Chapter 9
Coccinellids in a Changing World

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Abstract Current rates of biodiversity change and loss exceed those historically recorded and show no indication of slowing. Comparisons of recorded extinctions of known species over the last 100 years with rates of extinction of characteristic species in the fossil record indicate that humans have increased the species extinction rate by 100 times. The major drivers of biodiversity change are considered to be habitat change, climate change, invasive species, overexploitation and pollution but changes in biodiversity and ecosystems are most often caused by the interactions between multiple drivers, across both spatial and temporal dimensions. Dietary and habitat generalist and specialist coccinellids should exhibit differing responses to these drivers of change. On continental scales, coccinellids move rather than adapt and when possible, maintain environmental constancy rather than geographic constancy. Only when dispersal is not possible due to barriers of unfavourable habitats must they evolve or die. This means that permanent, relatively continuous latitudinal wildlife corridors are essential to allow species (particularly stenotopic species) to mobilize for survival as environments change. This chapter will review evidence relating specifically to the impacts of drivers of change on coccinellids.

Keywords Coccinellidae · Ladybirds · Environmental change · Habitat destruction and fragmentation · Climate change · Invasive species · Overexploitation · Pollution

9.1 Introduction

> Changes in biodiversity due to human activities were more rapid in the past 50 years than at any time in human history, and the drivers of change that cause biodiversity loss and lead to changes in ecosystem services are either steady, show no evidence of declining over time, or are increasing in intensity. (Millennium Ecosystem Assessment 2005)

Human actions have dramatically transformed virtually all of Earth's ecosystems (Millennium Ecosystem Assessment 2005). Current rates of biodiversity change

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P. Kindlmann et al. (eds.), *Aphid Biodiversity under Environmental Change*,
DOI 10.1007/978-90-481-8601-3_9,

and loss exceed by orders of magnitude those historically recorded and show no indication of slowing. Comparisons of recorded extinctions of known species over the last 100 years with rates of extinction of characteristic species in the fossil record indicate that humans have increased the species extinction rate by 100 times (Millennium Ecosystem Assessment 2005). Less direct estimates suggest that current extinction rates are 1,000–10,000 times higher than rates recorded among fossil lineages (Millennium Ecosystem Assessment 2005). Biodiversity change is caused by a range of direct and indirect drivers, whereby direct drivers unambiguously influence ecosystem processes and indirect drivers act diffusely by changing one or more direct drivers. Habitat change, climate change, invasive species, overexploitation and pollution are considered direct drivers with the greatest impact on biodiversity (Millennium Ecosystem Assessment 2005). However, changes in biodiversity and ecosystems are most often caused by the interactions between multiple drivers, across both spatial and temporal dimensions. Following a brief introduction to the biology of ladybirds (Coleoptera: Coccinellidae), this chapter will review evidence relating to the impacts of drivers of change on coccinellids.

9.2 Ladybirds (Coleoptera: Coccinellidae)

Ladybirds belong to the Coleoptera (beetles), a very successful order of insects that evolved about 280 million years ago (Lower Permian). All the modern superfamilies of Coleoptera were established as distinct lineages by the end of the Jurassic. Morphological phylogenies suggest that ladybirds are advanced beetles but molecular evidence suggests that the ladybirds are more closely related to an ancient lineage of Coleoptera, the ground beetles (Carabidae). However, it is widely accepted that the ladybirds constitute a monophyletic family that includes over 5,000 described species worldwide (Howland and Hewitt 1995; Majerus 2003).

There are seven subfamilies of Coccinellidae: Sticholotidinae, Chilocorinae, Scymninae, Coccidulinae, Ortalinae, Coccinellinae, Epilachninae. Most species in the Epilachninae are phytophagous, while the majority of species in the other subfamilies are predatory. The preferred diets of the two feeding stages in the life-cycle, the larval and adult stages, are generally the same. Most predatory ladybirds feed on either aphids or coccids (a few feed on both), however some predatory species feed on mites, adelgids, aleyrodids, ants, chrysomelid larvae, cicadellids, pentatomids, phylloxera, mycophagous coccinellids and psyllids (Dixon 2000). One wingless and blind species, *Cleidostethus meliponae*, has been found in the nests of the bee, *Melipona alinderi*, in East Africa (Salt 1920). A small number of species within the Coccinellinae and Epilachninae are mycophagous, feeding on the hyphae and spores of fungi. There is also considerable variability in the degree of dietary specialisation between species. Thus, whereas some species have a very narrow range of preferred prey, such as a single species of mite, aphids of a single genus, or plants of a single family, other species have a wide prey range. For example, *Harmonia axyridis* will feed on aphids, coccids, adelgids, psyllids, many other insects, including other coccinellids and lepidopterans, and also mites. Adaptations to specific or more general diets are complex, including mandibular dentition, gut length and structure, and morphological features that affect mobility. When preferred prey are scarce, many predatory coccinellids will feed on alternative foods, such as pollen, nectar, honey-dew and fungi, and many also resort to cannibalism (Hodek 1996a).

There is a strong interaction between the dietary preferences of coccinellids and their geographic distributions. At a global scale, for example, aphids are more abundant than coccids in temperate regions and a higher proportion of ladybirds in this climatic zone specialize on aphids than coccids (Dixon 2000). The reverse is the case in the wet tropics. Locally, ladybird densities are strongly correlated to food availability (Majerus 1994).

Ladybirds are holometabolous insects and as such begin their life cycle as an egg, which hatches to give rise to a larva that generally passes through four instars before pupation and metamorphosis into an adult. With only a few exceptions the aphidophagous species lay their eggs in clusters and the coccidophagous species lay their eggs singly or in very small groups. Development rate is dependent on temperature and food quality (Majerus 1994; Dixon 2000). Although the relative lengths of time that coccidophagous and aphidophagous coccinellids spend as egg, larva, pupa and adult are similar for a given temperature, ladybirds specializing on aphids develop faster than coccidophagous, phytophagous or mycophagous species (Dixon 2000).

