Chapter 4

DISTRIBUTION AND HABITATS

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4.1 INTRODUCTION

In the present epoch of molecular and mathematical approaches to biology we may ask, at the beginning of this chapter, why should one review and stimulate research of something as basic and simple as studies of coccinellid habitats? Our response is that habitat studies, i.e. the study of where coccinellids live, are indispensable. Knowledge of where the coccinellid lives provides basic information necessary for studies of ecology (determining species niches), ecophysiology (food and microclimatic preferences), biogeography (the factors limiting coccinellid distribution) and other disciplines. Habitat studies thus link natural reality with theory. Predictions of hypotheses derived from biological theories could of course be tested in the laboratory, if not solely on a computer. However, the final proof of the reality of such predictions can be done only after relating the ideas back to nature, and this means studying the presence and habits of coccinellids in natural habitats. Therefore the methods and results of habitat studies are of utmost importance. In this chapter we review the methods of collection and description of data concerning habitats, and interpret them in terms of the factors that cause variation in abundance while trying to keep a balance between earlier results and recent. Examples of coccinellid communities from economically important crops or intensively studied natural biotopes are provided and discussed at the end of this chapter.

The main difficulty of habitat studies is to define **what is the 'habitat'**. Man has a tendency to view his environment in terms of his own activities. Crops, gardens, forests or urban areas are automatically recognized as habitats. However, the vegetation, although uniform from our point of view, may be a mosaic of environments with often dramatically differing qualities. On the other hand, natural objects which appear different to our perception may be part of an integral habitat from the point of view of coccinellids. Two adjacent and evenly developed crops of different cereal species, two rows of garden trees each of a different species may represent a uniform habitat because of the absence of any difference that is important for the coccinellids. Since coccinellids can distinguish and select habitats with the qualities important to them, we too should aim to distinguish the boundaries of habitats and consider the environment from the 'point of view of a coccinellid'. Here we try to show some factors important for coccinellid decisions. The selection of these factors is based on our personal experience and is probably far from complete. However, we believe that considering at least these factors may contribute to understanding coccinellid distribution.

A habitat is populated by a specific **community of coccinellid species**. Here, the term 'community' is used in its broadest sense as a set of coccinellid individuals present in a given habitat at a particular time. We prefer this vague terminology over a detailed definition. Such a definition usually includes information concerning the previous history of the community (permanence in time, details of its origin) or the motivation of the animals that make up the community (hibernation, search for food). In the field, even the obvious causes are difficult to understand and including further criteria would only add a good deal of speculation. Perhaps this remark is superfluous since, in fact, use of the vast terminology attempting to classify communities is in decline, leaving room for new understanding of factors contributing to the structure of communities.

4.2 SAMPLING

Sampling is the initial phase in investigating the presence of coccinellids in a particular habitat. We may be interested in the proportion of different species in the entire family Coccinellidae (relative abundance), or in the absolute abundance (i.e. numbers per unit area). Maximizing the reliability of sampling is a prerequisite for making correct ecological conclusions and already at this stage of investigation there arise problems. Each sampling method only provides a differently biased estimate of relative and absolute abundance. The bias may arise from several sources: uneven distribution of species in the vegetation cover; different behaviour of coccinellids in relation to daily changes of light intensity, temperature and humidity; fluctuations of weather; different escape reactions of species and stages during the sampling procedure; different conspicuousness to the collector. Generally, it is easier to collect adults than larvae, and the first and second instars cannot be counted with any accuracy in the field. Here we review the different methods used for sampling coccinellids, how they are influenced by environmental factors and the efforts that have been made to standardize their results under different conditions, as well as attempts to recalculate 'absolute' from 'relative' abundance.

Several methods were tested for sampling from **herbaceous stands**. Collecting coccinellids by **hand-picking** from small plots ('quadrat sampling') was the sampling technique that gave the highest estimates of numbers per unit area, probably giving densities close to the true coccinellid abundance (Michels et al. 1997). True numbers of coccinellid adults and larvae were established by sampling out a 1 m^2 area fenced by a 40 cm plywood enclosure, until both plants and ground were clean of the insects. This method could be recommended for future studies as the yardstick of 'true abundance' of coccinellids for evaluating the efficiency of other methods. Lower abundances were obtained by 'removal sampling', which consisted of two 15-min periods of picking coccinellids from an unfenced area of 25 m^2. The differences between the results of both these methods were not significant for three (*Hip. convergens, Hip. sinuata, C. septempunctata*) species but not for *Col. maculata* (Michels et al.1997).

Sweeping with a sweep net is probably the most widely used method which measures an unknown function of coccinellid numbers and activity. It samples a narrow upper stratum of vegetation and the number of insects available for collecting is therefore dependent on plant stand height (Elliott et al. 1991). This relative method is also sensitive to the weather and to diurnal changes in coccinellid activity. Studies on the efficiency of this method have established a significant although sometimes low correlation between abundance established by sweeping and hand-picking. The magnitude of the error of the estimate of coccinellid abundance decreases and species presence increases with the number of sweeps in a non-linear convex manner (Elliott & Kieckhefer 1990).

Hand-shaking plants, an alternative to sweeping, is not used frequently, but is a convenient way of sampling wild herbaceous plants. Arefin and Ivliev (1988) compared its efficiency with sweeping in capturing different species (*C. septempunctata*, *Har. axyridis* and *P. quatuordecimpunctata*) and different developmental stages and found a high correlation between the results of both methods.

Visual counting on a transect (walking counts) is quick but weather sensitive; it is particularly convenient for recording highly visible brightly coloured adults, e.g. *C. septempunctata*. This method exploits the thermoregulatory behaviour of ladybirds – basking in the sunshine on cool days. The basking individuals are counted by a person who walks with the sun behind them. The method could be used for a quick comparison of coccinellid abundance in different crops and can supplement or replace sweeping (Honěk 1978a, 1982a, Lapchin et al. 1987, Iperti et al. 1988). Michels & Behle (1992) found that visual counting was the best method for estimating abundance of *Hippodamia* species in grain sorghum. Differences between observers could be removed, since there was a high correlation between the counts of those that worked in parallel (Frazer & Raworth 1985). By contrast, in strawberry crops where sweeping was not practicable, walking counts were influenced by temperature, solar radiation and time of day to the extent that they were of little practical use (Frazer & Raworth 1985).

Vacuum sampling by D-Vac has also been used for coccinellid studies. Like hand picking, it samples all development stages from the whole vegetation profile but its efficiency is limited by the influence of plant architecture. As with sweeping, efficiency is good if coccinellids sit at the top of the plants but low when they hide in the lower strata of the plant stand (Cosper et al. 1983). Ellington et al. (1984) found that the efficiency of D-Vac was superior to that of sweeping, as it collected more than twice the number of *Hippodamia* spp. adults than the latter method, but this was still only a fraction of the population counted by hand-picking. In stands of soybeans, D-Vac sampling was inferior to sweeping (Bechinski & Pedigo 1982).

Several studies have **compared the efficiency of sampling methods** in crop stands in relation to the crop and microclimate characteristics. For wheat, Elliott et al. (1991) proposed regression methods for converting the data from several sampling methods to absolute coccinellid numbers. Michels et al. (1997) compared hand-picking with timed sampling and sweeping. Hand-picking accurately estimated adult but underestimated larval density. Timed counts and sweeping results were correlated with the absolute density established by hand-picking. Regression models for converting the data of four coccinellid species to their absolute abundance included the number of tillers per 0.3 m of row, plant growth stage, height and number of aphids per tiller and these variables accounted for 89–93% of the variance. This study was further continued in alfalfa, where Elliott & Michels (1997) compared hand-picking, time-limited visual counting and sweeping; they proposed methods of converting the results of timed and sweep samples to absolute numbers of four coccinellid species. For sweeping and timed counting, plant height was included in the best regression models for adults. For larvae, the regression explained a low proportion of variance and included plant growth stage and aphid abundance. In sorghum crops, the efficiencies of hand-picking, timed sampling, sweeping and D-Vac sampling were compared and regression methods of calculating absolute abundance were established (Michels et al. 1996). In soybean crops, Arefin and Ivliev (1988) compared the efficiency of shaking the plant and sweeping, and found a high correlation between the results of both methods ($r^2 = 0.64–0.98$ for adults and larvae of *C. septempunctata*, *Har. axyridis* and *P. quatuordecimpunctata*). However, the slope of the regression for abundance determined by sweeping differed from that found by shaking ($b = 0.16$ and 1.06, respectively). In cotton, Ellington et al. (1984) found that D-Vac sampling captured 34% and sweeping only 14% of the *Hippodamia* spp. adult population established by hand-picking.

Methods of sampling coccinellids from **trees and shrubs** have been less investigated than for herbs. Studies of tree faunas have been based on accessible parts of the crown, the lower stratum of large trees or whole small trees. Coccinellid faunas of upper parts of large trees remain uninvestigated. Three sampling methods have been used most frequently: (i) direct examination of a fixed number of twigs or leaves (Brown 2004, Michaud 2004, Oztemiz et al. 2008); (ii) collecting into a sheet by shaking (branch jarring) or beating (LaMana & Miller 1996, Brown & Schmitt 2001); and (iii) sweeping (Honěk & Rejmánek 1982, Honěk 1985b, Honěk et al. 2005). As yet no comparative studies of these methods are available. Sampling from trees and shrubs is made somewhat easier by the fact that their rigid architecture enables permanent localization of particular sampled twigs and leaves and counting prey. This enables precise counting coccinellid larvae whose distribution is largely determined by prey availability, but adults move in response to light and temperature conditions. Measuring leaf temperature is complex; it has been studied since the 1920s and is reviewed by Thofelt (1975). Microclimatic effects on coccinellid communities on trees have not yet been analyzed but are certainly important.

Besides sampling from plants, various **traps** can be used which collect coccinellid adults during flight. Such catches provide samples of adults of unknown origin, although the beetles probably mostly come from nearby stands, and are influenced by species-specific orientation (leading to different attractiveness of different kinds of trap), diurnal periodicity and flight ability.

Sticky cards are most frequently used because they catch large numbers of coccinellids. The numbers of adults stuck on the cards depends on the card colour. Yellow-coloured traps are better than red, green and white ones (Udayagiri et al. 1997) and are therefore generally used to study coccinellid movement within a field (Ives 1981a). Kokubu (1986) designed his experiments to estimate the numbers of immigrant and emigrant coccinellids in maize plots. He placed yellow sticky panels in parallel with the sides of the plot so that surfaces facing the plot sampled emigrant beetles while the opposite surface trapped immigrant ones. For *A. bipunctata*, *C. septempunctata* and *P. quatuordecimpunctata* there was, however, only a poor correlation between abundance on maize plants and trap catches. Similarly, Stephens and Losey (2004) found a poor correlation between sweeping, visual counts and sticky trap catches of *Har. axyridis*, *Col. maculata* and *C. septempunctata* in alfalfa. However, using sticky traps demonstrated different flight activity of *Col. maculata* and *C. septempunctata* in central and marginal parts of maize crops (Udayagiri et al. 1997, Bruck & Lewis 1998, Colunga-Garcia & Gage 1998) and were also useful in detecting long-term changes in abundance of coccinellid species that occurred before and after arrival of the invasive *Har. axyridis*. Yellow sticky traps can also be used for detecting the height which particular coccinellid species prefer when in flight (Parajulee & Slosser 2003).

