MINI REVIEW

Aphidophagous ladybirds (Coleoptera: Coccinellidae) and climate change: a review

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Abstract

1. I here review the potential effects of climate change on aphidophagous ladybirds and their future diversity. Aphidophagous ladybirds face challenges arising directly from climatic change and indirect challenges due to the effect of climate on their aphid prey and other organisms with which they interact.

2. Ladybirds show at least some potential to respond to changes of climate through genetic change or phenotypic plasticity, notably through changes in colour pattern, dormancy and voltinism but also through thermal physiology and microhabitat or habitat plasticity.

3. Phenological changes will likely occur in many aphidophagous species arising from relations with their prey. Changes in aphid abundance may lead to changes in ladybird prey associations over the season. The tendency to prey on multiple aphid species will insulate many ladybird predators from decline resulting from changes in the abundance of particular aphids.

4. Like other insects, the geographic ranges of aphidophagous ladybird species will change as they track the climate. This is evidenced by the fossil record of ladybirds and by recent changes in ladybird biogeography. Such changes may be accompanied by a degree of thermal or phenological adaptation.

5. It is likely that cold-adapted ladybirds and some island species will go extinct. Specialised species may also be threatened. A problem in assessing the threat to the latter is the minimal amount of research carried out on specialised species.

6. In summary, aphidophagous ladybirds exhibit some potential resilience against climate change, but future climatic effects on their overall biodiversity are not fully clear.

Key words. Aphidoidea, biodiversity, Coccinellini, global warming, habitat, Insecta, phenology, predator, specialization, thermoregulation.

Introduction

Insects, like many other taxa, are claimed to be facing a precipitous decline in both diversity and abundance (Didham et al., 2020; Wagner, 2020). This was recently characterised as ‘death by a thousand cuts’, with wide diversity of stressors linked to this decline, including changes in land use and climate, exotic species, pollution (including light) and insecticide and herbicide use (Wagner et al., 2021). There are many gaps in our understanding of insect declines that still need to be addressed, including the geographic and taxonomic spread of such declines and the stressors involved (e.g., Saunders et al., 2020). In this article, I focus on one group of widespread insects – the aphid-eating ladybird beetles – and one stressor – climate change.

The ladybird family, the Coccinellidae, is estimated to comprise 6000 species (Bouchard et al., 2017), which include phytophagous, fungivorous and predatory species (Giorgi et al., 2009; Hodek & Evans, 2012). The aphid predators are often considered to play a significant role as pest control agents (Michaud, 2012), and a very small number of them have gained particular attention as invasive alien species (Evans et al., 2011; Roy et al., 2016). Nonetheless, research generally has focused rather narrowly on a few species and we know rather little about many of them, especially the more specialised ones (Sloggett, 2005).

The motivation for this article arises from several considerations. Interest in the negative impacts of invasive ladybirds, including Coccinella septempunctata L. in North America, but...
especially Harmonia axyridis (Pallas), on native ladybirds has been intense (reviewed by Koch, 2003; Evans et al., 2011; Roy & Brown, 2015; Rondoni et al., 2021). This focus has arguably acted to distract attention from other possible anthropogenic threats to ladybird species. Nonetheless, some evidence from long-term datasets points to declines in aphidophagous species pre-dating the introduction of invasive species (Honek et al., 2016) and the situation even with respect to invasives appears to be highly complex (e.g., Harmon et al., 2007; Evans, 2017). Other factors likely influence aphidophagous ladybird diversity including changes in land use or habitat degradation, climate change and pollution (Roy & Majerus, 2010; Honek et al., 2017).

There are a number of good reasons to focus on climate change and ladybird aphidophages. There is an extensive body of work on the effect of climate change on aphids (e.g., Hullé et al., 2010; Kindlmann et al., 2010; Blanchard et al., 2019), making the possibility of understanding future conditions for their predators more achievable. There is also an extensive general body of work on aphidophagous ladybirds (e.g., Majerus, 1994, 2016; Dixon, 2000; Hodek et al., 2012), even if it is imperfect and biased towards particular species. Our knowledge of both predator and prey make aphidophagous ladybird good potential models for the effects of climate change on predatory insects or, more generally, secondary consumers. Additionally, an important legacy of studies of invasive species is an interest in the conservation of coccinellid species (e.g., Adriaens et al., 2015; IUCN, 2021), which should be further extended beyond its origins. There is a scattered literature on the impact of climate change on aphidophagous ladybirds, much of it focused on agroecosystems. Additionally, two previous reviews have broadly addressed the possible effects of anthropogenic change on ladybirds, including sections on climate change (Roy & Majerus, 2010; Honek et al., 2017).

This review aims to address critically and in greater depth than previously how climate change will affect aphidophagous ladybird communities in the future. I particularly draw attention to the less well-studied specialist species and how they might fare relative to generalists. Although the focus is on the larger aphidophagous species, mainly members of the tribe Coccinellini (Nedvěd & Kovář, 2012), some of what is discussed is more broadly applicable to the Coccinellidae. Except in passing, this review does not address how the biological control potential of ladybirds may change. The subject is a complex one that would warrant a review of its own, and most likely has a minimal bearing on how ladybird diversity can be affected by climate change.

The future conditions that ladybirds face

Like all organisms, aphidophagous ladybirds can be affected by climate change via direct and indirect effects (Fig. 1). The most obvious direct effect is the gradual global increase in temperature (see IPCC, 2014); however, the changes in atmospheric carbon dioxide (CO₂) or climate-sensitive pollutants such as ozone (O₃) (see Seinfeld & Pandis, 2016) can also have an effect. Climate change involves not only gradual warming but also changes in precipitation and extreme weather events and associated impacts, including heatwaves, excessive rainfall and droughts (IPCC, 2014; WMO, 2020). All the factors given here can potentially affect ladybirds directly, the most obvious example being temperature via ectothermy and thermal tolerance. However, there are also a diversity of indirect effects arising due to impacts on the habitat and the organisms with which ladybirds interact, which include natural enemies, competitors, prey and the host plants on which the prey live (Majerus, 1994, 2016; Hodek et al., 2012).