Coccinellids are found on all the continents of the world with the exception of Antarctica. In the context of this chapter, the distribution of ladybirds needs to be considered at both geographic and local scales. The current geographical distributions of ladybird species are the result of historical events relating to climatic changes, vegetation changes, geographic topography, plate tectonics, and more recently, anthropogenic impacts on land usage (Majerus 1994). Locally, coccinellid distributions depend on food availability, habitat preferences and the degree of habitat specialisation. Thus, while some species are habitat generalists (eurytopic), and may be found in a diverse array of environments, others are restricted to one or a small number of habitat types (stenotopic), and display a suite of adaptations to these specific habitats. *Myzia oblongoguttata* and *Myrrha octodecimpunctata* only breed on needled conifers and, therefore, are stenoptopic. In contrast, *H. axyridis* is little restricted by habitat and so is eurytopic. The distributions of some coccinellids are further affected by the distributions of non-prey species. Thus, for example, some species have little or no tolerance to aggressive ants, and are excluded from foraging within the ranges of these ants. Conversely, other coccinellids, such as *Coccinella magnifica* and *Platynaspis luteorubra* are myrmecophilous, having specific adaptations for living in close proximity to ants (Sloggett and Majerus 2003; Völkl 1995).

Most coccinellids exist in complex ecosytems. Aspects of their life-histories, dietary preferences and habitat preferences, as well as their behaviour, all have pertinence to the issue of coccinellids in a changing world. For example coccinellids vary in mobility and habitat plasticity, particularly the ways in which they cope with unfavorable habitats (*sensu* Southwood 1977), and their interactions with their enemies and competitors and, consequently, will differ in their responses to global drivers of change.

9.3 Main Drivers of Biodiversity Change

9.3.1 Habitat Destruction and Fragmentation

Nearly all of Earth's ecosystems have been dramatically altered through human actions (Millenium Ecosystem Assessment 2005). Indeed the Millennium Ecosystem Assessment (2005) highlights some striking statistics: more land was converted to cropland in the 30 years after 1950 than in the preceding 150 years; 35% of mangrove swamps have been lost in the last two decades; over half of the 14 biomes assessed have experienced a 20–50% conversion to human use, with temperate and Mediterranean forests and temperate grasslands being the most affected. The rate of destruction of some ecosystems has begun to slow but in some cases this is because little habitat remains. Moreover, remaining areas of habitat are often fragmented. Larger remnants and fragments that are close to other remnants exhibit less biodiversity loss than small and unconnected fragments, which are more vulnerable to species extinctions. Furthermore, the edges of habitat fragments, have different climates and favour different species compared to the habitat interior; small fragments are unsuitable for species that favour the habitat interior (Woodroffe and Ginsberg 1998; Laurance et al. 2001). Stenotopic species, which exhibit a narrow relationship with a particular habitat, could be at greater risk from habitat destruction than eurytopic species, particularly if their dispersal ability is also weak. However, the consequences of fragmentation and community dynamics in response to fragmentation are difficult to assess because of the complexity caused by biotic and abiotic interactions at multiple scales (McGarigal and Cushman 2002).

Habitat fragmentation is known to affect arthropods differently depending on the trophic guild with which they are associated and the degree to which they specialize (Davies et al. 2001). Species with a wide host range are more likely to find sufficient resources within a fragment compared to specialists. In addition, generalists are more likely to utilize corridors connecting fragments for nutrition and harborage than are specialists. The habitat and food requirements of different species of coccinellid are diverse and many species are known to be restricted to specific habitats (Honěk and Hodek 1996). At a geographic scale, for example, *Coccinella alta* and *Bothrocalvia lewisi* are high montane species, while *Hippodamia arctica* and *Anisosticta strigata* are sub-arctic species. In Europe, *Anisosticta novemdecimpunctata* and *Macronaemia episcopalis* are restricted to the vegetation of wetlands (fen, marsh and moist meadows); *Adalia conglomerata* and *M. oblogoguttata* to coniferous forests; *Coccinella magnifica* to habitats close to *Formica* ant nests (Honěk and Hodek 1996; Majerus et al. 2006a). A small proportion of coccinellids are much more eurytopic, with species such as *Adalia bipunctata* and *H. axyridis* occurring in a wide range of arbivorous and lower herbage habitats, including many crop systems. The proportion of specialist to generalist species has not been assessed globally, but in Britain, of 42 species, Majerus (1994) categorised 11 to be habitat generalists, ten to be generalists within the constraint of breeding either on trees or on low growing herbage, but not both, and 21 to be habitat specialists.

Studies based on metapopulation and island biogeography theory predict that species occupying higher trophic levels will be more susceptible to the effects of habitat loss than those occupying lower levels (Dobson et al. 2006). It has been demonstrated that parasitoids tend to be more extinction-prone than their herbivore hosts (Cronin 2004) and declines in diversity and abundance of parasitoids result in declines in parasitism rates with increasing fragment isolation or fragment size (Rand and Tscharntke 2007). The loss of higher trophic levels ultimately disrupts top down control of prey populations in natural habitat fragments (Dobson et al. 2006). Many species of ladybird are predatory, occupying higher trophic levels, and have been shown to respond directly to fragment isolation in experiments (Kareiva 1987; Banks 1999). Ladybirds are further predicted to respond to landscape level factors such as habitat fragment area, shape and the structure of neighbouring fragments (Stoner and Joern 2004). In a study on insect communities in tall grass prairie remnants, Stoner and Joern (2004) demonstrated that fragment shape was an important variable in explaining changes in the community composition of coccinellids. This study concluded that species associated with higher trophic levels, such as ladybirds, are more susceptible to fragmentation because of the challenges of recolonisation following local extinction events.

Conversely, it has been speculated that predictions based on island or metapopulation based theory may not apply to generalist predators because they can exploit the intervening landscape matrix (Rand et al. 2006). Indeed, in situations where anthropogenically modified matrix habitats provide resources for generalist predators, such as agricultural systems, spillover into adjacent natural systems could result in increased predator abundance (Rand et al. 2006). Abundance of *Coccinella septempunctata* and *Propylea quatuordecimpunctata*, two relatively generalist ladybird predators, was shown to be decoupled from local resource density but was consistent with spillover effects (Rand and Tscharntke 2007). Both species were more abundant within nettle patches in simple compared to complex habitats, suggesting that these species benefit from the surrounding agricultural habitats (Rand and Tscharntke 2007).