In contrast to coloured cards, **window traps** (=impaction traps) collect a supposedly unbiased sample of flying coccinellids. The beetles bump into a transparent glass wall and fall into a collecting trough below. However, it remains unknown whether the glass wall is really ‘invisible’ to them. The species-selective capture by yellow sticky traps and window traps was demonstrated by Storck-Weyhermueller (1988); with both types of trap, the height and position above the ground influencing the catch of particular species. Boiteau et al. (1999) collected 21 species of coccinellids using window traps placed at heights of 0.8 to 14.3 m. *Hip. convergens*, *C. septempunctata* and *C. trifasciata* flew mostly near the ground while other species were less selective.

Malaise traps, tents catching flying insects that enter their interior through a gap and are led by phototaxis to collecting bottles, have been found to be convenient in detecting the peak of flying *C. septempunctata* during migration and non-migration flights. Sarospataki & Marko (1995) hung Malaise traps within a shrub stratum (0–2 m height), at the tree canopy stratum (12.5–14.5 m height) and above all the vegetation (25–27 m height). While the lower traps captured adults throughout the vegetative period, the traps placed above the vegetation captured adults only at the time of migration, in late July.

Although coccinellids are mostly day active, they are frequently caught in **light traps**. Trap efficiency is influenced by trap design and depends both on light source and the reflective surface behind the light. Light traps collect a mixture of species from coccinellid communities of different habitats near the trap and the samples have a great diversity (Honěk & Rejmánek 1982). Catches were used to compare the annual variation of species abundance (Honěk & Kocourek 1986) and long-term changes in the colour morph proportions of the different species (Honěk et al. 2005). Interpreting seasonal variation of catches in terms of number of generations per year (trivial flight) and flight to overwintering sites (migratory flight) needs background knowledge of species biology (Koch & Hutchinson 2003).

There certainly exist further methods used to capture other insect taxa but not applied to sampling coccinellids as yet. To use them the kind reader may stimulate her/his powers of imagination by reading standard reference books, e.g. Southwood and Henderson (2000).

Abundance of coccinellid individuals in a habitat is a dynamic state of balance between immigrating and emigrating individuals. The process of exchange of individuals at a place could be studied by **mark–recapture method**. A known number of individuals of a species are marked and released, then the individuals are sampled after some time and the proportion of released individuals in the total recaptured population is established. This method is convenient for study of abundant species and can determine total number of individuals at a place, their residence time, emigration rates, and distance of emigration from the place of their release. Calculation of these values was described for aphidophagous (van der Werf et al. 2000) and phytophagous coccinellids (Koji & Nakamura 2002). For marking individuals the authors use paint (van der Werf et al. 2000, Grez et al. 2005, Seko et al., 2008) or proteins, established after recapture by biochemical methods (Hagler & Naranjo 2004, Hagler & Jones 2010).

4.3 FACTORS DETERMINING THE COMPOSITION OF COMMUNITIES

The coccinellid community present at each site is a sample of the **local fauna** which is a total of all the species present in a geographic area. The **characteristics of a site** include the prey abundance and species, host plant, microclimate, surrounding landscape characteristics, as well as intraguild (Chapter 7) and other biotic factors. The **probability of being sampled** within a particular community is a function of the size of the coccinellid population. The probability of capturing rare species decreases with their rarity, and so their disappearance from samples for a time is no evidence of short-term extinction followed by recolonization. The estimated diversity of communities increases as sampling intensity increases to a maximum which is the full composition of the local fauna. This may be attained at any location if sampling effort is maximized and time is unlimited.

4.3.1 Local faunas

The relationship between the coccinellid faunas of particular geographic areas and the composition of their communities in particular habitats within these areas has still been little studied. There is probably no study that demonstrates geographic trends in abundance and diversity of species in particular habitats along a transect long enough to cross a range of geographic areas. Most studies have been performed in temperate regions with a similar diversity of coccinellid species, or limited to particular crops. It can be hoped that this section will stimulate further research.

4.3.1.1 Geographic differences

Unlike for other groups of organisms, for coccinellids there has been no study dividing the Earth's surface into a rectangular grid showing local variation in species diversity and abundance. Local lists of species for particular areas are not useful, because they are biased by different sizes of the areas and different sampling activity within them. Regardless of this limitation, it is clear that richness in genera and species is inversely related to the **geographical latitude** of an area. This may be illustrated by the example of faunas of areas of similar size and geography in Russia, sampled with comparable effort and separated by 15° of latitude. The fauna of the Magadan territory (60 °N) contains 18 species from 9 genera (Ivliev et al. 1975) while that of the Primorskii Region (45 °N) has 63 species from 29 genera (Kuznetsov 1975).

4.3.1.2 Invasion and extinction

The number of species in a geographical area may decrease through extinction, or increase through immigration by or artificial introduction of a new species. There is no record of any global **extinction** of a coccinellid species, but some species may become locally extinct from island faunas (Majerus 1994). However, the case of *C. undecimpunctata*, which invaded and spread in North America but now is nearly extinct after some 100 years of co-existence with the local fauna (Wheeler & Hoebke 2008), indicates that extinction could occur more frequently. More data are available for coccinellid introductions than for extinctions. Recent **introductions** of coccinellids into new areas have not been spontaneous but instead have followed human activity. Since the 1890s, 179 coccinellid species have been introduced deliberately or inadvertently to the USA and Canada, and 27 have become established. These species originally represented an insignificant fraction of the coccinellid species in the local communities, but this situation lasted only until the 1980s (Harmon et al. 2007). Since then immigrant species have come to replace indigenous species to an alarming extent, so that now introduced coccinellid species, mainly *C. septempunctata* and *Har. axyridis*, typically represent 60 to 80% of adult coccinellid communities (Gardiner et al. 2009). Mechanisms involved in the replacement by new species of the original fauna, and the fatal consequences for the latter thereof, include intraguild predation (Chapter 7) and 'marginalization' of native species – their displacement from preferred habitats to habitats that they had not occupied before. An example is provided by *C. septempunctata,* established in Utah (USA) between 1992–2001. Since then this species has increased in numbers while densities of native species, *Hip. convergens*, *Hip. quinquesignata*, *Hip. sinuata* and *C. transversoguttata*, have decreased. The decline of these native ladybirds mirrored a decline of pea aphid *Acyrthosiphon pisum*. As *C. septempunctata* depressed prey availability for the adults of native species, these have shifted their foraging away from alfalfa to other crops and wild herbs. The reality of this scenario was confirmed by field experiments which revealed that native ladybirds were more sensitive to local aphid density than was *C. septempunctata* (Evans 2004). In eastern USA, Finlayson et al. (2008) compared composition of coccinellid communities on several habitats and in all places found prevalence of non-native over native species of coccinellids.

The limits that environmental conditions impose on the distribution of introduced species were demonstrated for *Har. axyridis*. At the northern boundary of its distribution in North America survival is limited by severe winter cold and this species only survives winter inside human houses. In northern marginal regions the distribution of human settlements coincides thus with distribution of this coccinellid species (Labrie et al. 2008).

4.3.1.3 Climatic changes

Recently a lot of attention has been paid to the consequences for coccinellids of the expected climatic change. Simulation, using data from the United Kingdom, revealed that warming of the climate could change the interaction between coccinellids and aphids in that the abundance of prey may decrease by 40–60% and the Julian date of their peak population could be advanced (Skirvin et al. 1997) (Fig. 4.1). As individual coccinellid species show a different response to prey abundance (Honěk et al. 2007), changes in prey number and their timing due to climate warming might change the composition of coccinellid communities. Other studies, however, throw a different light on the importance of local climate in determining the presence of coccinellid species. The accuracy of predictions of the geographic range of a species based on climatic characteristics was tested using data for 15 *Chilocorus* species introduced to various areas in tropical and subtropical zonse, with the CLIMEX programme simulating the effect of climate on species distribution. This programme tests for a match between climate and biological characteristic of the species. Predictive models of distribution of the different *Chilocorus* species were based on the likelihood of their establishment with respect to their physiological characteristics and climatic tolerances. Model predictions were compared with data on the actual distribution of the species. The real distribution of four (27%) species was predicted

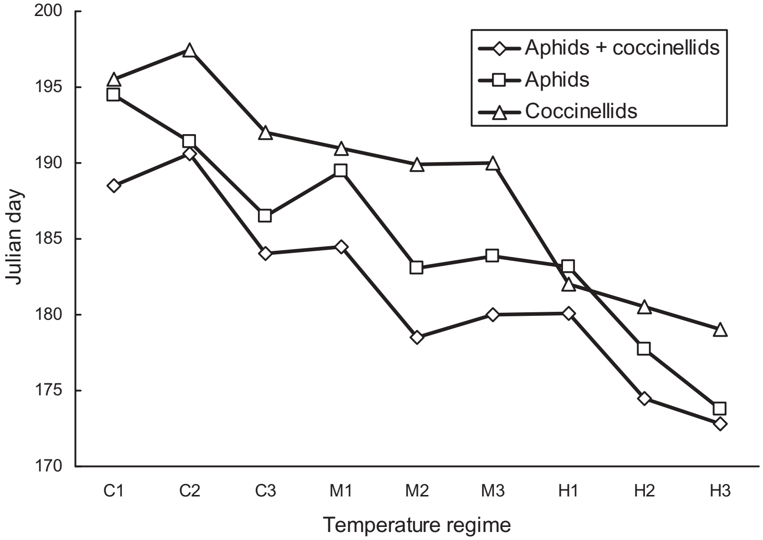

Figure 4.1 Simulation of timing (Julian day) of peak abundance of the grain aphid *Sitobion avenae* and its coccinellid predator *Coccinella septempunctata* in the UK under different scenarios of climatic change. Timing of maximum abundance was predicted using the model of Carter et al. (1982), three temperature regimes, cold (C), moderate (M) and hot (H) and three within-regime temperature modifications. The figure shows shortening of the vegetation period in terms of calendar time by c. 20 days for the *S. avenae* population alone, the *S. avenae* population subject to *C. septempunctata* predation, and the population of *C. septempunctata* (redrawn from Skirvin et al. 1997).

with 100% accuracy from climate data, but accuracy for the other species was limited by factors other than climate. Thus most predictions of change in the geographic distribution of species based on climatic data are likely to be wrong (Samways et al. 1999). Similarly a study of climatic limits for the geographic distribution of *Har. axyridis* showed that **climate** was **not** the **limiting factor**. Establishment and spread of this species was found to be likely in many regions, including ones which had not yet been invaded (Poutsma et al. 2008). In fact, a climate suitable for the establishment of *Har. axyridis* existed in many areas not occupied by this species for thousands of years before its recent nearly worldwide invasion.

4.3.2 Locality determinants

By analogy with a theatre performance, that of a coccinellid community at a particular site also involves 'scenery' which is the landscape, the host plant and the microclimate (the components dealt with in this chapter), and 'players' which comprise the prey, conspecific and heterospecific members of the same trophic guild, as well as natural enemies. Except for prey which is dealt with here, the other 'players' are treated in Chapters 7 and 8. Here we present the factors that determine the presence or absence of a species in a particular habitat in the order of their importance which is prey, host plant, microclimate, and landscape.

4.3.2.1 Prey

Prey availability is the primary factor that brings together coccinellid assemblages; adults seek prey not only for their own welfare but as a resource for their progeny (Chapter 5). Assemblages are also formed because of satiation before hibernation (Chapter 6). It is still open for further research as to in which situations **abundance** of prey is **more important than** prey **species** in determining coccinellid presence in a habitat, and where the order of importance of these two determinants is reversed.