For aphidophagous ladybirds, the most important and ubiquitous interaction is with their aphid prey. The occurrence and abundance of aphids exerts a clear effect on ladybird abundance, with predatory ladybird populations generally accepted as being ‘bottom up’ rather than ‘top down’ regulated (Dixon, 2000; Hodek et al., 2012). A large body of research exists on the effect of climate change on aphids and the patterns observed are complex and often species specific (e.g., Harrington et al., 1995; Hullé et al., 2010; Kindlmann et al., 2010; Bell et al., 2015; Blanchard et al., 2019), but some generalisations are made for the purposes of this article. The first, which is well supported, is that there are general changes in aphid phenology resulting from climate change. Warming temperatures generally advance early season activity (mainly measured as first flight) and lead to a longer overall season (Bell et al., 2015, 2019; Durak et al., 2016; Wu et al., 2020).

The effect of climate change on aphid abundance is much less clear than its effect on aphid phenology. Higher future temperatures could potentially lead to higher aphid abundances (Harrington et al., 1995; Dixon, 1998; Hullé et al., 2010), but this may not happen due to a variety of factors including temperatures extending beyond the upper limits of species’ tolerances.
host plant quality and the impact of natural enemies (e.g., Dixon & Hopkins, 2010; Murrell & Barton, 2017; Straw et al., 2019). An additional further effect is that of carbon dioxide and ozone: both influence plant growth, but their effects on aphid abundance appear to be very variable (Ameixa, 2010; Hullé et al., 2010; Blanchard et al., 2019). Further complexity arises because, there may be other effects showing locally long-term trends, such as pollution or fertiliser use, which can increase aphid population size (e.g., Bell et al., 1993; Duffield et al., 1997) or pesticide use, which can cause a decrease (Bell et al., 2020). At least some data indicate a small increase in aphid abundance (Bell et al., 2015; Martay et al., 2017, but see Bell et al., 2020). This effect may be more pronounced if the effects of natural enemy activity are removed (e.g., Percy et al., 2002, 2003; Murrell & Barton, 2017).

Arguably though, the overriding trend seems to be that there is not one. Aphid responses to identical temperatures and atmospheric pollutants can be species-, host plant- or even clone specific (Ameixa, 2010; Dixon & Hopkins, 2010; Blanchard et al., 2019). Additionally, there are marked fluctuations in aphid numbers each year (Dixon, 1998; Bell et al., 2020). These may in part be linked to extreme weather events (e.g., Ma et al., 2015; Rodríguez-del-Bosque et al., 2020), which will increase with climate change (Easterling et al., 2000; Filazzola et al., 2021). Combined, these considerations suggest that aphid responses to climate change are likely to vary considerably across species. Fossil evidence and current distributional changes indicate that the ranges of aphid species will change as the climate warms (Ameixa, 2010; Dixon & Hopkins, 2010). Habitat fragmentation may pose a significant problem for this, notably for non-crop aphids due to the loss of natural habitats, potentially leading to species extinction (Ameixa, 2010).

Direct effects on ladybirds

It is not possible to separate fully direct and indirect effects of climate change on aphidophagous ladybirds, because they clearly overlap. However, the most obvious direct effects involve issues relating to thermoregulation and other climatic variables. Because ladybirds are ectotherms, increasing overall temperature has predictable effects, causing an increase in metabolism, activity, growth rate and food consumption up to a certain threshold value (termed the thermal optimum or thermal maximum), and then a decrease, as heat stress causes a drop-off in biological function and, eventually, death (e.g., Mack & Smilowitz, 1982; Acar et al., 2001; Auad et al., 2014; Khan et al., 2016). There are emergent developmental and life history characteristics, including changes in size, which vary, and temporal development and longevity, which generally decrease with increasing temperature (Nedvěd & Honěk, 2012). The thermal requirements of aphidophagous ladybirds clearly differ interspecifically (Nedvěd & Honěk 2012) and climatic warming could therefore impact on or even extinguish local populations of particular species. Other climatic effects could also play a significant, though likely subsidiary, role. In a study of factors affecting local colonisation and extinction of ladybirds in the United Kingdom, Comont et al. (2014) noted that ladybirds were less likely to colonise grid squares characterised by a lot of rain: they attributed this to an inhibitory effect of rainy weather on insect activity.

Extreme events associated with climate change, many of them of short duration, including drought, intense precipitation, hail and storms, but especially extremes of temperature, exert a strong effect on local populations of insects (Harvey et al., 2020; Filazzola et al., 2021; Skendžić et al., 2021). In laboratory experiments, immature Harmonia axyridis acclimated to 20°C were exposed to a temperature close to the upper developmental threshold of this species, 33°C, for a single continuous period of 48 h. This caused significant mortality in eggs and younger larvae, as well as smaller adult size (Knapp & Nedvěd, 2013). In further experiments, there was also an increase in developmental rate (Knapp, 2014). Thus, there are diverse potential damaging effects of relatively short duration extremes of temperature. Other extreme weather events may also have impacts. In July 2020, in Eindhoven, The Netherlands, high winds blew large numbers of arboreal ladybirds and their larvae from trees during breeding (J.J. Sloggett & I. Zeilstra pers. obs.). Although effects such as this act only in the short term, combined with other factors such as temperature, they may increase stress on local populations of ladybirds.