It can be concluded that dietary and habitat generalist and specialist coccinellids should exhibit differing responses to habitat loss and fragmentation. It is widely accepted that some species of coccinellid are dominant predators, impacting aphids in natural habitats as a consequence of spillover from cropland habitats (Kareiva 1987; Müller and Godfray 1997). In addition, coccinellids are highly voracious compared to many other natural enemy taxa (Müller and Godfray 1997) and so their impact on prey populations is likely to be disproportionate to their abundance (Rand and Tscharntke 2007). However, there is an absence of empirical work examining the effects of habitat loss on the abundance of a broad assemblage of natural enemies, including coccinellids. Understanding the cumulative effects of habitat loss on predator-prey interactions, and even single species, requires such an approach. Meanwhile the literature is in conflict. The prevailing view that the loss of natural habitat will disrupt predator-prey interactions in natural systems is disputed by Rand

and Tscharntke (2007). This ambiguous view is undoubtedly a consequence of the concentration of research on a relatively small number of coccinellid species that have economic importance as biological control agents. For example, in an analysis of the literature on coccinellids published between 1995 and 2004, Sloggett (2005) showed that in 623 papers found, only 62 species were studied. Moreover 40% of the studies described concerned just two species, *C. septempunctata* and *H. axyridis*, with three further species, *Coleomegilla maculata*, *A. bipunctata* and *Hippodamia convergens* together comprising another 29% of the studies. All of these species are eurytopic and aphidophagous. Given this extreme knowledge bias, it is obvious that research is needed on the habitat requirements and responses to habitat change of a suite of coccinellids with differing levels of habitat specialization before informed conclusions on the effect of habitat destruction and fragmentation can be made. Undoubtedly, the impact of habitat destruction and fragmentation on a particular species of coccinellid will crucially depend on the degree of specialization of that species.

9.3.2 Climate Change

Recent changes in climate, particularly warmer temperatures, have already begun to impact on biodiversity and ecosystems. Changes in species distributions, population sizes, the timing of reproduction and migration events, and in the frequency of pest and disease outbreaks have all been documented and linked to elevated temperatures. The Intergovernmental Panel on Climate Change predicts an increase in global mean surface temperature of 2–6.4°C above pre-industrial levels by 2100, increased incidence of floods and droughts and a rise in sea level of an additional 8–88 cm between 1990 and 2100. In some regions, ecosystem services could be enhanced by low levels of climate change but at high levels detrimental impacts will vastly outweigh the benefits in most biomes (Millenium Ecosystem Assessment 2005). Indeed, climate change scenarios are predicted, with medium to high certainty, to increase the loss of biodiversity and the risk of extinction for many species (Parmesan and Yohe 2003). There are a number of factors that will exacerbate the situation for some species: low population sizes, limited range of accepted food, high degree of habitat or host plant specificity and limited climatic range.

The importance of the relationship between ladybirds and temperature is widely recognized. Interestingly, the names adopted by some nations for these much loved insects exemplify this; in the Czech Republic they are called slunéčka (small suns) and in Japan they are known as tento mushi (sun loving insects). The importance of climate, particularly microclimate, to coccinellid development and behaviour has been demonstrated in a number of studies. Smith (1971) working in maize, showed that the temperature difference between low density stands and cooler high density stands could be as much as 8.6°C. *Coccinella transversoguttata* and *Coccinella novemnotata* preferred the higher temperature, low density stands, while *C. maculata* and *Hippodamia tredecimpunctata* sheltered from the hottest temperatures in the high density crop. Honěk (1979) found a similar situation in temperate cereal crops, where *C. septempunctata* and *Coccinella quinquepunctata* preferred sparse and well-insolated stands with a warm microclimate, while *P. quatuordecimpunctata* tolerated dense stands with a much cooler microclimate. Ewert and Chiang (1966) demonstrated that ladybirds also exhibit humidity preferences. The vertical distribution of *H. convergens*, *H. tredecimpunctata* and *C. maculata* in barley corresponds to preference for specific humidities within the crop. The humidity preferences of these species were correlated with their resistance to desiccation. The daily movement of ladybirds on host plants further illustrates the importance of microclimate. For example, Benton and Crump (1981) observed a regular pattern of *C. maculata* climbing up the vegetation in the morning, and returning to lower levels in the afternoon. Some species, such as *C. septempunctata*, increase their body temperature through thermoregulatory behaviour that leads them to seek out bare ground, or insolated regions of the host plant (Honěk 1985).

Oviposition behaviour also reflects microclimatic preferences. *Coccinella septempunctata* often lay eggs on bare, insolated soil or upper leaf surfaces (Ferran et al. 1989). *Adalia bipunctata* and *Anatis ocellata* lay eggs on lower leaf surfaces, which is thought to be an anti-predator strategy, but the lower leaf surface also provides a humid and cool environment (Hodek 1996a). Risk of predation on the lower leaf surface is likely to be lower than on the upper leaf surface because predatory insects will forage primarily on the warmer, upper leaf surface. The reduced risk of mortality may outweigh the advantage of faster development that could be achieved on the upper leaf surface. Indeed, Lövei et al. (1991) demonstrated that ladybirds select more sheltered oviposition sites as temperature increases. Therefore, it appears that at elevated temperatures the cost-benefit balance tends towards oviposition site selection that reduces predation at the expense of rapid development.

Coccinellids usually survive seasonally unfavourable conditions in the adult stage. For ladybirds, unfavourable conditions may be a consequence of lack of food or adverse climatic factors, i.e. low temperatures, very high temperatures, or very dry conditions. If climatic conditions are favourable when food becomes scarce, ladybirds generally disperse to seek food elsewhere. Conversely, under unfavourable climatic conditions, ladybirds become inactive, some species entering programmed diapause, while other species simply become dormant or quiescent. The difference between these states is important in the context of potential climatic change. Quiescence involves a response to periods of sudden, unpredictable weather; the ladybirds simply become inactive but resume activity as soon as conditions become favourable again. Dormancy (also known as oligopause) is a response to unfavourable conditions that are seasonally predictable. Ladybirds become inactive, generally for a fixed period, surviving on fat reserves, but they are capable of becoming active to feed for short periods within the unfavourable period if conditions permit. Diapause is also a response to predictably unfavourable seasons, and follows a preparatory period in which ladybirds build up their fat reserves and either do not mature their gonads, or reabsorb their eggs. Ladybirds in diapause do not become active in brief favourable periods, and cannot reproduce until diapause is terminated.

