestation and ladybird reproduction, such as leaf damage, mould infestation and ladybird larval and pupal skins. These signs are generally apparent even up to leaf fall in autumn (figure 3). However very little evidence of aphids or ladybirds was detected (Table 1). Aphids on some other trees may have been less heavily affected.

3. Leaves from a tulip tree (a) that had not previously been infested with aphids compared to (b) those that had previously been infested with the aphid *Illinoia liriodendri*. The damage to the edges of the uninfested leaves was apparently due to drought. The previously infested leaves show spotting and mottling and a ladybird pupal skin (foreground, bottom leaf). Both pictures were taken late August 2019 in Maastricht. Photos: John Sloggett
3. Bladeren van (a) een tulpenboom die niet geïnfecteerd zijn geweest met bladluis vergeleken met (b) bladeren die wel geïnfecteerd zijn geweest met de bladluis *Illinoia liriodendri*. De schade aan de rand van de niet geïnfecteerde bladeren was blijkbaar ontstaan door droogte. De eerder geïnfecteerde bladeren laten vlekken en verkleuringen zien en de huid van een lieveheersbeestjespop (op de voorgrond, onderste blad). Beide foto's zijn genomen eind augustus 2019 in Maastricht.

Table 1. Summary of surveys of limes and tulip trees carried out in July and August, looking for evidence of aphid infestation or ladybird reproduction. The trees surveyed had harboured large aphid and ladybird populations in previous years.
Tabel 1. Samenvatting van inventarisaties van lindes en tulpenbomen uitgevoerd in juli en augustus, kijkend naar bewijs van bladluisinfectie of lieveheersbeestjesreproductie. Op de geïnventariseerde bomen waren in voorgaande jaren grote populaties bladluis en lieveheersbeestjes aanwezig.

Date / datum	**Location**/ locatie	**Tree** / boom	**No. of trees** / aantal bomen	**Result** / resultaat
19.vii.2019	Maastricht, Monseigneur Nolenspark	Lime	17	Very few aphids. No signs of previous infestation by aphids or earlier occurring ladybird immature stages. One *C. septempunctata*, one clutch of hatching *H. axyridis* eggs.
26.viii.2019	SE Maastricht	Tulip tree	40	No aphids. No signs of previous infestation by aphids or earlier occurring ladybird immature stages; trees showing signs of drought stress. Two *H. axyridis* adults.
27.viii.2019	Maastricht, Monseigneur Nolenspark	Lime	19	Few signs of previous infestation by aphids or earlier occurring ladybird immature stages. Two *H. axyridis* adults.
28.viii.2019	Eindhoven, Onze Lieve Vrouwestraat	Tulip tree	21	Few signs of previous infestation by aphids or earlier occurring ladybird immature stages. Two *H. axyridis* adults.
29.viii.2019	Eindhoven, TU/e campus	Lime	25	Few signs of previous infestation by aphids or earlier occurring ladybird immature stages.

Oaks *Quercus* at one site in Eindhoven were still found to harbour aphids, most likely *Tuberculatus annulatus* (Hartig) and some *Lachnus roboris* (Linnaeus), and numbers of *H. axyridis*, *A. bipunctata* and *Oenopia conglobata* (Linnaeus) on 8th September.

Overall effects

The vast majority of Dutch ladybirds do not survive more than a year, and die in midsummer (Cuppen *et al.* 2017), so numbers of ladybirds towards the end of the active season in 2019 reflect that year's ladybird reproduction and initial survival of the new ladybirds. A number of species, including the ones discussed above, were collected or observed just prior to overwintering in autumn of 2019 at sites from which ladybirds had been collected at the same time in previous years. In spite of the phenological changes of aphids and the observed ladybirds earlier in the year, effects on the abundance of many ladybird species at the end of the season appeared to be relatively small. The species-specific response depended on the species' habitat preferences and diet. The generalist *C. septempunctata*, which is found on diverse low-growing plants, appeared unaffected. This is explained because although the timing of aphids on herbaceous plants and shrubs changed, their abundance did not, or was even enhanced, facilitating ladybird reproduction. The same may be true for *Propylea quatuordecimpunctata* (Linnaeus), which also showed no effect, although this species sometimes does also utilise trees for breeding. By contrast, *A. bipunctata* and *H. axyridis* appeared less abundant at some sites compared to other years, but were equally abundant or even more abundant elsewhere, such as on the oaks previously described in Eindhoven. This can be explained because although these broad generalists utilise deciduous trees, there were sufficient alternative aphid-rich plants on which to breed, especially herbs, like nettles, and shrubs, like roses, but also some trees, like oaks. The ladybird *O. conglobata*, which is generally restricted to trees, showed little change in abundance, but this can be explained by this species' strong association with oaks, observed over several years, which did not exhibit an aphid decline. A ladybird species that did appear to be affected was *Adalia decempunctata* (Linnaeus). The population size at an overwintering site in Maastricht (an ornamental weeping beech tree *Fagus sylvatica* 'Pendula') was reduced two- to four-fold, compared to the preceding three years. This is likely because although *A. decempunctata* breeds on a diversity of trees, it regularly utilises lime trees infested with the aphid *E. tiliae*, which, though usually common in Maastricht, occurred in such low numbers in 2019. Other trees utilised by *A. decempunctata* likely also had lower aphid numbers.