Coccinellid communities of particular habitats begin as assemblages of mobile adults which turn into assemblages of larvae after selective oviposition and selective larval survival. Larval communities thus usually are a copy of the composition of adult coccinellids. The **mechanisms whereby coccinellid assemble** and then oviposit have been reviewed by Evans (2003). Adult ladybirds are highly mobile in traversing the landscape (5.4.1.5), but become less active and produce more eggs as their rate of encounter with prey and aphid consumption increases, with the result that most eggs tend to be laid at sites of high aphid density. Females use their resources to produce eggs in modest numbers when prey consumption is limited. They may thus be prepared to lay some eggs quickly when they succeed in finding aphids in high numbers, but otherwise they may have little choice but to lay eggs at suboptimal sites. Upon locating patches of high prey density, females are faced with the decision of how long to remain. It is frequently thought that they become passively trapped at such patches until the aphid density there collapses. However, there is no such positive trapping. Oviposition has already terminated by the middle of the course of the prey population's development, and the cause is an **oviposition-deterring pheromone** (Ruzicka 1996, Klewer et al. 2007) secreted by the larvae from the anal disk that helps their locomotion (Laubertie et al. 2006). In this, the larvae are mainly responding to cues associated with presence of conspecific larvae (Yasuda et al. 2000, Hemptinne et al. 2000a). Oviposition-deterring pheromones may promote their departure from prey patches well before prey resources are exhausted. Females may also have an innate tendency to disperse regardless of local conditions.

Prey is an attractant and arrestant for immigrating adults. The minimum **prey density** capable of attracting adult *C. septempunctata* is below10 aphids per square metre (Honěk 1980) and imigration may occur simultaneously with aphid immigration (Arefin & Ivliev 1988). At this low threshold density of prey, the coccinellids can just capture sufficient prey to maintain their body weight (Frazer & Gilbert 1976). A proportion of the adult population will leave the site but be replaced by new immigrants (Ives 1981a). Immigration and emigration rates depend on the **frequency of encounters** between coccinellids and their prey, which is how a positive correlation between the abundance of aphids and coccinellids arises. This was shown in alfalfa stands populated by different aphid and coccinellid species (Neuenschwander et al. 1975, Radcliffe et al. 1976, Honěk 1982a), in strawberry plantations of British Columbia populated by the aphid *Chaetosiphon fragaefolii* and *C. californica* (Frazer & Raworth 1985), and bean stands infested with the aphid *Aphis craccivora* and populated with *Menochilus sexmaculatus* and *C. transversalis* (Agarwala & Bardhanroy 1999; Fig. 4.2). In tobacco stands, numbers of the aphid *Myzus persicae* and those of *Cer. undecimnotata*, *A. bipunctata*, *Hip. variegata* and *P. quatuordecimpunctata* were only loosely correlated because of a negative coccinellid response to the many aphids parasitized by hymenopteran parasitoids (Kavallieratos et al. 2004). However, evidence for a parallel increase in aphid and coccinellid abundance has been found to vary between coccinellid species. In cereal plots where aphid density was experimentally manipulated, numbers of *C. septempunctata* and *Hip. convergens* increased in parallel with aphid density while those of *Hip. tredecimpunctata*, *Col. maculata* and *Hip. parenthesis* were not significantly correlated (Elliott & Kieckhefer 2000). In soybean stands a positive relationship between the aphid *Aphis glycines* and coccinellid abundance was demonstrated for *Har. axyridis*, while with *C. septempunctata* increasing aphid abundance only prolonged residence time in experimental plots (Costamagna & Landis 2007). Only a few studies found that aphid and coccinellid abundance were not correlated (Sakuratani 1977). A positive correlation between the size of aphid colonies and the abundance of *A. bipunctata* was demonstrated in stands of three weeds, stinging nettle (*Urtica dioica*), scentless mayweed (*Tripleurospermum maritimum*) and wormwood (*Artemisia vulgaris*), where abundance of this ladybird and, in parallel, its dominance in coccinellid communities increased with aphid abundance and colony size (Honěk 1981).

Minor details of prey distribution may affect the decision by coccinellids to invade stands of a host plant. Coccinellids were found to aggregate more on grouped than on isolated aphid-infested plants of maize (Sakuratani et al. 1983) and alfalfa (Evans & Youssef 1992). The effect of aphid aggregation was also demonstrated in wheat stands where *A. bipunctata* preferred being on inflorescences (Hemptinne et al. 1988) where aphid populations are more densely aggregated than on leaves.

Recent studies have revealed mechanistic feedbacks on coccinellids of their effects on aphid behaviour. The **anti-predator defensive behaviour of prey** may reduce foraging by coccinellids and confound the density relationship between them. This behaviour

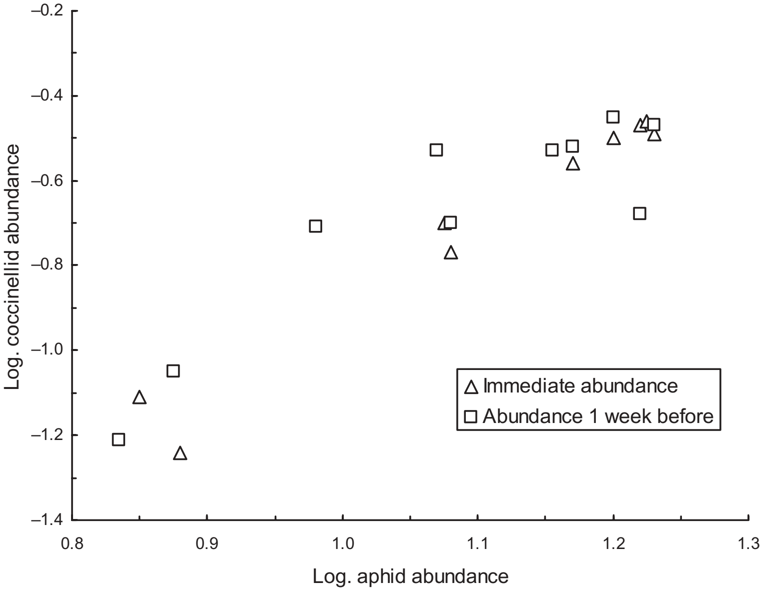

Figure 4.2 The cumulative abundance of adult *Menochilus sexmaculatus* and *Coccinella transversalis* in bean crops infested with *Aphis craccivora* in India. The figure shows the relationship between coccinellid and aphid abundance measured on a particular day (immediate abundance), and the abundance of coccinellids in relation to aphid abundance established 1 week earlier (redrawn from Agarwala & Bardhanroy 1999).

includes the **prey dropping** from the host plant, as happened in 60% of encounters between the aphid *Acyrthosiphon pisum* and *C. septempunctata* on alfalfa while only 7% of aphids drop spontaneously. The antipredator dropping behaviour is specifically directed against coccinellid attack. Encountering heteropteran predators, *Nabis americoferus, Geocoris punctipes* and *Orius insidiosus*, resulted in only 14% drop of the aphids. Adult aphids had a significantly higher propensity to drop than nymphs but the density of aphids had no effect (Losey & Denno 1998). Also dropping of the aphid *Macrosiphum euphorbiae* from potato plants was increased by interaction with *Har. axyridis* (Narayandas & Alyokhin 2006). Dropping of aphids from host plant may lead to their predation on the ground, e.g. by carabids (Losey & Denno 1999). The efficiency of dropping as a protective strategy of the prey was demonstrated in *Har. axyridis*, whose predation of *A. pisum* doubled when dropping was artificially prevented (Francke et al. 2008). In practice, however, only a few encounters of coccinellids with aphid prey result in predation. Thus in *Hip. convergens* preying on *A. pisum* the ratio of encounters leading to prey disturbance only to encounters resulting in prey consumption was 30:1 (Nelson & Rosenheim 2006). Whether similar mechanisms of predator–prey interaction are important in determining abundance of particular coccinellid species and affecting composition of coccinellid communities of particular habitats remains uncertain.

In addition to prey abundance, qualitative **taxonomic differences between prey species** are important for stenophagous coccinellids, and probably also for generalists. A review of prey specificity is given in 5.2. How might prey preferences influence selection of a particular habitat? In their review, Sloggett and Majerus (2000) address the concept of ‘habitat preferences’ from the point of view of diet specificity. They argue that limitations of consumption and competition for prey were probably important factor in the evolution of coccinellid preferences. Dietary specialization and associated preference for particular habitats has probably occurred in some lineages derived from generalist ancestors to avoid costs associated with migration between habitats and prey switching. Adaptation to particular food could be rather quick (Rana et al. 2002). In the generalist *A. bipunctata, A. pisum* is a preferred and *A. fabae* a non-preferred, but often consumed, aphid species. The initially poor performance of *A. bipunctata* improved during six generations of rearing on *A. fabae* prey, as development time decreased and adult weight and longevity increased. After six generations of selection, the strain by then adapted to *A. fabae* performed worse on *A. pisum* diet than the strain reared continually on that species. Thus the specialization on one kind of prey entails a trade-off in performance on another.

The 'innate' mechanisms leading to **preference for a particular species of prey** include perception of its chemical composition which may be **reflected** already **by its odour**. This was shown in females of *Cycloneda sanguinea* which were attracted to tomato plants infested by their preferred prey the aphid *M. euphorbiae* as opposed to plants infested by non-preferred prey, the mite *Tetranychus evansi* (Sarmento et al. 2007).

The **size** of the coccinellid relative to that of the prey is also a factor determining coccinellid preference. An analysis of the prey of ladybirds indicates that, the larger the ladybird species, the larger also the prey and/or the greater the mobility (Dixon & Hemptinne 2001). The smallest ladybird species feed on mites, and the largest on caterpillars and beetle larvae. On a global scale, the size of coccinellid species inhabiting a geographic area is correlated with the size of the prey prevailing in this area. This means that the ratio of the numbers of species of aphidophagous and coccidophagous ladybirds in the Nearctic and Palearctic regions reflects the ratio of the number of species of aphids to the number of species of coccids in the two regions. Large coccinellid species, in particular the predators of large and/or active prey, also lay larger eggs than small species which are predators of small and/or slow moving prey (5.2.3; 5.2.4).

Variation of **quality acquired during prey development** may also influence coccinellid performance. The same prey fed different food may have different nutritive value for coccinellids. The aphid *A. pisum* reared on alfalfa had a 6.3-times greater content of myristic acid, a 2.7-times higher content of total fatty acids and a 1.7-times higher caloric content than *A. pisum* reared on beans. Individuals of *A. pisum* with as high a fat content fed to larvae of *Col. maculata* and *Hip. convergens* decreased their mortality and development time. This beneficial effect of high quality prey was significant when aphids were scarce, but not significant if food was in surplus (Giles et al. 2001, 2002). Also the aphid *A. fabae* reared on hoary orache (*Atriplex sagittata)* was toxic to *A. bipunctata* while the same aphid species reared on other host plants was an acceptable (though not preferred) food for this coccinellid (Kalushkov 1998).