In some species, a diapause before reproduction is obligatory and genetically programmed (Dobrzhanskii and Dobzhansky 1922), but for many species, induction of diapause is a very plastic response initiated by one or more environmental factors. The factors that induce dormancy or diapause vary among species of coccinellid, with the nature and availability of food, day length, temperature, humidity and the physiological state of host plants all being involved in some species (reviewed by Hodek 1996b). The likelihood that an individual ladybird survives through a dormant period is dependent on the level of reserves that it has accumulated prior to dormancy (Hodek and Cerkasov 1963; Barron and Wilson 1998). Fat, glycogen and water reserves all diminish during dormancy, with rates of reduction being affected by changes in ambient temperature, and in the case of water loss, humidity. For overwintering coccinellids, fluctuating temperatures or abnormally high temperatures generally cause reserves to be used up faster than do constant low temperatures (Majerus 1994). Consequently, increases in winter temperature or in fluctuations in winter temperatures due to climate change may lead to increasing rates of winter mortality in species with genetically controlled obligatory diapause.

Some coccinellids make lengthy migration flights to and from dormancy sites, but others remain in, or close to, their preferred breeding habitats during unfavourable seasons. Some of the species that migrate before becoming dormant form large overwintering (e.g., *H. convergens*) or aestivating (e.g. *Micraspis frenata*) aggregations. Such behaviour is most common in species that feed on aphids, which are notoriously ephemeral. These overwintering sites are often at high altitude, where temperatures through the winter are low and so the rate of depletion of reserves is minimised. In some species, such as *H. convergens* in California, movement to and from montane overwintering sites is dependent upon specific autumn and spring winds (Hagen 1962). Such movement may be perturbed by climate changes to the detriment of the ladybird populations.

The relationship between coccinellids and climatic factors are complex, varying temporally and spatially, and with life stage. Although it may be expected that ladybirds will be negatively affected by climate change, direct empirical evidence is sparse. However, at a local level there are some indications that climatic changes are already influencing annual cycles. In Britain, survey data from 1980 to the present day suggest that *C. septempunctata* movement from overwintering sites, earliest mating and earliest eclosion have all shifted 11–18 days earlier in spring over the last 25 years (Majerus unpublished data). There is no indication whether these changes have had a positive or negative effect on populations of this species. However, such rapid changes do have the potential to temporally decouple predators from peaks in abundance of their preferred prey. There are several potential consequences of such a decoupling: aphid populations may suffer reduced predation by coccinellids, intraguild predation may increase as coccinellids turn to alternative prey, and cannibalism may increase, reducing coccinellid numbers.

Some of the more generalist species of ladybird have been shown to exhibit phenotypic plasticity, which could be adaptive under scenarios of climate change, and help buffer these species against some of the detrimental effects of changing climatic factors. *Adalia bipunctata* is a highly polymorphic species (Majerus 1994), in which the various genetic forms can be broadly classified into melanics (black with red spots) or non-melanics (red with black spots). The frequency with which these colour morphs occur varies geographically (Brakefield 1984). Clines in melanism in The Netherlands have become shallower (relative decrease in melanic forms) over time (1978–1998) and this change has coincided with an increase in local ambient spring temperatures (De Jong and Brakefield 1998). The authors invoke the thermal melanism hypothesis, whereby an increase in temperature is predicted to reduce the contribution of radiation to warming up of ladybirds. It is speculated that lower minimum temperatures (east Netherlands) are consistent with a large advantage to melanics when warming up early in the day. Other highly polymorphic species include *H. axyridis*, *Cheilomenes sexmaculatus*, and *Propylea japonica*, all of which are eurytopic.

Some species are euryotopic near the centre of their geographic distributions and stenotypic at the edges of their range (Majerus 1994). Indeed, close to the edge of their range they may only be able to survive through adaptation to some specific type of habitat. *Coccinella quinquepunctata* appears highly eurytopic in continental Europe, but in Britain (Fig. 9.1) its known distribution is confined to unstable river shingles in west Wales and the Spey Valley in Scotland. Global warming could result in *C. quinquepunctata* increasing in distribution across Britain. *Hippodamia tredecimpunctata* (Fig. 9.2) is sporadically reported on the south and east coasts of Britain where it appears to arrive from continental Europe and establish small colonies that soon become extinct (Majerus 1994). Climate change may be favourable for the long term establishment of *H. tredecimpunctata* in England in the future. *Halyzia sedecimguttata* has increased in abundance in Britain over recent years. This mildew feeding species was considered to primarily feed on mildews on sycamore but recently has been found more widely on deciduous trees (UK Ladybird Survey, unpublished data). Warmer, wetter springs in Britain could have increased the prevalence of mildew and the distribution of *H. sedecimguttata* could have increased in response to this available food. The UK Ladybird Survey (www.ladybird-survey.org) will be investigating this further. There will undoubtedly be winners and losers as a consequence of climate change but the exact nature and balance of outcomes is hard to predict because of the complexity of interactions and lack of available data.

Climatic factors are likely to influence the dynamics of interactions between ladybirds and their prey, predators and parasites. For example, short range clinal variation in the prevalence of a sexually transmitted Laboulbeniales fungus (*Hesperomyces virescens*) infecting *A. bipunctata* is associated with urbanization and has been linked with increased temperatures within the urban environment (Welch et al. 2001). A second sexually transmitted parasite of *A. bipunctata* may also be affected by climate change. The ectoparasitic mite *Coccipolippus hippodamiae* infects *A. bipunctata* over much of continental Europe, but is absent from Britain (Webberley et al. 2006). Hurst et al. (1995) have attributed the absence of this mite from British populations of *A. bipunctata* to the lack of transmission between generations in the occasional years when the species is fully univoltine (in most of continental Europe, *A. bipunctata* has two or more overlapping generations per year) and the old generation dies before the new generation is reproductively