Climatic changes also affect voltinism and dormancy, both via direct effects of temperature, but also through indirect effects on aphids. Both are considered in more detail below, and the discussion here is limited to the challenges that ladybirds face due to a warming climate. Increased temperature causes faster development, potentially increasing the number of generations through which ladybirds can pass over time, although this effect is modified by prey availability. Such faster development may also cause overlap of adult generations, leading to the occurrence of sexually transmitted parasites, such as mites and fungi, to which ladybirds are prone (Welch et al., 2001; Roy & Majerus, 2010; Pastok et al., 2016). These generally occur in the warmer parts of the ranges of temperate ladybirds (e.g., Webberley et al., 2006) and may spread as the climate warms, especially if aphid populations increase (cf. Welch et al., 2001; Sloggett, 2017). Dormancy can occur in ladybirds in winter or summer as a means of avoiding temperature extremes or periods of aphid scarcity (Hodek, 2012; Honek et al., 2017) and is population specific, depending on local conditions (Hodek, 2012). As the local climate changes, different patterns of dormancy become necessary. The length of dormancy could change, for example, winter dormancy could be shorter if temperatures are higher (Roy & Majerus, 2010), although the factors regulating dormancy are not limited to temperature (Hodek, 2012; see also below). Climate could also have a direct effect on mortality during dormancy: increased temperatures pose a possible risk of higher dormancy metabolic rates leading to depletion of stored reserves (Roy & Majerus, 2010).

Evolutionary and plastic responses to direct climatic effects

Potentially ladybirds could adjust locally to climate change through adaptation or phenotypic plasticity. Our knowledge of how they might do this is patchy and often arises as a consequence of studies focused on other subjects, such as
polymorphism (Sloggett & Honěk, 2012) and invasiveness (e.g., Boher et al., 2018; Logan et al., 2020). A variable number of studies exist in a diversity of areas, notably thermoregulation related to colour pattern, physiology and behavioural plasticity, and dormancy and vortonism. However, in many of these areas, a broader focus is required than is currently the case.

Colour pattern

The best-studied aspect of ladybird thermoregulation is the impact of colour pattern. Many aphidophagous ladybird species exhibit considerable variation in their colour patterns; these range from fully discontinuous genetic polymorphisms to more subtle variation in spot number or strength arising from continuous genetic variation or phenotypic plasticity (Majerus, 1994, 1997; Sloggett & Honěk, 2012). Although many factors have been implicated in this colour pattern variation, climate clearly plays a significant role (e.g., Dobzhansky, 1933; Brakefield, 1984a, b; Okuda et al., 1997), notably temperature, sunshine duration and humidity (e.g., Honěk, 1996; Okuda et al., 1997; Purse et al., 2015). This colour-pattern variability argues that, to some extent, populations of ladybirds could be buffered against changes in climate through changes in colour pattern (Roy & Majerus, 2010). These can operate irrespective of its underlying control, be it genetic or environmental, via selection or phenotypic plasticity.

If this is the case, then it is to be expected that the frequencies of different colour forms should change long term and parallel changes in the climate. Current evidence from polymorphisms is inconsistent on this point, although given that the selective factors underlying colour pattern variation are diverse and not limited to climate, this is perhaps unsurprising. Certainly long-term trends exist. These were noted over 50 years ago in the polymorphic Harmonia axyridis of Japan where an increase in melanics and decrease in non-melanics were presumed to be linked to a warming climate from 1912 to 1965 (Komai & Chino, 1969).

More recently, studies on Adalia bipunctata (L.), also polymorphic, in the Netherlands covering 1978 to 2004, show a decline in the frequency of melanics in the east, leading to a flattening of a cline from the Dutch coast; these changes were associated with increased temperatures in these regions, especially in spring (de Jong & Brakefield, 1998; Brakefield & de Jong, 2011).

However, such patterns are not universal or consistent. The studies given above exhibit opposite changes in the frequency of melanics in response to temperature. A recent study by Honek et al. (2020) found no change in invasive H. axyridis morph frequencies over a 9-year period in the Czech Republic and no general relationship between climate and morph frequencies in Europe. Another study by Honěk et al. (2005) summarises a number of long-term Central European trends for A. bipunctata but failed to find any evidence of a decrease in melanics over a timeframe similar to that of de Jong and Brakefield. However, an increase was observed in non-melanic (spotted) Adalia decempunctata (L.), which is also polymorphic. As pointed out by Honek et al. (2020), the effects of climate likely vary across populations. It seems probable that in many cases, trends related to climate change may be modified or overridden by other of the diverse selective factors that can maintain ladybird colour pattern polymorphisms. This in its turn suggests that selection in polymorphic species can only modulate the effects of climate in a limited range of circumstances, when other selective factors are very weak or climatic selection is very strong.

Only a single study has addressed long-term changes in spot strength or number, which are more likely polygenic or the product of phenotypic plasticity. In this study, the frequency of low-spot forms (0–3 spots per elytra) in Hippodamia variegata (Goeze) increased from 1981 to the 2000s, but this followed a decrease from 1937 to 1981; thus the pattern was inconsistent (Honek et al., 2012). The study was hampered by a lack of background knowledge of the exact underlying basis of the variation; furthermore, the authors claimed that differences in the degree of melanisation were too small to affect thermoregulation. The relationship of this variation with climatic factors would be worthy of detailed physiological investigation (sensu de Jong et al., 1996) for this and other species that vary in spot strength or number. Other studies of geographic variation and phenotypic plasticity would argue that a relationship does exist (e.g., Dobzhansky, 1933; Okuda et al., 1997).