Oviposition follows successful predation, and so gives rise to the community of larvae. The number of eggs laid and the duration of oviposition are influenced by several factors. In the field, *C. septempunctata* start to oviposit after the aphid population has attained density of about one aphid per 300 cm^2 of leaf area, a threshold similar in different crops (Honěk 1980). In laboratory experiments with *A. bipunctata*, a species that prefers aggregated aphid populations, the minimum density for laying eggs was four-times higher at two aphids per 150 cm^2 leaf area, and females required at least 10 aphids per 150 cm^2 to achieve maximum oviposition (Hemptinne & Dixon 1991). In the field (an alfalfa crop), the threshold aphid density was not reached everywhere at the same time, and this caused a conspicuous asynchrony in ovariole maturation of *C. septempunctata* in different parts of the field (Honěk 1978b). As mentioned earlier in another context, limited prey consumption results in females producing only modest numbers of eggs given their restricted resources, and these eggs are frequently not laid and remain retained in the ovariole. As a consequence, the females are ready to lay eggs quickly when they succeed in finding aphids in high numbers (Evans 2003). In the field, the number of eggs deposited (Wratten 1973, Wright & Laing 1980, Ives 1981b, Kawauchi 1981, Ferran et al. 1984, Ghanim et al. 1984, Coderre et al. 1987) as well as egg cluster size (Agarwala & Bardhanroy 1999) is then frequently directly proportional (on a log–log plot) to the density of aphids. This is not only because of an increase in fertility but also because of an increasing number of coccinellid females (Neuenschwander et al. 1975, Turchin & Kareiva 1989, Ofuya 1991). Furthermore, females discriminate between preferred and non-preferred prey and lay eggs preferentially in patches of suitable prey. Under laboratory conditions *A. bipunctata* laid 13 eggs /8 hours when provided with a suitable aphid, *A. pisum*, 11.4 eggs with the moderately suitable *A. fabae* and only 7.6 eggs when provided with the toxic aphid *Megoura viciae* (Frechette et al. 2006). The enhancing effect of prey abundance on oviposition is further magnified by suitable substrates available for oviposition. The availability of a suitable site was a significant factor in the selection of oviposition site and determination of cluster size in *Aphidecta obliterata* and *A. bipunctata* (Timms & Leather 2007).

4.3.2.2 Host plant

The prey of coccinellids is always encountered on its host plant, the effects of which on coccinellid attraction and oviposition are sometimes hard to separate (5.4). Plants, alone or in interaction with prey, are sources of **chemical cues** attracting coccinellid adults. Although the beetles' sensory capacities were thought to be poor, recent studies have revealed that their sense of smell is good (Pettersson et al. 2008, Hatano et al. 2009; and Chapter 9). Firstly, it may be the smell of intact plants that is detected. In the field, adult *C. septempunctata* were more abundant in barley plots containing the weeds creeping thistle (*Cirsium arvense*) and couch grass (*Elytrigia repens*) than in clean barley plots. In olfactometer experiments, adults then showed a significantly more positive response to odours of each of the two weeds than to that of barley alone (Ninkovic & Pettersson 2003). Similarly with *Col. maculata*, Zhu et al. (1999) observed significant electroantenogram responses to volatile compounds produced by intact maize plants at the three-leaf stage, i.e. the period when this crop is attractive to aphids. Odours emanating from host plants have also been found to stimulate coccinellid oviposition. Pieces of Eastern red cedar (*Juniperus virginiana*) wood split from the plant but not damaged by prey species attracted *Cycloneda munda*, *A. bipunctata*, *C. transversoguttata* and *Col. maculata* and initiated oviposition (Boldyrev et al. 1969). Shah (1983) demonstrated that *A. bipunctata* and *C. septempunctata* laid more eggs on the twigs of European barberry (*Berberis vulgaris*) than on the twigs of other woody plants, apple tree (*Malus pumila*) wild cherry (*Prunus avium*), sour cherry (*P. cerasus*), cotoneaster (*Cotoneaster tomentosus* and *C. integerrima*), common honeysuckle (*Lonicera periclymenum*) and common snowberry (*Symphoricarpos rivularis*). The aphids (*Acyrthosiphon pisum*) provided in this experiment to stimulate coccinellid oviposition were evenly dispersed over the experimental twigs but did not cause any damage on all species of experimental plants.

Other studies have demonstrated that **prey-induced plant chemicals** (5.4.1.2) can become arrestant or possibly attractant stimuli for adult coccinellids. *Hip. convergens* was attracted not only to radish leaves infested by *M. persicae* but also to radish leaves cleaned after previous colonization by this aphid (Hamilton et al. 1999). Also *C. septempunctata* females preferred not only odours of turnip, mustard and rape plants (*Brassica* spp.) actually populated with *M. persicae* but also odours of previously damaged and subsequently cleaned leaves (Girling & Hassall 2008). The adults of this species also responded positively to volatiles from barley plants infested or previously infested by the aphid *Rhopalosiphum padi*. while the volatiles emanating from uninfested plants or undisturbed aphids alone (placed on a filter paper and not releasing alarm pheromone) were not attractive (Ninkovic et al. 2001). Well known are the attractant and arrestant effects of **honeydew** (Carter & Dixon 1984, Pettersson et al. 2008). These roles of honeydew were shown in the open in experiments in which a synthetic mimic of honeydew was spread onto the crops to provide food for predators during the initial development of the aphid population. The honeydew mimic was either yeast autolysate or a suspension of the yeast *Saccharomyces fragilis* (as a source of amino acids) and sugar. Spraying the mimic on the fields increased the numbers of different coccinellid species in several crops (Hagen et al. 1971, Ben Saad & Bishop 1976, Nichols & Neel 1977, Evans & Richards 1997).

In contrast to adults, sensing by larvae is of aphid rather than host plant odours. This may help them to find prey on the host plant surface which is large relative to the size and movement capacities of larvae. Searching by larvae of *Hip. convergens* became more intensive after exposure to the odour of tobacco leaves infested with the aphid *Myzus persicae nicotianae* (Jamal & Brown 2001) while searching by *A. bipunctata* increased in response to the odour of crushed aphids, an odour made up mainly of aphid alarm pheromone (*E*)-β-farnesene (Hemptinne et al. 2000b; 9.3.2).

Of plant characteristics correlated with the presence of particular coccinellid species, the most obvious is **plant stature or architecture**. It is well established that some coccinellid species occur mainly in herbaceous stands, whilst others prefer shrubs or trees (4.4). The differences in coccinellid preference for plant type persist even when the host plants are populated by the same species of aphid (Iperti 1966; Fig. 4.3). The composition of coccinellid communities can even vary with plant species within stands consisting of plants of identical growth type, i.e. herbs or trees (Pruszynski & Lipa 1970). Although it is difficult to show conclusively that it is the particular species of plant that can be the real cause of coccinellid presence, it has been convincingly

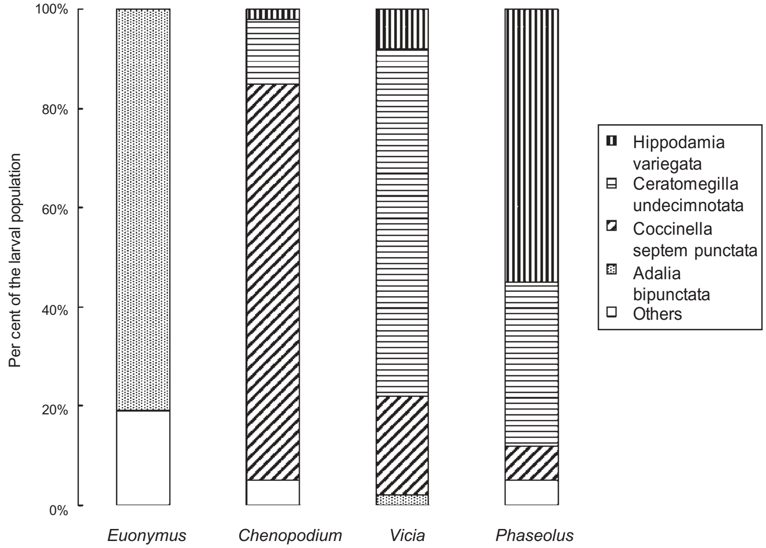

Figure 4.3 Proportion of larvae of different coccinellid species on four host plant species infested with the same aphid, *Aphis fabae*, in southern France (redrawn from Iperti 1966).

demonstrated in some cases. Among three crops, all infested by the aphid *M. persicae* at the same density, *C. transversoguttata* preferred sugar beet (*Beta vulgaris*) while its numbers on broccoli (*Brassica oleracea* Italica group) and radish (*Raphanus sativus*) were lower. *Scymnus marginicollis* preferred radish to broccoli and sugar beet (Tamaki et al. 1981). Sometimes species-specific host-plant effects become manifest only in combination with specific environmental conditions. In a study of herbaceous weeds, coccinellid communities were more and more dominated by *A. bipunctata* as the abundance of aphids increased. The only exception was the coccinellid community on the scentless mayweed (*Tripleurospermum maritimum*) growing on saline soils where *A. bipunctata* was replaced by *C. undecimpunctata*. The communities on stinging nettles (*Urtica dioica*) and wormwood (*Artemisia vulgaris*) were not affected by soil salinity (Honěk 1981). Preference for a particular host plant is sometimes affected by small details of its morphology. Floral architecture is critical in whether or not pollen and nectar of the host plant are accessible to predators. For *Col. maculata,* dill (*Anethum graveolens*) and coriander (*Coriandrum sativum*) both have a floral morphology that complements the head morphology of the adult ladybird (Patt et al. 1997).

That a host plant is suitable for coccinellids is indicated by the presence of larvae (5.2.2). Using this criterion LaMana and Miller (1996) found that, among common North American coccinellids, there were six species that preferred trees and five that preferred herbs. Although adults of all 11 species were present on both trees and herbs, larvae were found only on the preferred plant type. The difference between communities that occur on particular crops may be due to the timing of aphid presence. In Greece, *C. septempunctata* was the most abundant species on durum wheat, while *Hip. variegata* dominated cotton (Kavallieratos et al. 2002). This was probably because the monovoltine *C. septempunctata* dominated the early maturing durum wheat while populations of polyvoltine *Hip. variegata* increased in numbers with the course of the season to dominate in the late maturing cotton.

Co-existence of several coccinellid species on the same host plant is facilitated by them occupying different horizontal strata within the plant stand (4.3.2.3). Musser & Shelton (2003) found the adults of *Col. maculata* in the lower stratum of a maize crop while *Har. axyridis* was less selective (Fig. 4.4). The same vertical distribution of both species was found in field cage experiments by Hoogendoorn and Heimpel (2004). As vertical separation of different coccinellid species

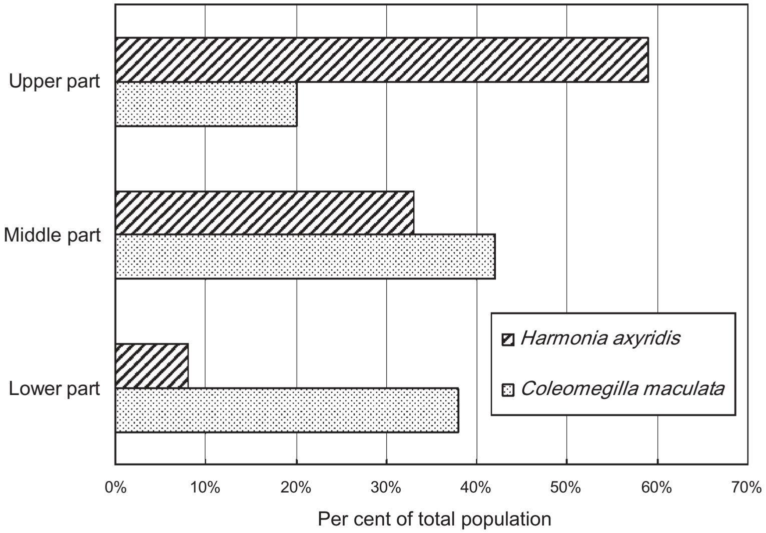

Figure 4.4 Differences in the vertical distribution (as proportion of the population of each species dwelling in the upper, middle and lower third of the plants) of adult *Harmonia axyridis* and *Coleomegila maculata* on a maize crop in the eastern USA (redrawn from Musser & Shelton 2003).

reduces competition between them, preferences for particular strata became exaggerated in cages that contained a mixture of both species; c. 70% of *Col. maculata* were in the bottom and lower sections of the maize plants and c. 80% of *Har. axyridis* were in the middle and top sections. In wheat, *A. bipunctata* preferred the inflorescences while *P. quatuordecimpunctata* preferred the lower parts of the plants (Hemptinne et al. 1988). In cotton, *Hip. convergens* and *Col. maculata* preferred leaves and terminals early in the season but later on the preferences differed and *Hip. convergens* was found on the fruits, whereas *Col. maculata* was found on both leaves and fruits (Cosper et al. 1983).