Subsequent observations and conclusion

Observations made in Eindhoven in 2020 suggested that aphid and ladybird phenology returned to the pattern observed prior to 2019. In 2021, the spring was again characterised by fluctuating temperatures (www.knmi.nl/nederland-nu/klimatologie/maand-en-seizoensoverzichten/2021/lente). Although it was not possible to carry out such extensive observations as in 2019, some were made on lime trees and tulip trees in Eindhoven in summer. As in 2019, observations on both types of tree suggested low populations of their respective aphids, associated low numbers of ladybirds and very little ladybird reproduction. These provide additional support that the changes in aphid and ladybird phenology in 2019 described above resulted from spring weather conditions. It is worrying that this situation has occurred in two of the last three years, possibly a result of larger scale climatic change.

The fluctuating temperatures in April and May 2019 apparently affected insect phenology, with high temperatures enhancing reproduction and low temperatures retarding it, and even possibly causing mortality. Differences in aphid population responses were therefore observed, likely due to the differing times when aphids began to reproduce in spring and the extent to which they are affected by cold temperatures. This in turn affected ladybird phenology, which was also affected in part directly by temperature. The variation in the ultimate population responses of the ladybird species arose because of the variability in how aphid species responded to the temperature fluctuations and because ladybird species differ in their feeding preferences and dietary breadth. Generalist species, like *A. bipunctata*, which consume a wide diversity of aphids occurring on herbs, shrubs and trees, are insulated against a decline in certain prey species by their wide dietary breadth. By contrast, more specialised species, like *A. decempunctata*, breeding on trees, are vulnerable because they rely on fewer prey species for reproduction.

Although this report is observational and anecdotal, it might provide some pointers on how larger scale climatic change or meteorological extremes resulting from global warming could affect aphids and their ladybird predators in the future

generally. At a more local level, it could indicate changes currently occurring in the Netherlands and surrounding regions as a possible consequence of climate change.

Acknowledgement

I thank Ilja Zeilstra for providing translations for the parts of this paper in Dutch and proofreading the paper.

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Accepted: September 2, 2021

Samenvatting

Ongewone fenologie van bladluizen (Aphidoidea) en hun lieveheersbeestjes predatoren (Coccinellidae) als gevolg van fluctuerende lente temperaturen

Waarnemingen in het veld van prooi-gerelateerde effecten van het weer, inclusief temperatuur, op de fenologie van lieveheersbeestjes zijn zeldzaam, maar kunnen inzicht geven in hoe lieveheersbeestjes mogelijk reageren op klimaatverandering. In 2019 zorgden ongewone temperaturen in de lente in het zuidoosten van Nederland voor veranderingen in bladluisaantallen en de fenologie van lieveheersbeestjes die zich voeden met bladluis. April en mei werden gekarakteriseerd door sterke temperatuurschommelingen. Bladluissoorten reageerden hier verschillend op. Sommige soorten die voorkwamen op een aantal kruiden en struiken bereikten grote aantallen, maar soorten op sommige bomen waren bijna helemaal afwezig. De soortspecifieke reactie van bladluizen was waarschijnlijk het gevolg van verschillende tijden van reproductie in de lente en hun reactie op de kou. Het lieveheersbeestje *Coccinella septempunctata* reproduceert vroeg, maar voor *Harmonia axyridis* heeft de koudegolf in april waarschijnlijk geleid tot mortaliteit waardoor de populaties kleiner waren dan normaal voorafgaand aan reproductie. Het leek erop dat generalisten, zoals *H. axyridis* en *Adalia bipunctata*, die normaal gesproken voornamelijk op bomen reproduceren, sterker geassocieerd werden met bladluis op kruiden en struiken. De populatiegrootte van lieveheersbeestjes aan het einde van het jaar suggereerde dat generalisten niet zwaar getroffen waren, waarschijnlijk omdat hun omvangrijke dieetbereik betekende dat zij konden reproduceren op de op dat moment aanwezige bladluissoorten. Het specialistische lieveheersbeestje *Oenopia conglobata*, dat een sterke associatie heeft met eik, was schijnbaar ook niet getroffen omdat op de eiken normale bladluispopulaties aanwezig waren in 2019. Daarentegen was *Adalia decempunctata* in veel kleinere aantallen aanwezig dan normaal, waarschijnlijk door de schaarste van één van zijn hoofdprooien, de bladluis *Eucallipterus tiliae* op linde, en andere op bomen voorkomende bladluissoorten. In 2021 zorgden vergelijkbare lentecondities nogmaals voor weinig bladluizen op bomen, wat de doet vermoeden dat sommige in 2019 waargenomen veranderingen mogelijk meer permanent worden.

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