Phenotypic plasticity in the colour patterns of ladybirds is well known, with adult ladybirds exhibiting decreasing spot size with higher temperatures (e.g., Timofeeff-Ressovsky, 1941; Sakai et al., 1974; Okuda et al., 1997; Michie et al., 2010). Across populations, this may interact with genetic effects on spot size (Okuda et al., 1997) and the effect extends to short periods of high temperature during development (Knapp & Nedvěd, 2013). The plastic effect of temperature is not limited to adult ladybirds, with pupae and even larvae exhibiting lighter pigmentation with increasing temperature (Okuda et al., 1997; Zhang et al., 2020).

Considered overall, it seems that in many ladybirds, including even non-polymorphic ones, the potential exists for a degree of buffering against climatic changes in the future through colour pattern change or modification. An open question, however, is to what extent. Studies of polymorphic or plastic species at the edge of their ranges or under conditions close to the limits of thermal tolerance may help clarify this further.

Selection on and plasticity in thermal physiology

At the moment, we know little about the potential of aphidophagous ladybirds to evolve physiological changes in response to the thermal challenges of climate change. A study of an invasive population of Harmonia axyridis in South Africa found limited heritability in most traits and high genetic correlations between them (Logan et al., 2020). However, as the populations were invasive ones that had been through at least two genetic bottlenecks, it is hard to extrapolate anything from this study to other species.

Physiological thermal plasticity, which would allow some adjustment to changing temperatures, has received some attention, although probably not as much as it deserves. A study by Sørensen et al. (2013) has shown the potential for A. bipunctata plasticity at different temperatures when reared under different thermal conditions. In this experiment, adults reared at 15, 20, and 25 °C fed on more aphids at their own...
rearing temperature than ladybirds from the other treatments (though generally ladybirds at higher temperatures ate more); additionally ladybirds reared at higher temperatures were more resistant to heat stress. A plastic effect of colour pattern cannot be ruled out in explaining these results, since Sørensen et al. did not look at the effects of rearing temperature on colour pattern. In contrast, Boher et al. (2018) used ladybirds of three species occurring in Chile [Eriopis chilensis Hofmann, Hippodamia variegata and Harmonia axyridis] that were reared at a common temperature and subsequently acclimated to three different temperatures: this makes colour pattern effects unlikely. They found no effect of acclimation on upper and lower lethal limits, when 50% of ladybirds died, and on minimum critical temperature, when ladybirds were no more able to turn themselves upright. The upper critical temperature was only affected in one of the three species tested (E. chilensis), when it increased with acclimation temperature. Irrespective of colour pattern, Shinner et al. (2020) point out that different traits should be affected depending on larval or adult thermal exposure, since larval exposure to a particular temperature is not necessarily a good predictor for similar adult exposure. Using H. axyridis, they found that some of the traits they measured, such as the critical thermal maximum of adults were unaffected by larval exposure, while some traits related to adult walking were. As reinforced by Shinner et al., acclimation studies need to test multiple traits resulting from acclimation at multiple points in the life cycle.

Although sometimes useful in understanding how ladybird thermal physiology can respond to climate, there has been an unfortunate tendency for studies of the thermal physiology of ladybirds to focus on issues related to invasiveness (e.g., Knapp & Nedved, 2013; Barahona-Segovia et al., 2016; Boher et al., 2018; Logan et al., 2020; Awad et al., 2021). For example, the study of Boher et al. (2018), discussed above, primarily aimed to identify whether invasiveness (in this case in Hippodamia variegata and Harmonia axyridis) was correlated with thermal tolerance; similarly, the study of Logan et al. (2020) aimed to examine how the thermal characteristics of an invasive species (H. axyridis) could evolve under climate change. Interestingly, there is rather little evidence for invasive species being better able to respond to climate change than native ones (Barahona-Segovia et al., 2016; Logan et al., 2020; Awad et al., 2021). The focus on invasive ladybirds suggests that thermal physiology comprises one area where invasive ladybirds have distracted researchers from carrying out studies more directly focused on climate change (see Introduction). Further thermal studies on a wider diversity of species are urgently required, specifically in order to assess how common and ecologically relevant thermal acclimation and physiological evolution could be in buffering local ladybird populations from the effects of climate change.

**Behavioural plasticity**

Behavioural changes can also act to maintain an association with a favoured climate and may initially buffer against a changing climate. In China, at the hottest time of day, ladybirds moved into maize whors in which the temperature was lower and the humidity higher (Pan et al., 2020). In Western Europe, Coccinella quinquepunctata L., which is limited to humid sparsely vegetated pioneer habitats, is spread across a wider diversity of habitats in the north compared to the drier south, where it appears to be mainly limited to the vicinity of rivers (Sloggett & Zeilstra, 2020). The ladybird also pupates more frequently under stones in the south. These behaviors apparently maintain the ladybird’s association with humid habitats in a hotter, drier climate. They most likely arise due to plasticity, rather than local adaptation (Sloggett & Zeilstra, 2020). Certain aphidophagous species of ladybird do change their habitat preferences geographically (e.g., Sloggett & Majerus, 2000), although it remains to be seen how much of this variation is driven by climate and how effective habitat or microhabitat plasticity is as a buffer against climate change. In the case of C. quinquepunctata, suitable river habitats are generally scarce and a change to exclusively river habitats in north-west Europe would still entail massive population losses (Sloggett & Zeilstra, 2020).