Coccinellid communities may also differ between **plants** of the same species but different **age** because ageing is accompanied by changes in size. Klausnitzer (1968) found a much higher incidence of *Myrrha octodecimguttata* adults (27%, *n* = 188) in crowns of old large trees than on young trees. By contrast, *Scymnus nigrinus*, the second species in order of abundance on the young trees was scarce in the crowns of old trees. Gumos and Wisniewski (1960) compared 10 and 40 year old pine stands and found a fourfold abundance of *Anatis ocellata* on the older trees. In general, coccinellid communities of young pines contained more species with a broader ecological range than did those of the crowns of old pines which are inhabited by a lower number of stenotopic species. The succession of coccinellid species in the course of ageing of red pine stands infested with the aphid *Schizolachnus piniradiatae* in Canada was apparently brought about by a gradual decrease in prey density (Gagné & Martin 1968). *Coccinella transversoguttata* and *Scymnus lacustris* were dominant in younger stands, whereas *Mulsantina picta* and *Anatis mali* were most common in older plantations. In Israel, *Chil. bipustulatus* was more abundant in mature citrus groves (23–30 year old) than in young ones (7–9 year old) (Rosen & Gerson 1965). The causes of differences in attractivity for coccinellids other than tree size (e.g. microclimate) remain to be studied.

Effects of intraspecific **genetic differences** between host plants have been investigated mainly because of public concerns over food safety and the environmental hazards of transgenic and herbivore-resistant crops in general. No difference in the abundance of *C. septempunctata*, *Har. axyridis* and *Hip. convergens* were found between transgenic potatoes containing Cry3A gene for *Bacillus thuringiensis* (Bt) endotoxin and classical non-transgenic ones (Riddick et al. 2000; Fig. 4.5). Direct exposure to the Bt toxin expressed in transgenic plants had little effect on the activity and

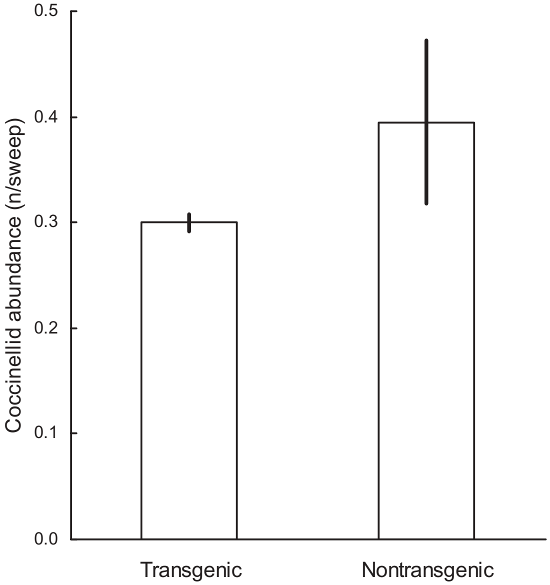

Figure 4.5 Cumulative abundance of adult *Coccinella septempunctata*, *Harmonia axyridis* and *Hippodamia convergens* on transgenic and nontransgenic potato. Average (±SE) results for 1994 and 1995. The differences between particular species and years were not significant (redrawn from Riddick et al. 2000).

abundance of *Menochilus sexmaculatus* (Dhillon & Sharma 2009). Differences in coccinellid abundance were only found (Torres & Ruberson 2005) when use of pesticides on transgenic crops ceased, and the increased numbers of predaceous Coccinellidae became part of an integrated pest management system (Obrycki et al. 2009). Selection of crops for resistance to phytophagous pests thus may result in decreasing abundance of pest populations with only minor effects on coccinellid assemblages so that the standard correlation between cocinellid and prey density (4.3.2.1) does not hold so strongly with host plant resistance. The synergism of lowering pest numbers as a consequence of breeding crops for resistance and simultaneous preservation of high coccinellid numbers in the crop stands may have positive consequences for using biological control (van Emden 2010). In stands of spring wheat cultivars resistant or susceptible to the aphid *Diuraphis noxia*, there were no differences in abundance of *C. septempunctata*, *C. transversoguttata*, *C. trifasciata* and *Hip. convergens* (Bosque-Perez et al. 2002). Francis et al. (2001) showed small differences in oviposition and larval development of *A. bipunctata* fed the aphid *M. persicae* on bean (*Vicia faba*, glucosinolate free), rape (*Brassica napus*, low glucosinolate content) and white mustard (*Sinapis alba*, high glucosinolate content). However, the effect of host plant substances on coccinellid performance mediated via the prey is not always negligible. Thus endophytic fungi (endophytes) in the host plant may change plant and prey quality with effects on coccinellids. Mycotoxins from perennial ryegrass (*Lolium perenne*) infected with *Neotyphodium lolii* were transmitted by the aphid *R. padi* to *C. septempunctata*, whose development took longer and adult survival and fecundity were reduced (de Sassi et al. 2006) (5.2).

The host plant may further affect coccinellid communities by providing **supplementary food** (=non-prey food), pollen, nectaries or damaged fruits attractive to adults and/or enhancing larval performance (Lundgren 2009). Pollen is particularly important for larvae of some species. With *Col. maculata*, oviposition and larval density in maize stands increased after anthesis but the abundance of adults did not. Nevertheless, larvae fed only maize pollen showed extended development time and finally decreased adult weight and fecundity compared to beetles reared on aphids (Honěk 1978b, Lundgren & Wiedenmann 2004, Lundgren et al. 2004). Also Cottrell and Yeargan (1998a) reported an increase of larval populations of *Col. maculata* in plots with abundant pollen. Nectar, provided by flowers or extrafloral nectaries supplement coccinellid food. Host plants with more nectaries may be more attractive to adults but the presence of such supplementary food may decrease predation by them. Under experimental conditions there was a significant reduction in predation on the aphid *Aphis spiraecola* by *Har. axyridis* on apple shoots when a peach shoot with extrafloral nectaria was also provided (Spellman et al. 2006). Damaged fruits also provide additional sources of food for the beetles. *Harmonia axyridis* adults preferred damaged pumpkin, apple, grape and raspberry fruits over intact fruits, because of the higher sugar content, and not only as a water source (Koch et al. 2004).

Finally, **plant surfaces** are important in the searching and prey capture efficiency of both larvae and adults (5.4). Cottrell and Yeargan (1999) established that larvae of *Col. maculata* born on hophornbeam copperleaf *Acalypha ostryaefolia* were unable to leave because they could not pass over the glandular trichomes on the leaf petioles. The only way they could

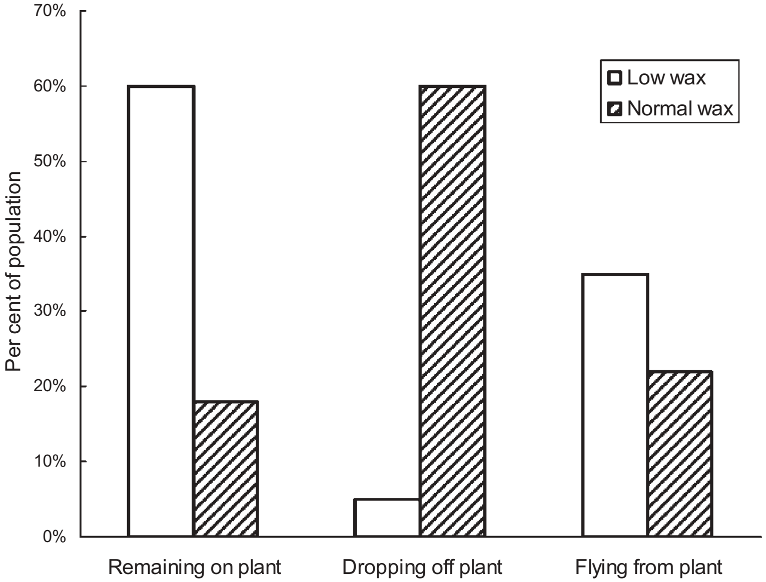

Figure 4.6 Different behaviours of adult female *Hippodamia convergens* on two isogenic lines of pea (*Pisum sativum*), one with a leaf surface with reduced wax cover ('low wax') and the other covered with a normal wax bloom ('normal wax') (redrawn from Eigenbrode et al. 1998).

escape was by dropping to the ground. The effect of plant surfaces on searching activity is well documented. Reduction in surface waxbloom in isogenic lines of pea (*Pisum sativum*) improved the effectiveness of movement and prey capture by adult *Hip. convergens* significantly at low prey densities (Eigenbrode et al. 1998) (Fig. 4.6). Indeed, the waxbloom on most pea varieties is slippery enough to cause many *Hip. convergens* and *C. septempunctata* to fall. Experiments by Kareiva and Sahakian (1990) showed percentage falls for the two coccinellids to be, respectively, 32 and 47%, while the comparable figures on 'leafless' pea varieties were only 9 and 26%. The latter varieties are resistant to powdery mildew *Erisyphe polygoni* because the leaf area has been largely replaced by a profusion of green stipules and tendrils; particularly the tendrils provide a firm hold for ladybirds. As a result, predation is much improved, and leafless peas show an apparent resistance to *A. pisum* which they do not possess in the absence of ladybirds. Similarly, predation of the lepidopteran *Plutella xylostella* larvae by *Hip. convergens* adult females was significantly greater on the less waxy 'glossy' than on normal waxbloom isogenic plants, again because of better adhesion on the former (Eigenbrode & Kabalo 1999). Glandular trichomes of tobacco leaves significantly decreased the search speed of *Hip. convergens* larvae (Belcher & Thurston 1982).

4.3.2.3 Microclimate

The effects of microclimate are obviously associated with the density and structure of host plants. It is thus hard to discriminate between the effect of both, and the importance of microclimatic effects is therefore frequently underestimated.