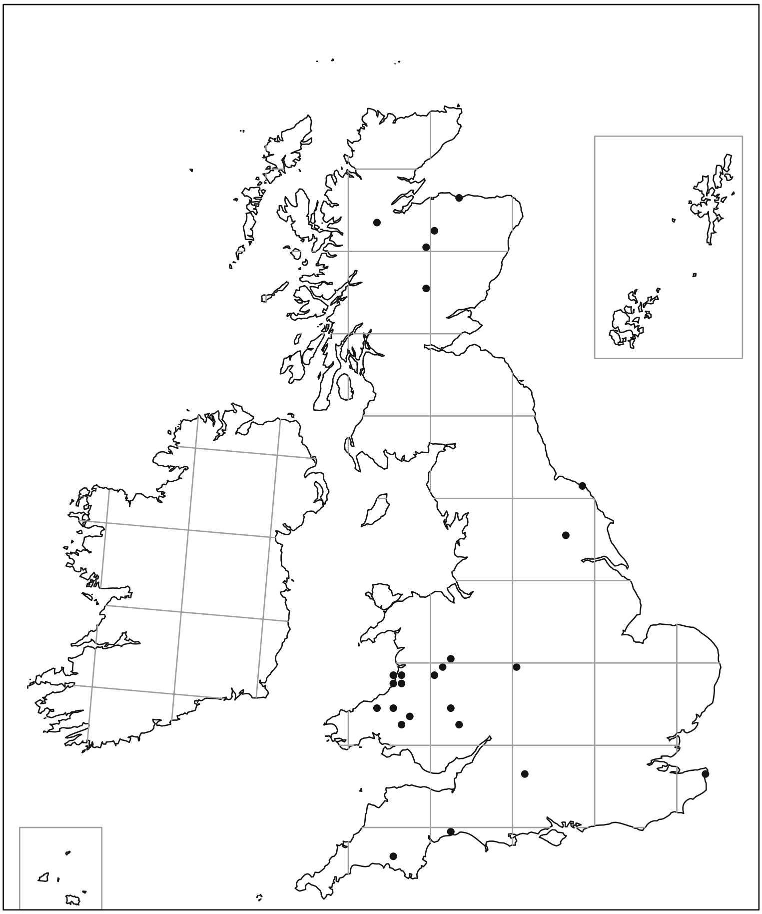

Fig. 9.1 Distribution of *Coccinella quinquepunctata* in Britain where it is confined to unstable river shingles in west Wales and the Spey Valley in Scotland (data from 1832 to present). Data from the UK Ladybird Survey, Biological Records Centre

active. From surveys over the last 28 years, such years are becoming less common, at least in southern England (Majerus unpublished data). Increasing temperatures are, therefore, likely to increase the probability of long-term survival of this mite in British populations of *A. bipunctata*. As *C. hippodamiae* has a severe impact on the female ladybirds it infects – eggs laid by females more than 3 weeks after becoming infected fail to hatch (Hurst et al. 1995) – this is likely to have a negative impact on *A. bipunctata* populations.

Studies of the effects of current climate changes on coccinellids at a more global scale are lacking. However, examination of coccinellid remnants in Quaternary deposits allows for some inferences. The Quaternary Period, from 2.4 million years ago to present, has been characterised by numerous intense climatic oscillations, particularly at higher latitudes. Climatic oscillations resulted in many coccinellids

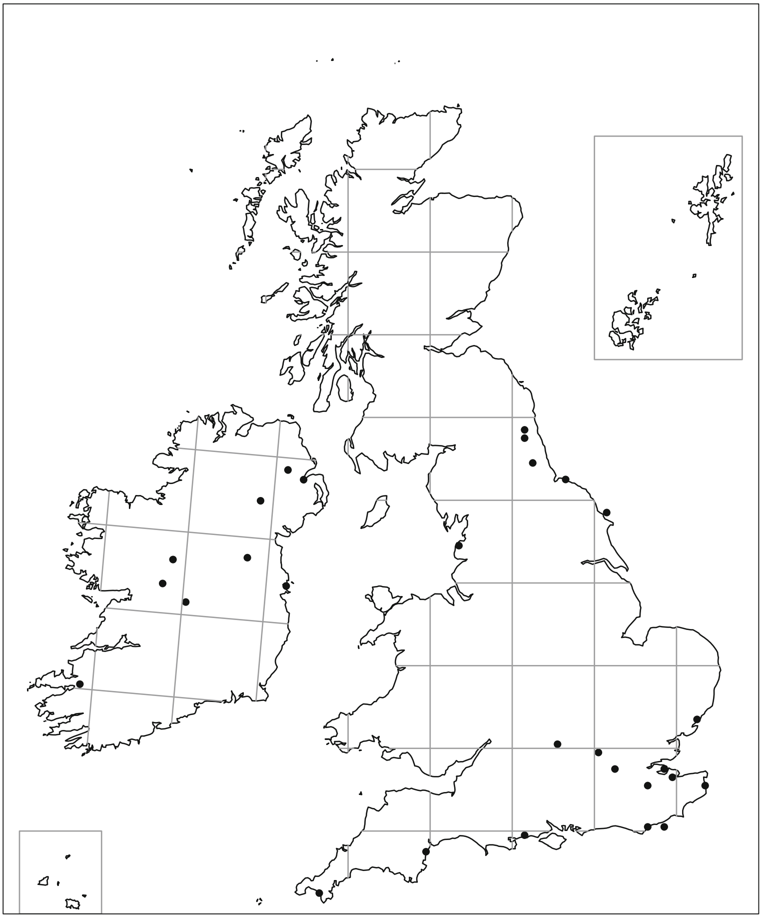

Fig. 9.2 Distribution of *Hippodamia tredecimpunctata* in Britain where it appears to arrive from continental Europe, establishes small colonies and these then become extinct (data from 1819 to present). Data from the UK Ladybird Survey, Biological Records Centre

changing their geographic ranges dramatically, particularly with respect to latitude, but also in some cases with respect to altitude. For example, *H. arctica* was common in Britain 40,000 years ago during the Upton Warren Interstadial and up until about 25,000 years ago, when it disappeared as temperatures declined further during the Late Weichselian Glaciation. A little over 13,000 years ago it reappeared, presumably from the south, moved northwards through Britain as temperatures increased, and disappeared again, only to reappear from 11,000 to 10,000 years ago in the cooler Younger Dryas period (Osborne 1971). It then disappeared yet again, and has not reappeared. In Europe, the species is now restricted to the north of Sweden and Norway, mainly within the Arctic Circle. A similar pattern is seen in *A. strigata* (Majerus 1994). The enormity of potential geographic range alterations is illustrated by the ladybird *Ceratomegilla ulkie* which was recorded from an organic silt from the River Thames around 40,000 years ago (Briggs et al. 1985), is now absent from Europe, but still occurs at high latitudes or high altitudes in north-western Canada and north-eastern Asia.