**Voltinism and dormancy**

Voltinism and dormancy (used here to include diapause and quiescence) are closely related, with periods of dormancy at times of year when conditions are adverse for ladybirds acting as ‘place-holders’ for patterns of volitnism over a year (Hagen, 1962; Hodek, 2012). Intraspecifically and interspecifically, there is considerable variation in these life history characters of ladybirds, although extensive knowledge is limited to a few species, most notably Coccinella septempunctata (Hodek, 2012; Suleman, 2015). At higher latitudes, aphidophagous ladybirds tend to be univoltine; in some species, there seems to be a requirement for a winter diapause before reproducing again, although this often is not for all individuals in a population (Hagen, 1962; Hodek, 2012; Roy et al., 2013). This ‘obligate’ diapause maintains univoltinism with a limited capacity for multivoltinism under favourable conditions (Hodek, 2012). At lower latitudes, where it is warmer and the aphid season is longer, ladybird populations are bi- or multivoltine; depending on climate, periods of reproduction may be broken by a winter or summer diapause quiescence or both (Hagen, 1962; Hodek, 2012). A wide variety of factors appear to play a role in determining diapause or quiescence predominantly daylength but also including temperature and food availability (Hodek 2012). In C. septempunctata, it is known that there is a genetic component to ‘obligate’ diapause and it is possible to select for the capacity to breed continuously under favourable conditions (Hodek & Čerkasov, 1961; Bonnemaison, 1964).

Hodek (2012) suggested that the underlying control of dormancy combines plasticity and resilience, with diverse genetic and environmental controls allowing aphidophagous ladybirds to respond to an environment that is already unpredictable for aphidophages. Thus although dormant ladybirds may potentially be threatened by, for example, warmer winters giving rise to stored reserves running out more rapidly (Roy & Majerus, 2010), it seems probable that through a combination of selection and plasticity, aphidophagous ladybird populations can respond to such challenges by altering patterns or the length of dormancy. The same is true for voltinism; with a warmer climate or a longer aphid season, univoltine populations...
may evolve towards being partially or fully bivoltine. This could occur in *C. septempunctata* through selection on pre-existing genetic variation for continuous breeding under favourable conditions; indeed, it appears already to have occurred in invasive populations of *C. septempunctata* in North America (Hodek, 2012). Bivoltine or multivoltine populations could evolve more generations through changes in sensitivity to environmental cues such as daylength, although this could also be a passive process of generation time becoming shorter due to increasing temperature.

Although these scenarios are persuasive, based on our current knowledge, it is worth noting Hodek’s warning that our knowledge of these life history characters is based on a narrow range of species (Hodek, 2012). These are almost entirely habitat and dietary generalists, which are expected to be more genetically and phenotypically variable due to the diversity of situations that they encounter. There is almost no work on more specialised species (but see Majerus, 1994; Roy et al., 2013) so we know very little of the capacity of these ladybirds to evolve or exhibit plastic responses in their life histories. Dietary specialists particularly might be expected to be less flexible in their synchronisation with aphid prey due to the lower diversity of prey on which they depend: this would give less potential for adjustment in response to climate change. Thus, further fundamental studies of voltinism and dormancy in specialists, including long-term studies, are necessary to better assess how well insulated their populations are against climatically mediated phenological change.

### Indirect effects mediated by aphid prey

Work on individual host-plant-aphid-ladybird systems has generally focused on pest aphid biocontrol. There are few generalities that arise from this work because the outcomes are very variable (Ameixa, 2010; van Baaren et al., 2010; Hullé et al., 2010). This is not least because even the effects of temperature and atmospheric gases on plants and aphids alone are so diverse (see above). Outcomes are then further modified by the responses of ladybirds, which also vary. In general, aphid consumption by ladybirds appears to increase disproportionately at higher temperatures (Schwarz & Franck, 2019), although conversion efficiency can vary (Krengel et al., 2013). Elevated carbon dioxide can increase aphid consumption and ladybird growth rate (Srinivasa Rao et al., 2018) or have a negligible effect (Chen et al., 2007). The effect of water availability on aphid consumption appears to vary with drought intensity (Banfield-Zanin & Leather, 2016). When combined together with variation in host plant and aphid responses, outcomes are highly specific to the system under examination.

Another system-specific concern is that of phenological mismatch between predator and prey, i.e., that changing environmental variables decouple the phenological match between specific predators and prey, or that differing thermal limitations cause the ranges of the two to diverge (van Baaren et al., 2010; Roy & Majerus, 2010). The current evidence for this in aphid-ladybird systems is limited and much of it largely theoretical (e.g., Eigenbrode et al., 2015; Fuchs et al., 2017). Although potentially problematic for biological control in individual systems, viewed overall from the perspective of the ladybird, this and other aphid-mediated effects do not appear to pose a universal problem. Many aphidophagous ladybirds have flexible and changing phenological relationships with their prey, as is illustrated by the capacity of ladybirds to integrate new prey, such as exotic species, into their diet (e.g., Goodarzy & Davis, 1958; Danilov, 2016). Furthermore, ladybirds can persist on atypical or non-aphid food during periods of aphid scarcity (Sloggett & Majorus, 2000; Evans, 2009). As pointed out elsewhere in this article, selection or plasticity can change ladybird dormancy or voltinism. For example, the first flight of aphids in the United Kingdom is getting earlier (Bell et al., 2015), but so is emergence from overwintering sites of British *Coccinella septempunctata* (Roy & Majorus, 2010). Nonetheless, some caution is necessary. Although some such considerations can still apply to more specialised species (e.g., Parry, 1992; Cook & Webb, 1995), they may not be universal. Dietary specialists are reliant on a narrower range of aphid prey and may not display the same degree of plasticity or variability as generalists.