The impact of microclimate on the distribution of coccinellid adults and larvae in cereals was demonstrated by Honěk (1979, 1982a). The **density** of cereal crops may vary widely and this influences plant, air and soil surface temperatures as well as humidity. On bright June days, the temperature difference between the coolest and warmest sites within a cereal crop may be as high as 17°C. Adult *C. septempunctata* and *C. quinquepunctata* preferred sparse, well-insolated areas with a warm microclimate, while *P. quatuordecimpunctata* was less choosy and tolerated dense areas with a cooler microclimate. Adult preferences at different

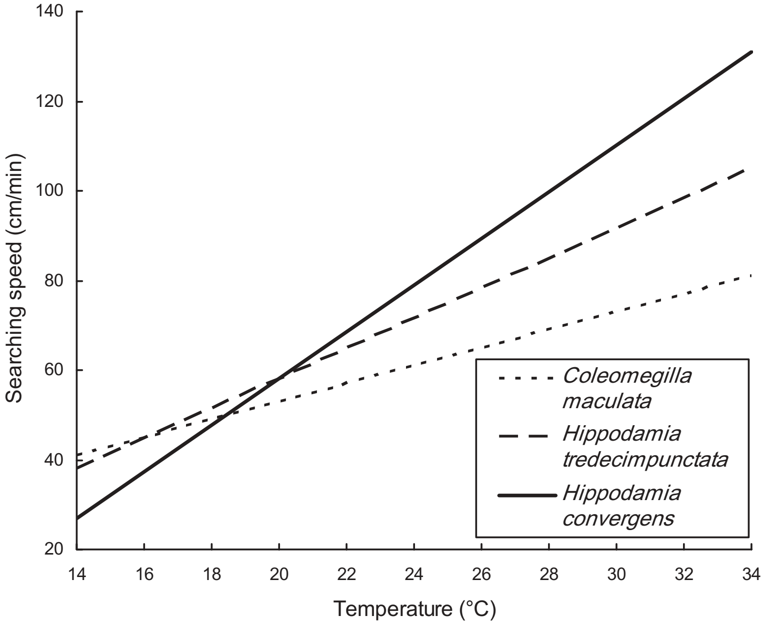

Figure 4.7 Searching speed of adults of three coccinellid species in relation to ambient temperature in stands of spring cereals in central USA (redrawn from Elliott et al. 2000).

places were correlated with larval density and apparently also with larval preferences (Honěk 1983). Preferences for a particular microclimate may be reflected in the daily movements of coccinellids on plants. During the cool morning hours, adult *C. septempunctata* may bask on the upper parts of the plants or on bare ground (Honěk 1985a). Within-plant movement may be facilitated by **innate circadian activity** of the species, as in *Col. maculata* (Benton & Crump 1981) or *C. septempunctata* (Zotov 1983, Nakamuta 1987; 5.4.1.1).

The causes of differences in vertical distribution of particular coccinellids on host plants are often preferences for **specific microclimate**. In crops of maize and barley, Ewert & Chiang (1966) found that *Hip. convergens* and *Hip. tredecimpunctata* preferred the upper parts of the plants, while *Col. maculata* preferred the lower parts. These differences could be attributed to the vertical gradient of decreasing humidity towards the top of the crop. The preferences of the coccinellids for plant stratum were correlated with their resistance to desiccation. *Coccinella septempunctata* prefers the top section of plants regardless of their height, probably because this provides the opportunity of **thermoregulatory basking**. A similar vertical distribution of *C. septempunctata* was observed on tall hop plants (J. Zelený, unpublished) and on about 10-times shorter dense cereal stands (A. Honěk, unpublished).

Recently, microclimate has attracted little attention but behavioural studies support earlier conclusions. Thus *C. septempunctata,* which prefer a warm microclimate, lay eggs at warm places which they may often find on the surface of unnatural objects including metal cans, wood and concrete structures (Sakuratani & Nakamura 1997). For pupation, the larvae select sites exposed to solar radiation, and pupate in positions that optimize body warming (Sakuratani et al. 1991). In warm-adapted *Hip. convergens*, *Hip. tredecimpunctata* and *Col. maculata,* the proportion of time spent in flight activity, searching for aphids and handling time to eat them were positively correlated with temperature (Elliott et al. 2000; Fig. 4.7).

4.3.2.4 Landscape

Recently much attention has been paid to the **effects of surroundings**, spatial distribution and composition of plant stands as well as to the effects of orographic diversity of landscape, on the coccinellid community at a particular habitat. The effect of alien plant species was first shown as an influence of other plants mixed into the stand of host plant of the prey. Coccinellids frequently benefit from diversification created by **planting different crop** species **together**. The abundance of *Col. maculata* was increased by growing beans (*Phaseolus vulgaris*) or squash (*Cucurbita maxima*) with maize providing a source of pollen and aphids (Wetzler & Risch 1984, Andow & Risch 1985). A positive **effect of weeds** in a crop stand on reducing phytophagous pests and/or increasing coccinellid density has frequently been demonstrated (Horn 1981). As an example of this, the abundance of *Col. maculata* was higher in maize crops containing the weed hophornbeam copperleaf (*Acalypha ostryaefolia*) than in weed-free stands (Cottrell & Yeargan 1998b) because the ladybird preferred to oviposit on the weed (Cottrell & Yeargan 1999).

Coccinellid communities on the prey host plant are also influenced by plants growing at the **edge of a crop**. The adults leave crops to evaluate the quality of surrounding habitats, a movement termed 'resource mapping'. This opens access to spatially separated resources and may cause an 'edge effect', i.e. the accumulation of individuals at the edge of the crop (Ries et al. 2004). **Adjacent uncultivated** land may also provide refuge and food for ladybirds when prey is scarce on the agricultural crops and to bridge gaps in synchronization with the pest species serving as prey. Parts of a field may also have a similar function (van den Bosch et al. 1959). These results led to the idea of '**strip cutting**' of alfalfa in California in the 1950s (Schlinger & Dietrick 1960). This practice allowed the movement of adult *C. transversalis* from harvested to unharvested strips during the 24 hours following a harvest. The coccinellids colonized these strips near the edge; therefore densities decreased with increasing distance from the borders with the harvested strips (Hossain et al. 2002). Such a decline in density of coccinellids also occurs on non-crop plants at the edge of the crop. Wormwood (*Artemisia vulgaris*), tansy (*Tanacetum vulgare*) and stinging nettle (*Urtica dioica*) planted as bordering vegetation, significantly increased the density of adults and larvae of *C. septempunctata*, *A. bipunctata* and *P. quatuordecimpunctata* on lettuce (*Lactuca sativa*) plants compared to the control lettuce field not surrounded by weedy margins (Sengonca et al. 2002). In northern Italy, coccinellids were also more abundant in crops with weedy field edges bordered by hedgerows of young trees than in crops bordered by hedgerows consisting of old trees (Burgio et al. 2006).

The increasing interest in nature conservation has made it clear that **fragmentation** of the habitat, the size of fragments and their distance one from the other can affect coccinellid abundance. In a pioneer study, Kareiva (1987) showed that, in a stand of Canada golden-rod (*Solidago canadensis*) populated by *Uroleucon nigrotuberculatum* aphids, that fragmentation of the stand into 1 × 1 m plots led to more frequent local explosions of aphid than in unfragmented area. The population dynamics of *U. nigrotuberculatum* in the fragmented plots became less stable than in the unfragmented area because of differential predation by *C. septempunctata*. Experimentally established aphid colonies were eliminated (eaten by ladybirds) twice as frequently in the unfragmented area (67% of colonies destroyed) than in the fragmented area (only 30% of colonies destroyed). In contrast, Grez et al. (2004) showed that dividing an area of alfalfa into several plots separated by bare ground, resulted in coccinellid abundance being only slightly influenced by plot size and distance between them. The optimum for coccinellid abundance was fragmentation into small patches a short distance apart. The **effect was transitory** and influenced *Hip. variegata* and *Hip. convergens* more than *Eriopis connexa*. The same authors later showed that the effect of the loss of habitat area (84% of the alfalfa crop removed from the 30 × 30 m experimental plots) and extent of its fragmentation (experimental plots divided into 1, 4 or 16 fragments) did not affect overall coccinellid abundance but that particular species, *Hyperaspis sphaeridioides* and *A. bipunctata* were most abundant in plots where 84% of alfalfa stand had been removed. The difference in population density persisted for long time only for *A. bipunctata* (Grez et al. 2008). Coccinellids avoided bare ground, remained longer in alfalfa plots than on bare ground and were more prone to move between crop fragments if these were close to each other. Coccinellids tended to stay longer in non-fragmented than in fragmented plots, although aphid abundance was similar throughout the experimental area (Grez et al. 2005). In experiments by Banks (1999), strips of broccoli were interspersed with sections sown to weeds representing 25, 50 and 75% of the total strip area. The strips containing particular percentages of weed cover were sown each in three replicates with weedy area divided into 2, 4 or 8 fragments. The abundance of *C. septempunctata* was not affected by the proportion of total strip area sown by weeds but was significantly but not consistently influenced by the extent of its fragmentation.

Finally, the global **character of the landscape**, which includes not only fragmentation and composition of the vegetation cover but also the agriculture practices used, has its effects on coccinellid abundance. Several examples have accumulated in the last years. Bianchi et al. (2007) showed that the long-term decrease in the abundance of *C. septempunctata* in the Czech Republic may have been caused by **changes in agricultural practices**, including reduced use of fertilizers and changes to the crop species grown. These changes occurred after agricultural production ceased to be subsidized. *C. septempunctata* only partially coped with these changes in spite of the plasticity of its life cycle based on 'phenotypic polymorphism', i.e. the element of its plasticity that enables it to occupy a wide ecological niche and extensive geographical area (Hodek & Michaud 2008). In the USA, Gardiner et al. (2009) showed that domestic *Hip. convergens* was replaced by the invasive *C. septempunctata*, *Har. axyridis*, *Hip. variegata* and *P. quatuordecimpunctata*, but less so in grassland dominated landscapes with low structural diversity and low amount of forests than in landscapes with other characteristics. Intensively managed agricultural areas therefore represent **landscape-scale refuges** for native coccinellid diversity (Gardiner et al. 2009). The effect of landscape varies with geographic area and more information on the impact on coccinellids is needed from the tropics. In a study in Swaziland, Magagula & Samways (2001) showed that the highest coccinellid abundance and diversity was in orchards, smaller in riparian areas and least in dry savannah. Prey availability was the most important determinant of coccinellid presence; humidity, temperature and ground insolation had no effect.

Switching between habitats is important for the maintenance of coccinellid populations, which in this way can exploit **seasonal changes** of quality in different habitats. A number of case studies have documented coccinellids switching between stands of wild herbs, trees, shrubs and crops. In a typical case, which represents the life cycle of coccinellids in temperate zones, adults leave the overwintering sites to feed on wild herbs, shrubs or trees populated with prey early in the season, move between them, then fly to crops which have been infested early by aphids; they occasionally change between crops where they reproduce. Adults of the last generation of the year finally again move to tree, shrub and wild herb hosts before hibernation. These movements have been amply documented for coccinellids in Europe (Banks 1955, Lusis 1961, Hodek et al. 1962, 1966, Iperti 1965, Honěk 1982b,1989, Hemptinne & Naisse 1988) and central Asia (Yakhontov 1966, Aleksidze 1970, Savoiskaya 1970) and hold also for North America where the distribution of coccinellid species follows the sequence of aphid populations as they become available in different crops (French et al. 2001). The factor determining these seasonal migrations between habitats is the search for food. In the spring, *Col. maculata* **migrate from hibernacula** to first arrive in wheat, but later on in June–August they move to maize because of the changing availability of aphids (Nault & Kennedy 2000). Similar food-motivated changes of habitat were observed in subtropical and tropical areas (Wiesmann 1955, Brown 1969, Iperti et al. 1970, Laudého et al. 1970).