This pattern suggests that, on continental scales, coccinellids move rather than adapt. When possible, they maintain environmental constancy rather than geographic constancy. Only when dispersal is not possible due to barriers of unfavourable habitats must they evolve or die. This means that permanent, relatively continuous latitudinal wildlife corridors are essential to allow species (particularly stenotopic species) to mobilize for survival as climate changes. The alternative is that these species will have to adapt to new environmental conditions, and due to the speed of the climatic changes that we are now experiencing, it is likely that some stenotopic species will simply not be able to adapt quickly enough to avoid extinction.

9.3.3 Invasive Species

> I have an unnerving nagging at the back of my mind that faunal and floral homogenisation is among the most detrimental of the ways in which humanity is affecting the Earth (Majerus 1994, p 311)

The distribution of species on Earth is becoming increasingly homogeneous for two main reasons: species are experiencing higher rates of extinction and rates of invasion and introduction are accelerating with increased trade and transportation (Millenium Ecosystem Assessment 2005). Invasion and extinction are not mutually exclusive; invasive alien species have been a major cause of extinction, particularly on islands and in freshwater habitats. Many coccinellids are threatened by invasive species and a small number of species have been implicated as invasive species themselves.

Classical biological control involves the introduction of a non-native natural enemy to control an exotic pest. Ladybirds have a long history of use as biological control agents against pest insects (Majerus 1994). In 1888, the Australian vedalia ladybird, *Rodolia cardinalis*, was released in California to control cushiony scale, *Icerya purchasi*, which were having devastating impacts on the citrus industry (DeBach 1964; Majerus 1994). This ladybird established and effectively reduced the scale insect population, an event widely regarded as marking the advent of modern biological control. Indeed, ladybirds are often considered flagships of biological control and the predatory habits of many species of ladybird have no doubt contributed to their popularity. Ladybirds are much-loved worldwide, but there is one species *H. axyridis*, that has become extremely unpopular outside of its native range over the last two decades for a number of reasons (Roy et al. 2006; Majerus et al. 2006b). First, it threatens the diversity of native aphidophagous species through direct competition for prey and as a voracious, intraguild predator (Majerus et al. 2006b; Pell et al. 2008). Second, it is considered a pest species in the USA because at times it feeds on soft fruits, adversely affecting the wine and fruit growing industries (Koch 2003; Koch et al. 2004; Kovach 2004). Third, it overwinters at high densities in buildings (thousands of individuals) and is consequently regarded as an urban nuisance (Kovach 2004). In addition, it is likely to adversely impact many non-target aphids and coccids, and has been shown to attack the immature stages of butterflies and many other insects. *Harmonia axyridis* has become perhaps the most infamous of invasive insects in the twenty-first century.

Harmonia axyridis was first introduced into the USA as a biological control agent of pest insects in 1916 (Gordon 1985). Many further releases were made, but the species failed to establish until the 1980s, when it was found in south-eastern Louisiana (Chapin and Brou 1991). It is now widespread across the USA and has spread into Canada (Koch and Galvan 2008). Intentional introductions of *H. axyridis* were made across Europe (Belgium, Czech Republic, France, Germany, Greece, Italy, Netherlands, Portugal, Spain and Switzerland) beginning in the early 1980s and the species is now considered established in all these countries, with the exception of Portugal and Spain (Brown et al. 2008). Inevitably, *H. axyridis* arrived in countries where it had not been deliberately introduced. By 2004. it had arrived in England and Luxembourg; in 2006 it was reported in Austria, Denmark, Wales and Norway; in 2007 Liechtenstein, Sweden and Northern Ireland (Brown et al. 2008). It has also been introduced and established in Egypt, South Africa and Argentina. In many parts of North America and Western Europe it is now the most abundant coccinellid species (Fig. 9.3).

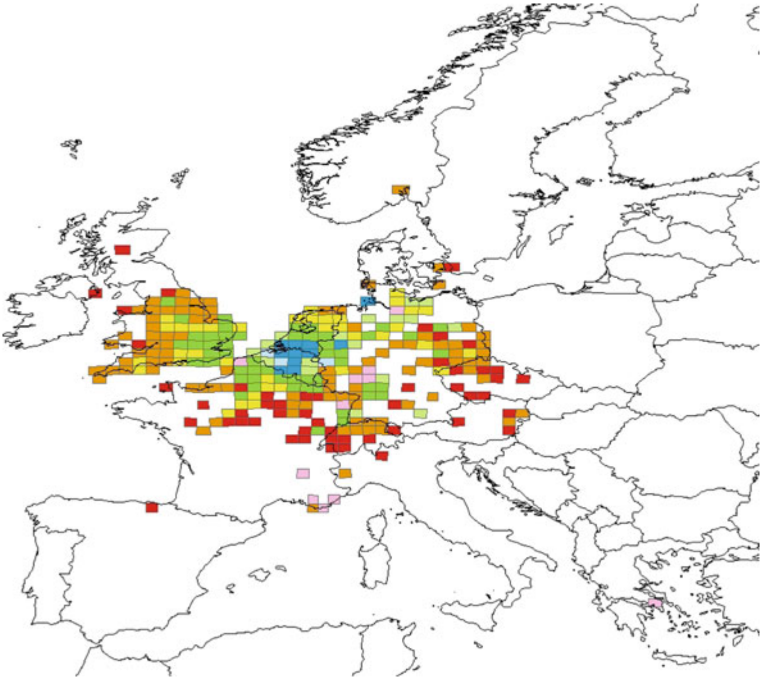

Fig. 9.3 European distribution of *Harmonia axyridis*. Adapted from Brown et al. (2008)

The success of *H. axyridis* as an invasive species is attributed to a number of factors including its size, voracity, reproductive potential, dispersive ability, eurytopy, and polyphagous habits (Evans 2000; Majerus et al. 2006b). Moreover, *H. axyridis* is a unidirectional intra-guild predator (Hironori and Katsuhiro 1997; Cottrell and Yeargan 1998; Phoofolo and Obrycki 1998; Michaud 2002a; Sato et al. 2003; Felix and Soares 2004; Snyder et al. 2004; Amkar 2006; Kajita et al. 2006; Cottrell 2007). As such, it is thought to be an important force in structuring aphidophagous guilds through direct impacts on other species of coccinellid (Yasuda and Shinya 1997; Kajita et al. 2000) and their prey (Majerus et al. 2006b).