Observations of my own, of interspecifically variable aphid responses to fluctuating spring temperatures and their ultimate effects on different ladybird predators, support a view that the phenological responses of aphidophagous ladybirds are to some extent species specific (Sloggett, 2021). The observations were made in 2019 in the southern Netherlands following a spring in which temperatures had fluctuated from above to below average. The effect of this on herbaceous aphids was limited and some may have even benefitted from the conditions. However, populations of some tree aphids, such as *Eucalypthus tiliae* L. on limes, *Tilia* spp., were much lower than normal all year. *Coccinella septempunctata*, a generalist that feeds on aphids on diverse herbaceous plants was unaffected, as was the more specialised *Oenopia conglobata* (L.), whose predominant prey, aphids on oak (*Quercus* spp.), did not noticeably decline. Generalist species such as *Adalia bipunctata* and *Harmonia axyridis* that usually breed heavily on *E. tiliae* as well as other aphids on trees and herbs, bred predominantly on herbaceous plants, with limited ill effects. In contrast, *Adalia decempunctata*, an arboreal species, which in cities is heavily reliant on *E. tiliae*, declined in number in the immediate aftermath of this season (Sloggett, 2021). Thus, changes in climate could affect aphidophagous ladybirds differently via their aphid prey, if they persist. Particularly interesting are the responses of the two *Adalia* species, with the more generalist *A. bipunctata*, insulated from effects by its broad dietary range, but the more specialised *A. decempunctata* being adversely affected. It is worth noting that other types of climatic change than temperature can also affect ladybirds via aphids. In 1994 in Cambridge, UK, and elsewhere, low early season rainfall apparently led to smaller than usual aphid populations and ladybirds switching to a variety of alternative food sources, such as ant-tended aphids (J.J. Sloggett pers. obs.).

If climate change did lead aphids to become more abundant (see above), this would likely favour dietary generalists, which perform better at higher densities of aphids. Generalists are optimised for relatively efficient prey capture across high densities of...
a diversity of aphid species; they invest less per egg in a larger number of eggs, which at high aphid densities have good probability of developing into adults. In contrast, specialists perform better at low aphid densities where higher investment per offspring is necessary (Sloggett, 2008a; Sloggett & Lorenz, 2008; Ferrer et al., 2015). This would make generalists the major beneficiaries of increased aphid densities due to climate change, including invasive species, which are typically generalists and possess the same reproductive characters (e.g., Hodek & Michaud, 2008; Roy et al., 2016). Increases in generalists could occur at a cost to more specialised ladybirds feeding on the same prey. However, it is worth repeating that a climate change-related increase in aphid density remains an open question and other factors unrelated to climate change can lead to increased aphid densities.

Other indirect factors

Effects of climate on the host plants of aphids can be considered as prey effects but are discussed separately here to distinguish them from phenological effects. Perhaps most noteworthy are potential effects on conifers, which harbour a large and diverse specialised ladybird fauna (e.g., Iablockoff-Khnzorian, 1982; Gordon, 1985; Majerus, 1994). A range of conifer species are in decline due to warming temperatures, drought and climate-related bark beetle outbreaks (e.g., Schuldt et al., 2020; Andrus et al., 2021; Kharuk et al., 2021); if this trend continues, there is likely to be a knock-on effect on the aphids feeding on them and on their natural enemies, including conifer-specialised ladybirds. In the south of the Netherlands, loss of Norway spruce, Picea abies (L.) Karst (cf. Mohren & Vodde, 2006; Schuldt et al., 2020), already appears to have affected the ladybird Aphiecta obliterata (L.), which preys on spruce aphid Elatobium abietum (Walker). The ladybird is now often more easily collected from non-native Douglas fir, Pseudotsuga menziesii (Mirbel) Franco, infested with the invasive adelgid Gilletteella cooleyi (Gillette) (J.J. Sloggett & I. Zeilstra unpub. data).

A small number of aphidophagous ladybirds have close or obligate interactions with other organisms, notably ants (Majerus et al., 2007). As with host plants, these species may also encounter problems if their ant associates are affected by climate change, although in at least some cases, the ladybirds may be buffered by multiple ant associations or facultative ones (e.g., Völkl, 1995; Sloggett et al., 2002). Arguably, the most important associations that ladybirds have with other animals, apart from with their prey, are with natural enemies, especially specialised parasites. Changes in ladybird phenology could increase the occurrence or prevalence of sexually transmitted parasites (see above), but we currently know little for other parasites of ladybirds and it is likely that any effects are specific to the host–parasite interaction. From the point of view of the ladybird, any such effects are likely to be minimal in their impact. The statement of Ceryngier & Hodek (1996) that there is no evidence that natural enemies exert regulatory effects on coccinellid populations still largely holds true, especially for aphidophagous species (Ceryngier et al., 2012).

Changes in geographic distribution

Although the potential exists for evolutionary, plastic and ecological changes; in many cases, it is also expected that organisms will respond to climate change by habitat tracking, leading to changes in geographic range matching climatic preference (Parmesan, 2006). In aphidophagous ladybirds, two lines of evidence support climate-related habitat tracking and changes of geographic range. The first uses the fossil record and the second, studies of current ladybird ranges.

Although largely limited to certain robust insect taxa that are more likely to fossilise, there is abundant evidence that the majority of insect fossils from the Quaternary, extending back 2.6 million years, comprise species that still exist today (Coope, 1995). During the climatic cycles of glacial and interglacial periods that characterise the Quaternary, these insects have repeatedly altered their ranges to match their climatic preferences (Coope 1995). Beetles have a particularly rich Quaternary fossil record due to their sturdy exoskeleton (Coope, 1995; Porch & Elias, 2000), and the evidence available supports ladybirds also exhibiting climate-related range changes (Majerus, 1994, 2016; Roy & Majerus, 2010). A diversity of different ladybirds that today are restricted to high latitudes or other cold climate regions are found as fossils from cooler glacial periods elsewhere, in areas that at that time would have exhibited a similar cool climate, though not today (e.g., Lemdahl, 1991; Schwert, 1992; Buckland & Buckland, 2018). In Britain and the European continent, for example, intermittent fossil records of Hippodamia arctica (Schneider) during glaciations extend back over 450 000 years to the Mid-Pleistocene (e.g., Coope & Sands, 1966; Ponel, 1995; Coope, 2013; Larkin et al., 2014). In contrast, the warmer interglacials and interstadials are characterised by species now characteristic of milder climates. For example, Coope and Angus (1975) recorded five fossil ladybird species in interstadial deposits at Isleworth in southern Britain, all currently occurring in Britain and/or the nearby continent. The records of Quaternary fossil ladybirds suggest that, like many insects, they may change their ranges relatively rapidly in response to climate change: possibly in the course of a few decades (cf. Coope, 1995). Unfortunately, we lack a similar fossil record for aphids, although it has been logically suggested that they would behave in the same way (Amézia, 2010).