Movement between habitats is by **flight** (6.3.1.3). Most displacements are probably accomplished by trivial flights, which occur near the ground. Boiteau et al. (1999) studied the altitudinal distribution of flights using window traps placed 0.8–14.3 m above the ground. Maximum catches, consisting mainly of *Hip. convergens*, *C. septempunctata* and *C. trifasciata*, were at 0.8 m. The flight of the other 18 species caught in this study was more evenly spread with respect to altitude. Sarospataki & Marko (1995) also established abundant trivial flight activity in a short period at the end of June of *C. septempunctata* at 0–2 m above ground level while migrants captured above the vegetation at 25–27 m height were very few.

4.3.3 Dominance, diversity and niche differentiation

The structure of coccinellid communities in different habitats shares common features that enable a few generalizations to be made. The spatial and trophic capacity of any habitat is limited, and the length of time that suitable conditions persist is rather short. Thus only a limited number of individuals and species may successfully survive and breed at a given place. This determines the general similarity in the numbers of species and their order of dominance in coccinellid communities in different parts of the world.

At any habitat, the coccinellid community will contain a few **dominant species**. Usually two to four species will represent more than 90% of the individuals. The other coccinellids, although often several times greater in number of species than the dominant ones, yet represent only a small fraction of the total number of individuals present. Comparative studies of diversity and dominance were made in maize crops and apple orchards in Hungary (Loevei 1981, Radwan & Loevei 1982, 1983, Loevei et al. 1991). Larval, pupal and adult communities in the maize crops grown under three different regimes consisted respectively of 7, 6 and 11 species, and the proportion of the most abundant species in the total population of each development stage ranged between 0.42–0.93, 0.31–0.47 and 0.41–0.68, respectively. The results for the apple orchards were similar regardless of whether they were treated with insecticides or not.

A frequent aim of habitat studies is to define the **niches** of individual coccinellid species and empirically compare the differences between these niches. The concept of niche with regard to coccinellids was reviewed by Snyder (2009). The species may be separated one from the other by using different habitats (**spatial niche**), using the same habitat at different time (**temporal niche**) or using a specific prey (**prey choice niches**). The knowledge necessary to recognize different kinds of niche separation in the open is to determine the relative abundance of a species which means its proportion in the sample of the coccinellid community of a habitat, and identifying the habitat by a number of characteristics each of which could influence coccinellid abundance. Honěk & Rejmánek (1982) classified 45 samples of adults captured in stands of 14 crop, wild herb and tree species (habitats). Five groups of communities were distinguished by differences in the dominance of particular species. Three groups consisted of communities of **herbaceous stands** inhabited by aphid populations of low or moderate density, mainly field crops. Communities of each of these three groups were dominated by one of the common species: *P. quatuordecimpunctata*, *C. septempunctata* or *Hip. variegata*. The other two groups consisted of communities inhabiting **trees or wild herbs** with dense aphid populations. These differed each other in the relative proportions of *A. bipunctata* and *C. septempunctata*. Using this data retrieved from habitat studies then enabled the calculation of **niche breadth for each species** and the overlap with the niches of other species (Honěk 1985b). Nedvěd (1999) developed this analysis further, and classified the preferences of particular species as reflected by their presence on host plant species which were each infested by a single species of aphid. He distinguished eight groups of coccinellid species which we list here with their main representatives: (i) tree canopy species (*Myrrha octodecimguttata*, *Har. quadripunctata*), (ii) steppe species also inhabiting field localities (*C. quinquepunctata*, *Scymnus frontalis*), (iii) tree-inhabiting species not restricted to feeding on aphids (*Calvia quatuordecimguttata*), (iv) generalist species characteristic of shrubs and trees (*A. bipunctata*), (v) common field species (*C. septempunctata*), (vi) species restricted to spruce (*A. conglomerata*), (vii) species restricted to oak (*Scymnus auritus*, *Stethorus punctillum*) and (viii) species restricted to pine (*Anatis ocellata*). Coderre et al. (1987) measured niche differences for oviposition preference, between four species of aphidophagous predators, including *Col. maculata* and *Hip. tredecimpunctata*. Oviposition preferences were clearly separable on each of the three principal axes which may be interpreted as (i) aphid abundance, (ii) timing of oviposition and vertical distribution of egg clusters on the host plant, and (iii) distance from the field margin.

4.4 COCCINELLID COMMUNITIES OF PARTICULAR HABITATS

As was pointed out in 4.1, the identification of coccinellid habitats according to units created by humans may be unjustified. By dividing the landscape in this way we may overlook differences in environmental quality that are unimportant from the human perspective but important for coccinellids. An apparently uniform stand thus may represent a mosaic of conditions perceived by coccinellids as different habitats. Nevertheless, faunas of different stands as distinguished by humans continue to be studied and here we summarize some recent results. The stands are classified into three groups: crops, wild herbaceous plants and trees. For each group the results are presented separately for the Palearctic (Europe) and Nearctic (USA and Canada) regions.

Stands of **crops** host ladybird communities made up of only few species. This is true for Europe (Table 4.1) where coccinellid communities were dominated (dominant species are those that make more than 5% of the total coccinellid population) by *C. septempunctata*. Less important were *C. quinquepunctata* and *P. quatuordecimpunctata*. The crop stands have not yet been dominated by the invasive *Har. axyridis* (Ameixa 2010).

Table 4.1 Relative abundance (%) of coccinellid species on crops, Europe.

	A	B	C	D
Adalia bipunctata	—	4.7	—	0.3
Adalia decempunctata	—	0.6	—	—
Anisosticta novemdecimpunctata	—	—	—	0.1
Aphidecta obliterata	—	—	—	0.1
Chilocorus bipustulatus	—	—	—	0.1
Chilocorus renipustulatus	—	—	—	0.1
Coccidula rufa	10.7	—	0.4	2.2
Coccinella hieroglyphica	+	—	—	—
Coccinella quinquepunctata	2.8	—	9.1	6.8
Coccinella septempunctata	86.0	89.2	90.5	80.1
Coccinula quatuordecimpustulata	0.1	—	—	0.2
Hippodamia tredecimpunctata	—	1.4	—	0.6
Hippodamia variegata	+	1.4	—	—
Myzia oblongoguttata	—	—	—	0.1
Propylea quatuordecimpunctata	0.4	2.5	—	9.0
Scymnus frontalis	—	—	—	0.1
Scymnus haemorrhoidalis	+	—	—	0.2
Scymnus suturalis	—	—	—	0.1
Scymnus sp.	—	0.3	—	—

+ species recorded in <0.1% frequency.

A Finland, cereals, *N* = 5824 (Clayhills & Markkula 1974); B Serbia, cereals, *N* = 361 (Tomanovic et al. 2008); C Finland, potato. *N* = 504 (Clayhills & Markkula 1974); D Finland, forage leguminosae, *N* = 1752 (Clayhills & Markkula 1974).

The communities of crops in the Nearctic are more diversified. Six species of coccinellids may become dominant in the communities of cereals (Table 4.2) and nine species in the communities of other crops (Table 4.3). This is because in communities of crops the dominant positions may be taken not only by native species typical for the herbaceous stratum, *Col. maculata*, *Cycloneda munda*, *Hip. convergens*, *Hip. parenthesis*, *Hip. sinuata* and *Hip. tredecimpunctata*, but also by species introduced from the Palearctic, *C. septempunctata* and *P. quatuordecimpunctata*. *Harmonia axyridis*, a species which in Europe is typical for communities of tree stands, became dominant in maize (Lucas et al. 2007, Musser & Shelton 2003), medicinal crops (Lucas et al. 2007) and soybean (Lucas et al. 2007, Schmidt et al. 2008). The coccinellid communities of crops in the Nearctic are thus originally more diversified but apparently less resistant to invasion of alien species than the communities of Europe.

The coccinellid communities inhabiting stands of **wild herbs** in Europe (Table 4.4) are more diversified than the communities inhabiting crops. This is because the coccinellid fauna of wild herbs consists both of species typical for the herbaceous stratum (*C. septempunctata*, *Hip. variegata*, *P. quatuordecimpunctata*) and of species typical for trees (*A. bipunctata*).

Trees host still more diversified communities of coccinellids. Recent studies in Europe (Table 4.5) have concerned communities of deciduous trees in the western and northern parts of the continent (Clayhills & Markkula 1974, Leather et al. 1999). Interestingly, the community of a **Mediterranean** citrus orchard was similar to that of deciduous trees (Kavallieratos et al. 2004). In contrast, a study of communities of **coniferous** trees (Selyemova et al. 2007) pointed out the distinct difference from broad-leaved trees. Several studies of North American apple orchards (Table 4.6) showed a dominance of alien species *C. septempunctata*, *Har. axyridis* and *P. quatuordecimpunctata* over native species (Brown & Miller 1998, Brown 2004, Lucas et al. 2007). On wild trees (Table 4.7) the dominance of alien species in the coccinellid communities was less prominent but *Har. axyridis* dominated in one study of Oregon (LaMana & Miller 1996).

Unlike European and North American communities, those of other parts of the world have been less studied (Table 4.8). Data from the East Palearctic (Yu 1999) and Africa (Woin et al. 2000, Magagula & Samways 2001) indicate that communities of **tropical** and **subtropical** areas may be more diverse than those of temperate zones. This is, of course, expected considering the greater species richness in the tropics.

The above data illustrate the limitations of current work on coccinellid communities. First, the examples of these communities have nearly all been retrieved from papers published in high-impact journals. Although this may guarantee quality, the other side of the coin is that the data are always published to illustrate something other than coccinellid community structure. Because of the difficulties in publishing raw community data in ‘high quality’ journals, the majority probably ends up in what is called the ‘grey literature’, i.e. local publications, conference proceedings or university theses. How much better would it be if this information was collected and subjected to meta-analysis! The second drawback is that there is enormous variation in the quality of species determination. If the data on aphidophagous species were limited to the subfamily coccinellinae, different studies

Table 4.2 Relative abundance (%) of coccinellid species on small grain cereals and maize, North America.

	A	B	C*	D	E	F	G	H	I
Adalia bipunctata	—	—	—	—	0.5	—	0.2	0.4	—
Coccinella septempunctata	7.5	6.5	1	2.0	3.9	2.5	2.1	5.5	3.3
Coccinella transversoguttata	—	1.3	6	—	—	—	1.3	—	—
Coleomegilla maculata	5.0	7.7	2	45.3	35.1	63.1	28.6	49.1	65.9
Cycloneda munda	—	1.1	5	2.0	—	28.0	0.6	—	1.6
Harmonia axyridis	—	—	—	—	54.8	—	—	32.5	—
Hippodamia convergens	59.4	45.6	1	32.4	—	5.1	41.9	—	27.6
Hippodamia glacialis	—	—	—	—	—	—	—	—	—
Hippodamia parenthesis	3.2	10.0	3	6.2	—	0.2	0.7	—	—
Hippodamia sinuata	—	—	5	—	—	—	—	—	—
Hippodamia sp.	—	—	—	—	5.7	—	—	—	—
Hippodamia tredecimpunctata	24.9	27.9	5	12.1	—	1.1	24.7	—	1.6
Olla v-nigrum	—	—	5	—	—	—	—	—	—
Propylea quatuordecimpunctata	—	—	—	—	0.4	—	—	12.6	—
Scymnus spp.	—	—	4	—	—	—	—	—	—

+ species recorded in <0.1% frequency.

*Abundances ranked starting from the most (1) to the least frequent (6) species.