Ware and Majerus (2008) examined intra-guild predation (IGP) of immature stages of British and Japanese coccinellids by *H. axyridis*. Thirteen species of coccinellid were included in this study: *H. axyridis*, *C. septempunctata*, *A. bipunctata*, *Adalia decempunctata*, *P. quatuorodecimpunctata*, *Calvia quatuordecimguttata*, *A. ocellata*, *Harmonia quadripunctata*, *C. quinquepunctata*, *C. septempunctata brucki*, *C. sexmaculatus*, *P. japonica* and *Eocaria muiri*. First instar *H. axyridis* larvae were considered unidirectional intra-guild predators of first instar *A. decempunctata*, *P. quatuordecimpunctata* and *C. quinquepunctata* and bidirectional intra-guild predators of *C. septempunctata*, *A. bipunctata*, *C. quatuordecimguttata* and *H. quadripunctata*. The only unidirectional intra-guild predator of *H. axyridis* was *A. ocellata*, a large British coccinellid (Majerus et al. 2006b). Fourth instar *H. axyridis* dominated as unidirectional intra-guild predators of other fourth instar coccinellid larvae (Ware and Majerus 2008).

These studies indicate the potential for *H. axyridis* to disrupt the community structure of aphidophagous coccinellids. Furthermore, the complexity and unpredictability of ecological impacts of invasive intraguild predators contribute to a high risk of adverse interactions when such species are intentionally introduced (Snyder and Evans 2006). *Harmonia axyridis* has been shown to be a dominant intra-guild predator in the field and in its native Japan it has limited the establishment of the introduced *A. bipunctata* (Sakuratani et al. 2000; Kajita et al. 2006). In contrast, *H. axyridis* has become abundant and widely distributed through North America and Europe (Brown et al. 2008) and is negatively impacting native ladybird species (LaMana and Miller 1996; Elliott et al. 1996; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Michaud 2002a; Nault and Kennedy 2003). *Coccinella septempunctata* has also become established widely in North America but *H. axyridis* is considered to be a more aggressive predator than *C. septempunctata* (Yasuda et al. 2004). Indeed, larvae of *H. axyridis* consume those of *C. septempunctata* but the reverse is considerably less frequent (Hironori and Katsuhiro 1997). Consequently, *H. axyridis* represents a considerable threat to indigenous ladybirds through intra-guild predation (Snyder et al. 2004).

9.3.4 Overexploitation

The one direct driver that is unlikely to have any strong negative impacts on coccinellids is overexploitation. This is because the coccinellids that have been exploited for biological control have a high reproductive potential, and because releases usually involve large numbers of ladybirds that have been cultured in captivity from relatively small samples of field-collected material. The one exception to this involves augmentative biological control using the North American coccinellid, *H. convergens*. This species has been collected in huge numbers from overwintering aggregations in mountains in America for over a 100 years. The ladybirds collected are bottled alive and stored in carefully controlled conditions until the spring when they are sold, by the pint or gallon, through garden centres or by mail. This practice does not appear to have had any detrimental effects on populations of *H. convergens* although the ladybirds are translocated away from their native habitat and released to control aphid species that may not even comprise suitable prey. For example, in the 1990s, a shipment of 30 million *H. convergens* were released onto *Tilia* trees lining roads in Dutch towns, to reduce aphid populations and thereby reduce amounts of aphid honeydew that fell onto parked cars. The project failed because the ladybirds all disappeared within a few weeks. One has to question the sense of releasing a species that relies on montane overwintering sites into a country that is devoid of mountains.

Although ladybirds have not suffered from overexploitation, it could be argued that the ill-advised releases of inappropriate species, such as *H. axyridis*, comprise cases of, if not overexploitation, then very unwise exploitation.

9.3.5 Pollution

Over the last 40 years pollution, particularly nutrient loading into ecosystems, has emerged as one of the most important drivers of change (Millenium Ecosystem Assessment 2005). More than half of all the synthetic nitrogen fertilisers ever used on Earth have been used since 1985 (Millenium Ecosystem Assessment 2005). Nitrogen application has increased five-fold since 1960 and up to 50% of the nitrogen applied will be lost to the environment and contribute to nitrous oxide emissions, eutrophication and hypoxia in marine environments (Millenium Ecosystem Assessment 2005). Global atmospheric CO_2 has risen from 280 μl/l in 1,700 to 370 on μl/l (Chen et al. 2007). It is predicted that elevated CO_2 will have profound impacts on species and communities altering trophic interactions between plants, herbivores and natural enemies. There have been many studies on the responses of plants and herbivores to elevated CO_2 (Coviella and Trumble 1999) but studies on higher trophic levels are lacking. Chen et al. (2007) assessed the impact of elevated CO_2 on *H. axyridis* and found no effect on growth and development. However, Chen et al. (2005) found that *H. axyridis* larvae consumed more cotton aphids, *Aphis gossypii*, fed elevated CO_2-grown cotton plants in order to compensate for the reduced soluble protein in cotton aphid. Plants grown in elevated CO_2 treatments have decreased foliar N and an increased C:N ratio. In contrast, elevated CO_2 did not influence aphid consumption rate by *H. convergens* (Stacey and Fellowes 2002). Clearly, there is a need for further studies on more species and with a greater range of environmental pollutants before any generalisations can be made.