A second line of evidence comes from aphidophagous species changing their ranges at the current time. For example Hippodamia (=Ceratomegilla) undecimnotata (Schneider), a ladybird of central and southern Europe, has recently expanded its range northwards (Akermans & Cuppen, 2020). It should be borne in mind, however, that ranges are not necessarily related to climate change but may also arise due to changes in land use, for example (e.g., Biezikowski & Orlova-Bienkowska, 2020), or a combination of factors. A case in point would be the spread of the conifer-dwelling Harmonia quadripunctata (Pontopiddan) from the European continent through Britain (Majerus, 1994; Roy et al., 2011); this might be attributable to climate change but could also be related to extensive planting of conifers in England in the 20th century (see Aldhous, 1997).

An established link between the climate and spread of a ladybird exists for Menochilus sexmaculata (=Cheilomenes sexmaculata, Menochilus sexmaculatus) (Fabricius), which spread...
northwards through Japan from 1910 to the 1990s (Kawakami et al., 2014). The spread of the beetle was linked to an increase in annual mean temperature above 15 °C, although not winter temperature. Interestingly further work has shown a degree of adaptation, in colour pattern, body size and dormancy, going hand in hand with this change of geographic range. As the species spread north, the more heavily melanised forms increased, most likely due to selection for increased absorbance of solar radiation (Kawakami et al., 2015; see also Kawakami et al., 2018). Body size also decreased; after excluding diet quality- or temperature-related plasticity, the authors concluded that this was most likely linked to the occurrence of melanism, since melanic individuals are smaller (Kawakami et al., 2015). As it spread to central Japan, *M. sexmaculata* developed previously unseen summer quiescence, based on field and historical records (Kawakami et al., 2016; Kawakami & Yamazaki, 2017). The authors attribute this to a lack of aphid prey (Kawakami et al., 2016), but it is not possible to exclude an additional direct effect of high temperatures, especially as the ladybird can apparently survive on non-aphid food (e.g., Jotwani & Verma, 1969; Syatrawati et al., 2020).

The studies of *M. sexmaculata* in Japan are particularly interesting as they show that climate-related changes in geographic range go hand in hand with the sort of genetic or phenotypically plastic changes discussed earlier in this article. The findings on body size are a notable addition to those discussed previously. Interspecifically, Honek et al. (2017) have argued that larger aphidophagous ladybird species will become scarcer in the Mediterranean due to aphid scarcity and shorter duration of aphid colonies under climate change. However, their arguments are not well supported by field evidence (Kindlmann et al., 2020). There are large species, such as *Coccinella septempunctata*, *Anatis ocellata* (L.) and *Myzia oblongoguttata* (L.) that extend well into the Iberian Peninsula (e.g., see www.gbif.org) and the authors’ assumption of a simple relationship between body size and aphid density is probably incorrect (Sloggett, 2008a).

### Extinction

If species cannot adapt or move in response to climate change, then they will go extinct. Thus far, we have no known examples of ladybirds going extinct at all, for any reason (Honek et al., 2017). This might suggest that this family is relatively resilient to environmental change. The analysis here, including potential for phenological adaptation and plasticity, dietary flexibility and habitat tracking, would suggest that could be the case for climate. However, some species may still be at risk.

The most obvious examples are species restricted to the colder high latitudes. As discussed previously, the ranges of some of these species have prehistorically extended to lower latitudes, but today many of these species are already restricted to high latitudes or altitudes. For example, among the North American Coccinellini, *Anisosticta borealis* Timberlake, *Ceratomegilla ulkei* Crotch, *Coccinella fulgida* Watson all have ranges restricted to above latitude 50°N (Gordon, 1985). As the climate warms, these species could be forced further and further north in search of a cooler climate, until there is nowhere left for them to go.

Island endemic species are also threatened because they are unable to disperse elsewhere in the face of changing climate, although their greatest threat may be from non-endemic species. In Gran Canaria, of 42 coccinellid species, 17 are endemic and

| Response group         | Character or characteristic | Response                                                                 |
|------------------------|-----------------------------|--------------------------------------------------------------------------|
| Adaptation/plasticity  | Colour pattern              | Mediates heat uptake and consequently thermoregulation. Can change through thermally mediated selection (notably in polymorphic species) or phenotypically plastic responses to temperature. |
|                        | Thermal physiology          | Physiological evolution or acclimation could buffer against changes in temperature. |
|                        | Behavioural Dormancy        | Plastic microhabitat or habitat preference buffers against changes in climate. Selected and plastic responses to changing seasonal length, as a consequence of temperature and prey availability. |
|                        | Voltinism                   | In many cases, voltinism will track changes in temperature and prey availability (i.e. if temperatures and prey are available ladybirds will reproduce). In some cases may change through plasticity and selection on dormancy, especially diapause and its relationship to reproduction. |
|                        | Diet                        | Ladybird species may incorporate new aphid prey into diet or switch prey aphid species if available prey spectrum changes. |
| Habitat tracking       | Geographic range            | Ladybirds will change geographic range according to climatic and habitat requirements, probably resulting in movement to higher latitudes. |
| Extinction             | High-latitude species       | Suitable climate no longer available. |
|                        | Island species (incl. high-altitude species) | No potential for dispersal to new areas. |
|                        | Specialists                 | Less adaptable than generalist species; possible competition with generalists; low potential for dispersal combined with habitat loss and fragmentation. |

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21 likely recent arrivals (Romanowski et al., 2020), illustrating the scale of the problem. High-altitude mountain species combine the problems of both high latitude and island species, being generally restricted to cold climate, ecological ‘islands’. Species inhabiting mountain ranges such as the Asian Coccinella alpigrada (Fablokoff-Khnzorian) and Oenopia shirkhahensis Khormizi and Nedvéd (Kovář, 2005; Khormizi & Nedvéd, 2020) could be forced to higher and higher altitudes, eventually going extinct if they cannot disperse to higher latitude mountain ranges elsewhere.