A USA, South Dakota, spring wheat, *N* = 4883 (Elliott & Kieckhefer 2000); B USA, South Dakota, small grain cereals, *N* = 5835 (Elliott et al. 1996); C USA, Midwest, wheat, *N* = not indicated (Obrycki et al. 2000); D USA, Nebraska, *N* = not indicated (Wright & DeVries 2000); E USA, New York, maize, *N* = not indicated (Musser & Shelton 2003); F USA, Iowa, maize, sticky trap, *N* = 1221 (Bruck & Lewis 1998); G USA, South Dakota, maize, *N* = 20753 (Elliott et al. 1996); H Canada, Quebec, maize, *N* = 8450 (Lucas et al. 2007); I USA, Nebraska, maize, *N* = not indicated (Wright & DeVries 2000).

Table 4.3 Relative abundance (%) of coccinellid species on stands of medicinal crops, forage leguminosae, sorghum and soybean, North America.

	A	B	C*	D	E	F	G	H	I	J
Adalia bipunctata	—	—	5		0.5	—	—	—	—	—
Anatis quindecimpunctata	—	—	—	—	—	—	—	—	—	0.3
Brachiacantha ursina	—	—	—	—	—	—	—	—	0.5	0.3
Coccinella californica	—	—	—	—	1.8	—	—	—	—	—
Coccinella septempunctata	20.1	5.7	1	17.2	27.4	0.2	0.2	5.2	8.2	5.5
Coccinella transversoguttata	—	1.2	7	—	—	—	—	—	—	—
Coccinella trifasciata	—	—	—	—	48.2	—	—	—	—	—
Coccinella undecimpunctata	—	—	—	—	3.6	—	—	—	—	—
Coleomegilla maculata	51.1	8.6	1	22.6	—	3.5	1.0	23.9	8.3	2.2
Cycloneda munda	—	0.6	3	1.2	—	—	—	0.4	—	2.5
Cycloneda polita	—	—	—	—	1.4	—	—	—	—	—
Harmonia axyridis	9.0	—	—	—	3.7	—	—	—	21.0	78.1
Hippodamia convergens	14.9	48.9	1	54.5	9.4	50.3	63.5	65.4	—	9.9
Hippodamia glacialis	—	—	6	—	—	—	—	—	—	—
Hippodamia parenthesis	—	16.5	2	4.0	—	—	0.1	0.8	1.0	1.0
Hippodamia sinuata	—	—	5	—	7.4	45.0	33.9	—	—	—
Hippodamia tredecimpunctata	—	18.4	5	0.6	—	—	—	4.7	—	0.1
Hippodamia variegata	—	—	—	—	—	—	—	—	1.0	—
Mulsantina picta	—	—	—	—	0.4	—	—	—	—	—
Olla v-nigrum	—	—	5	—	—	+	+	—	—	—
Propylea quatuordecimpunctata	4.8	—	—	—	—	—	—	—	60.0	—
Scymnus loewii	—	—	—	—	—	—	1.2	—	—	—
Scymnus spp.	—	—	4	—	—	0.2	—	—	—	—
Unidentified	—	—	—	—	—	0.2	—	—	—	—

+ species recorded in <0.1% frequency.

*Abundances ranked starting from the most (1) to the least frequent (7) species.

A Canada, Quebec, medicinal crops, *N* = 305 (Lucas et al. 2007); B USA, South Dakota, alfalfa, *N* = 7974 (Elliott et al. 1996); C USA, Midwest, alfalfa, *N* = not indicated (Obrycki et al. 2000); D USA, Nebraska, alfalfa, *N* = not indicated (Wright & DeVries 2000); E USA, Oregon, clover, alfalfa and peppermint, *N* = 780 (LaMana & Miller 1996); F USA, Texas, sorghum, *N* = 2872 (Michels et al. 1996); G USA, Texas, sorghum, *N* = 29,354 (Michels & Matis 2008); H USA, Nebraska, sorghum, *N* = not indicated (Wright & DeVries 2000); I Canada, Quebec, soybean, *N* = 334 (Lucas et al. 2007); J USA, Iowa, soybean, *N* = 1739 (Schmidt et al. 2008).

Table 4.4 Relative abundance (%) of coccinellid species on wild herbs, Europe.

	A	B	C
Adalia bipunctata	8.3	0.7	50.9
Chilocorus bipustulatus	0.5	—	—
Coccidula rufa	—	+	—
Coccinella septempunctata	4.9	12.0	49.1
Hippodamia variegata	21.6	48.1	—
Oenopia conglobata	2.8	0.3	—
Platynaspis luteorubra	—	+	—
Propylea quatuordecimpunctata	32.8	12.2	—
Psyllobora vigintiduopunctata	6.3	2.1	—
Scymnus apetzi	—	7.1	—
Scymnus auritus	—	1.4	—
Scymnus frontalis	—	6.3	—
Scymnus interruptus	—	0.1	—
Scymnus rubromaculatus	—	8.6	—
Scymnus subvillosus	—	0.4	—
Scymnus sp.	17.3	—	—
Stethorus pusillus	5.1	0.6	—

+ species recorded in <0.1% frequency.

A Italy, mixed herbs adjacent to old hedgerows, *N* = 656 (Burgio et al. 2006); B Italy, mixed herbs adjacent to young hedgerows, *N* = 2112 (Burgio et al. 2006); C United Kingdom, grasses and herbs, *N* = 112 (Leather et al. 1999).

Table 4.5 Relative abundance (%) of coccinellid species on trees, Europe.

	A	B	C	D	E
Adalia bipunctata	16.4	36.4	1.1	0.4	0.4
Adalia conglomerata	—	—	—	—	16.3
Adalia decempunctata	0.8	—	—	—	—
Anatis ocellata	—	—	—	—	7.7
Aphidecta obliterata	—	—	—	—	50.3
Calvia quatuordecimguttata	—	—	14.7	0.1	0.6
Ceratomegilla notata	—	—	—	—	2.8
Ceratomegilla undecimnotata	0.8	—	—	—	—
Coccinella quinquepunctata	—	—	—	11.0	+
Coccinella septempunctata	10.8	42.4	84.2	63.0	17.4
Coccidula rufa	—	—	—	0.3	—
Exochomus quadripustulatus	—	—	—	—	+
Halyzia sedecimguttata	—	—	—	—	0.6
Hippodamia variegata	—	—	—	—	0.1
Myzia oblongoguttata	—	—	—	—	0.6
Propylea quatuordecimpunctata	3.0	3.0	—	17.8	1.0
Psyllobora vigintiduopunctata	—	18.2	—	—	0.2
Scymnus abietis	—	—	—	—	1.6
Scymnus apetzi	51.4	—	—	—	—
Scymnus rubromaculatus	6.5	—	—	—	—
Scymnus subvillosus	10.2	—	—	—	—
Tytthaspis sedecimpunctata	—	—	—	—	+

+ species recorded in <0.1% frequency.

A Greece, citrus, *N* = 675 (Kavallieratos et al. 2004); B United Kingdom, deciduous trees, *N* = 33 (Leather et al. 1999); C Finland, apple, *N* = 95 (Clayhills & Markkula 1974); D Finland, black and red currant, *N* = 73 (Clayhills & Markkula 1974); E Slovakia, spruce, *N* = 3636 (Selyemova et al. 2007).

Table 4.6 Relative abundance (%) of coccinellid species in apple orchards, North America.

	A	B	C	D
Adalia bipunctata	3.2	—	—	+
Anatis labiculata	2.2	—	—	—
Brachiacantha ursina	—	—	—	22.0
Chilocorus stigma	—	—	—	+
Coccinella septempunctata	87.8	9.5	26.4	4.5
Coleomegilla maculata	1.7	14.0	2.0	30.0
Cycloneda munda	3.7	—	—	—
Harmonia axyridis	—	76.5	65.5	12.0
Hippodamia parenthesis	—	—	—	+
Hyperaspis binotata	—	—	—	+
Hyperaspis undulata	—	—	—	+
Nephus flavifrons	—	—	—	+
Olla v-nigrum	1.2	—	—	—
Propylea quatuordecimpunctata	—	—	—	15.0
Psyllobora vigintimaculata	—	—	—	+
Scymnus sp.	—	—	6.1	—

+ species recorded in <0.1% frequency.
A USA, West Virginia, 1989–93, *N* = 306 (Brown & Miller 1998); B USA, West Virginia, 1995–96, *N* = 276 (Brown & Miller 1998); C USA, West Virginia, *N* = 148 (Brown 2004); D Canada, Quebec, *N* = 691 (Lucas et al. 2007).

Table 4.7 Relative abundance (%) of coccinellid species on wild tree stands, North America.

	A	B	C
Adalia bipunctata	13.3	0.3	—
Anatis quindecimpunctata	—	0.3	—
Calvia quatuordecimguttata	0.6	—	—
Chilocorus sp.	0.1	0.3	7.1
Coccinella californica	0.2	—	—
Coccinella septempunctata	5.0	—	—
Coccinella trifasciata	0.8	1.1	—
Coleomegilla maculata	—	0.3	—
Cycloneda polita	3.9	—	—
Exochomus quadripustulatus	3.7	—	—
Harmonia axyridis	69.6	2.4	4.8
Hippodamia convergens	0.6	—	—
Hippodamia sinuata	1.0	—	—
Mulsantina picta	1.2	—	—
Mulsantina sp.	—	—	14.3
Myzia subvittata	0.1	—	—
Propylea quatuordecimpunctata	—	32.1	—
Psyllobora vigintimaculata	—	63.3	73.8

A USA, Oregon, mixed trees and shrubs, *N* = 2984 (LaMana & Miller 1996); B USA, Maine, yellow traps, deciduous forest, *N* = 1510 (Finlayson et al. 2008); C USA, Maine, yellow traps, coniferous forests, *N* = 126 (Finlayson et al. 2008).

Table 4.8 Studies of coccinellid communities out of Europe and North America.

Area	Host plant	No. of coccinellid species in the community	Reference
Cameroon	rice	13	Woin et al. (2000)
China	*Pinus armandii*	18	Yu (1999)
Swaziland	garden–savanna	23 (incl. 3 Epilachninae)	Magagula & Samways (2001)

would be more or less comparable in quality. However, when other subfamilies are included into sampling plans, the accurate determination of the collected material to species is far from common. Third, as stated above, more quantitative sampling of subtropical and tropical communities is necessary to fill the gaps ('white spots') in the distribution map of coccinellid communities.

4.5 CONCLUSION

Here we review knowledge of the distribution of coccinellid species among habitats. This includes the delimitation and characterization of what the habitat is, a description of its coccinellid community and a determination of the factors that attract particular species and hold the community together. We believe that this knowledge in itself is not only fundamental for coccinellid studies but also encourages the proposition of hypotheses. The review part of this chapter carries the risk that gaps which still exist in our knowledge may be hidden, in particular where the delimitation of a habitat has been erroneous, the time required for the development of coccinellid communities may have been underestimated, real causes determining species presence may have been overlooked, and, to us the most dangerous possibility, illusory causes may have been suggested and erroneous proofs of their effects have been done. In our view the new developments of discipline replicated results and strengthened hypotheses provided in Honěk and Hodek (1996). Our rather long experience of coccinellid habitat studies, however, may have made our evaluation of facts and causes too rigid. Our perspective is perhaps too much determined by the geographic conditions in which we have worked. We hope that future researchers, working under different conditions, may bring new ideas and make significant progress in the topic of this chapter.

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