The use of insecticides with low toxicity to natural enemies, including predatory coccinellids, is an important component of integrated pest management (Grafton-Cardwell and Gu 2003; Galvan et al. 2005). Consequently a number of studies have evaluated the toxicity of insecticides to species of coccinellid that are deemed agriculturally important by providing ecosystem services, namely pest control. *Harmonia axyridis* exhibits tolerance to fungicides (Michaud 2001), acaricides (Michaud 2002b) and some insecticides (Michaud 2002c). However, densities of *H. axyridis* were higher in field plots treated with spinosad or indoxacarb (new insecticides with high toxicity to pest insects and negligible toxicity to natural enemies) than in those treated with conventional insecticides such as carbaryl, chlorpyrifos, bifenthrin and λ-cyhalothrin (Galvan et al. 2005). Indeed, conventional chemicals were highly toxic to *H. axyridis*. The least toxic chemical insecticide to *H. axyridis* is spinosad; higher densities of *H. axyridis* were found in the spinosad-treated plots than the indoxacarb plots (Ochou and Martin 2003; Galvan et al. 2005). Toxicity of insecticides to this coccinellid varies with life stage: eggs and pupae are the most resilient stages to chemical insecticides and larvae followed by adults, which are the most susceptible (Youn et al. 2003).

Most studies on non-target impacts of insecticides consider only direct mortality through acute toxicity. Further work is required to examine residual activity and potential sublethal effects (such as reduced fecundity or disruption of predatory behaviour). Adult *Rodolia cardinalis* exposed to neonicotinoid imidacloprid and the pyrethroid cyfluthrin exhibited high mortality and progeny production was reduced by these chemicals and also fenpropathrin and buprofezin (Grafton-Cardwell and Gu 2003). Larval development to adulthood was also reduced after exposure to all these chemicals and also to pyriproxifen. Interestingly, neem-fed prey were not toxic to *Harmonia conformis* but were to the neuropteran *Mallada signatus* (Qi et al. 2001) indicating the specific nature of insecticidal activity.

In the UK, 47% of the 1.12 million tons (dry solids) of sewage sludge produced annually is applied to agricultural land as a fertiliser (Gendebien et al. 1999; Green et al. 2003). However, sludge contains a wide range of potentially toxic elements including cadmium and zinc. Indeed, although trace metals enter agroecosystems from other sources (atmospheric deposition and use of agrochemicals), sewage sludge is the principal source of trace metal addition to agricultural soils (Nriagu and Pacyna 1988). Green et al. (2003) examined the transfer of cadmium and zinc from sewage sludge amended soil through a plant-aphid system to newly emerged adult *C. septempunctata*. Cadmium was not biomagnified by the crop during transfer from soil to aphid but zinc was, resulting in concentrations four times greater in the aphids. However, there was no increase in the body burden of either metal in newly emerged *C. septempunctata*, larvae of which sequestered zinc in the exuviae and consequently regulated the body burden of zinc effectively (Green et al. 2003). The authors conclude that from an economic and ecological perspective soil trace metal concentrations added through sewage sludge application remain below levels detrimental to coccinellids. However, Green et al. (2003) add a precautionary note that is applicable to many studies relating to pollution effects on coccinellids: it has been demonstrated that increased trace metal concentrations in the diet of coleopteran larvae can cause changes in adult locomotive behaviour without significantly affecting the body burden of the adult. This highlights the need to assess the subtle interactions (on a species by species basis) that may be at play, but are often overlooked, in these systems. Indeed a study on copper-based fungicides (used for controlling foliar diseases in citrus production) demonstrated that three species of coccinellid (*Curinus coeruleus*, *H. axyridis* and *Olla v-nigrum*) exposed to residues survived to adulthood, but larvae of *O. v-nigrum* experienced a significant increase in developmental time, pre-reproductive period and decrease in fecundity than unexposed beetles. The other two species were unaffected by exposure (Michaud and Grant 2003).

9.4 Summary

Biodiversity and ecosystem services experience change due to natural causes, but current changes are dominated by anthropogenic drivers. The most important direct drivers of biodiversity loss and ecosystem service changes are habitat change, climate change, invasive alien species, overexploitation and pollution (Millennium Ecosystem Assessment 2005). All these, with the exception of overexploitation, impact coccinellid populations. However, empirical evidence is sparse or lacking for most of these drivers in respect of the vast majority of coccinellid species. Consequently, it is not possible to reliably predict the magnitude of these anthropogenic factors on coccinellid species worldwide. Moreover, there is a tendency in both research and review to consider each of these drivers independently, even though these drivers do not act in isolation from one another. In our discussion of habitat destruction and fragmentation, we noted that high levels of habitat specialisation and low mobility increase the vulnerability of coccinellids to loss of favourable habitats. In considering climate change, we have noted the importance of north–south wildlife corridors to allow specialised species to maintain environmental constancy. If one considers these two drivers together, it is obvious that habitat specialists, that also have limited climatic niches, are in a very precarious position. The habitats that they currently occupy may well become unfavourable, not due to habitat loss, but through climatic change. However, due to habitat fragmentation, the nearest favourable patch that provides a suitable climatic niche may now be far outside the dispersal range of these species. Add in additional pressures imposed by highly competitive invasive eurytopic species, such as *H. axyridis* and *C. septempunctata*, and pollution effects, and the future for many stenotypic species may be bleak. Strangely, the conclusions from the evidence available in the literature are conflicting. However, this is probably because the vast majority of studies on coccinellids have been on species that are of agricultural importance (providing an ecosystem service of pest control). Many of these species have been chosen specifically because they exhibit behaviours that contribute to their resilience, stability and success as biological control agents (polyphagous, eurytopic predators which exhibit phenotypic plasticity). Most known species of coccinellid have received little or no attention, and at least half of these are habitat specialists with both narrow food ranges, and narrow climatic niches. It is difficult to assess the impact that anthropogenic factors will have on most species of coccinellid but logic suggests that the direct anthropogenic drivers of environmental change, both individually and in concert, will be highly deleterious to all but the most adaptable and eurytopic coccinellids. We conclude with one of the key messages of the Millennium Ecosystem Assessment (2005):

Science can help ensure that decisions are made with the best available information, but ultimately the future of biodiversity will be determined by society.

Acknowledgements HER is supported by the Natural Environment Research Council through the Centre for Ecology & Hydrology. HER is based in the Biological Records Centre (Centre for Ecology & Hydrology) which is co-funded by the Joint Nature Conservation Committee. Professor Michael Majerus, an inspiration to many coccinellid biologists, sadly died in 2009. He will be missed tremendously by many collaborators and friends worldwide. Leaving the final words of this chapter to Mike (Majerus, 1994): *"If my ideas and theories are subsequently put to the test by others who are caught up in the fascination of ladybirds as much as I have been in the last dozen or so years, I will be delighted, whether my ideas are verified or refuted."*

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