A potentially more worrying, but as yet unsubstantiated, threat is that broadly posed to specialised aphidophagous ladybirds: there are reasons for thinking this might be the case. First, it seems likely that their specialisation makes them less likely to exhibit the genetic variation or phenotypic plasticity already observed in some generalist species (cf. Murzen et al., 2015), which has been discussed here. Second, they rely on a narrower range of prey or habitats: if their aphid prey decline or the habitat degrades, then there are limited alternative routes to survival. Third, even though habitat tracking remains a possibility, loss and fragmentation of suitable habitats for ladybirds and/or their prey poses a much greater problem for specialists when dispersing, because there are fewer suitable habitats available to a specialist and they are on average further apart. Specialist aphidophagous species tend to be more sedentary than generalists (Sloggett et al., 2008) and not to disperse widely (e.g., Vandenbergh, 1990; Humble, 1994), making them yet more vulnerable. Aphid-mediated competition from generalists could also play a role in suppressing specialist numbers. If these scenarios prove partially or wholly correct, some ladybird specialists might face a very challenging future indeed.

**Conclusion**

The main anticipated responses of aphidophagous ladybirds to climate change are summarised in Table 1. Broadly, the evidence suggests that the geographic ranges of many species will change, and that these changes will likely be accompanied by some degree of evolutionary change and phenotypically plastic responses. There will be phenological changes, including in relation to the prey species consumed, but the tendency of aphidophages to prey on multiple species will insulate many ladybirds from decline, due to changes in the abundance of particular aphids. Cold-climate species and some island ladybirds will go extinct. The extent to which more specialised dietary and habitat specialists will be affected by climate change is largely unknown and uninvestigated. The effects of climate change on aphidophagous ladybirds will interact with other anthropogenic stressors, especially habitat fragmentation and changes in land use, but certainly others as well, including other diverse factors responsible for habitat degradation, and probably also invasive (generalist) species.

Many of the responses of aphidophagous ladybirds to climate change are more widespread in insects (e.g., Parmesan, 2006; Eggleton, 2020). However, some particular aspects are worth singling out. Like many other secondary consumers (Thackeray et al., 2016), ladybird aphidophages may be less phenologically sensitive than insects at other trophic levels to the effects of climate change. They have the potential to change their patterns of voltinism and dormancy and, in spite of their relatively specialised food, they often show the capacity to alter their aphid diet to match what is available. This gives them some potential to respond to the direct, but especially indirect challenges posed by the changing climate. As an example, asymmetric changes in the seasonal phenology of predator and particular prey are unlikely to pose an issue for many aphidophagous ladybirds, although they may yet pose an issue for any biological control of specific aphid pests.

However, while true for many species, this may not be universal. Arguably, the most alarming feature to emerge from this review is a possible threat to more specialised species. Although specialisation is a continuum rather than a dichotomy in aphidophagous ladybirds (Sloggett, 2008a, 2008b), we can certainly say that many species exhibit some degree of specialisation and that the broad habitat and dietary generalists so often studied comprise a minority of aphidophagous ladybird biodiversity. This means that a large proportion of this biodiversity could be potentially under threat, and the threatened species are the very ones that are rarely researched. Rather little has changed in the 16 years since I published a paper suggesting that a focus on a few generalist species was distorting our overall understanding of the aphidophagous Coccinellidae (Sloggett, 2005). Many of the biological features discussed here remain poorly understood in specialists: these include colour pattern, dormancy, and thermal constraints. We might expect, for example, specialists to be less phenotypically plastic than generalists, and thus less able to respond to climatic warming, but, by and large, we do not have any evidence.

As another example, online recording schemes, often using citizen science data, have certainly enhanced our knowledge of some species’ ranges, but for many of the scarcer, more specialised ladybirds we still have too few observations to draw any conclusions about what changes are occurring. Some such schemes have rightly focused on tracking the spread of invasive species, especially Harmonia axyridis (e.g., https://www.coleoptera.org.uk/coccinellidae/home), but a greater focus on scarcer species, akin to that of the Lost ladybug Project (http://www.lostladybug.org/) would certainly be valuable. This should go hand in hand with a greater emphasis on studying natural history, for professionals and amateurs alike (cf. Saunders et al., 2020). This can form a starting point for understanding more broadly how humans are affecting ladybirds, including through climate change. Some, mainly Dutch, examples from the author’s experience are given in this article, as well as published examples (e.g., Akkermans & Cuppen, 2020). More diverse examples, not only with respect to species but also geographically, would be particularly valuable for researchers, making it easier to scale from individual cases to general patterns and from local effects to global ones.

Although further work is required to confirm it, climate change potentially could radically alter communities of aphidophagous ladybirds. It remains the case that the invasive species so intensively studied have not yet caused a single documented ladybird extinction (Honek et al., 2017); in contrast, climate change certainly can. That is reason enough to ensure that the climate, as well other non-invasive threats to ladybirds, receive
their fair share of attention and are not pushed into the background until it is too late.

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Conflicts of interest

The author has no conflicts of interest to declare.

Data availability statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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