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Ecology of *Harmonia axyridis* in natural habitats within its native range

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Abstract Originally distributed in northeast Asia, *Harmonia axyridis* (Coleoptera: Coccinellidae) is now found throughout much of the temperate zone. In its native area, *H. axyridis* maintains stable populations in heterogeneous and temporary habitats because of its great ability to find prey and reproduce, coupled with density-dependent and self-regulatory population regulation. A negative correlation of *H. axyridis* on the biodiversity of the aphidophagous community has been observed in its native range. The decrease in biodiversity may be mainly caused by the wider range of habitats available to *H. axyridis* than to the coexisting species. From a theoretical perspective, density-dependent regulation of *H. axyridis* populations, e.g., cannibalism, may be more important in maintaining the *H. axyridis*-dominated system, probably than is intraguild predation. Habitat heterogeneity may also be important to the coexistence of *H. axyridis* and other predators in both native and invaded areas.

Keywords Cannibalism · Coccinellidae · Coleoptera · Density dependence · Habitat heterogeneity · Population dynamics

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Introduction

Harmonia axyridis (Coleoptera: Coccinellidae) has been introduced into the United States, and more recently into European countries mainly for biological control of aphids (e.g., Koch 2003; Brown et al. 2008; Roy and Wajnberg 2008). However, *H. axyridis* is now regarded as a pest in the new areas it has colonized for a number of reasons including aggregations of beetles on grapes in autumn that are potential threats to the wine and fruit-growing industries (e.g., Koch et al. 2004; Roy and Wajnberg 2008), and the beetles' pattern of aggregation during winter is considered a nuisance to humans (Kovach 2004). In addition, this species may have negative impacts on endemic ladybird species in the US and European countries (e.g., Colunga-Gracia and Gage 1998; Adriaens et al. 2003; Brown 2003; Roy and Wajnberg 2008; Brown et al. 2011). Much attention has been paid to the invasion and establishment of *H. axyridis* because it can successfully invade and establish in an area in a short period, and *H. axyridis* abundance can increase considerably, both in absolute numbers and also relative to other native aphidophagous ladybird beetles. The rapid establishment and increase in abundance in a short period of time in invaded areas by generalist predators such as *H. axyridis*, through intentional or unintentional human activity, may be rare in the history of introductions for biological control and insect invasion. Therefore, *H. axyridis* invasions have received much attention from conservation ecologists as well as biological control scientists because of fears that *H. axyridis* may cause extinctions in the endemic aphidophagous predators of the invaded areas (e.g., Brown et al. 2011).

Harmonia axyridis is native to northeast Asia, including China, Korea, Japan, and Siberia (e.g., Sasaji 1971). Less common in natural forests, this species is generally found in agricultural fields, orchards, parks, and residential yards and gardens, suggesting that the original natural habitat of *H. axyridis* is disturbed areas (e.g., riversides and shrublands) (Osawa N, personal observations). *H. axyridis* also tends to prefer tree and shrub lands, whereas *Coccinella septempunctata*, another common aphidophagous species in Japan, prefers grassy habitats, although these generalizations have exceptions (e.g., Osawa 1991; Hironori and Katsuhiro 1997). These habitat preferences are reflected in differences in larval dropping behavior: the *H. axyridis* larva has a sucker on the tip of the abdomen, which prevents it from dropping accidentally to the ground, whereas *C. septempunctata* feigns death when it senses vibrations caused by predators and often falls to the ground as a result (Sato et al. 2005). These differences in dropping behavior play an important role in intra-guild differences in predation between the two species (Sato et al. 2005). In Japan, *H. axyridis* coexists with other aphidophagous predators (Osawa 1991). To predict the impact of *H. axyridis* on the native aphidophagous guilds of invaded areas, it is important to understand characteristics of the life history and population dynamics of the species, as well as its role within aphidophagous guilds in its natural native habitats.

In this paper, I summarize characteristics of *H. axyridis* populations in natural habitats by reviewing published works and analyzing unpublished data. I thus clarify the role of *H. axyridis* in the aphidophagous community in its native range.

Life history of *H. axyridis*

Harmonia axyridis is generally considered to have two generations per year in Japan, although it potentially has three or more in some years and localities (e.g., Tanigishi 1976; Osawa 1991). In Kyoto, in the center of Japan, adults of the overwintering generation, i.e., the second and/or third and fourth generations, terminate overwintering in late March and mate and lay eggs in April and May (Osawa and Nishida 1992; Osawa 2000). Adults of the first generation emerge in mid May to June (Osawa 2000; Osawa and Nishida 1992). In midsummer, the beetles aestivate in small groups in leaf-shelters on trees, e.g., *Quercus glauca* (Toda and Sakuratani 2006). Aestivation probably is an adaptation to survive high temperatures. Adults of the second and/or third and fourth generations reappear in autumn and mate and oviposit (Osawa, unpublished data). They gradually fly toward whitish or light-colored objects on hilltops or in valleys and at the bases of mountains, and thereafter aggregate at overwintering sites in early November (Obata 1986). The intensity of white as an attractant compared with other colors was confirmed by intensive field research at the native range in China (Wang et al. 2010). Except for natural rocks on mountainsides, the selected overwintering sites were artificial objects, e.g., houses, bridges, chimneys, wooden structures, and telegraph poles (e.g., Tanigishi 1976). Field experiments including different numbers of overwintering individuals suggested that one adaptive role of winter aggregation in *H. axyridis* is increased survival rate of overwintering adults in larger groups (Tanigishi 1976). This is largely consistent with results of intensive field research at the native range in China, which found that winter aggregation in human habitats is a behavioral adaptation for cold avoidance (Wang et al. 2010).

Dinocampus coccinellae (Hymenoptera: Braconidae) is known to be an adult parasitoid of *H. axyridis* (e.g., Maeta 1969). At the pupal stage, *Phalacrotophora* sp. (Diptera: Phoridae) is known to be a parasitoid of *H. axyridis* (Osawa 1992a). The percentage of *H. axyridis* pupae killed by parasitism in the field was 10.3% (Osawa 1992a). Interestingly, prior to the pre-pupal stage, *H. axyridis* larva provides an escape from parasitism through behavioral means (Osawa 1992a). No egg parasitoids have been observed in *H. axyridis*.

Alkaloids are traditionally regarded as a chemical defense against predators in ladybird beetles (e.g., Brakefield 1985; Sloggett et al. 2009a, b), although the intensity of toxicity of different species is highly variable in alkaloids (e.g., Majerus 1994; Sloggett et al. 2009a). Recent research has confirmed that alkaloids also play an important role in the intensity of intraguild predation in *H. axyridis* in invaded areas (e.g., Kajita et al. 2010; Sloggett et al. 2009a; Sloggett and Davis 2010; Sloggett et al. 2011).

Cannibalism

Cannibalism plays an important role in the life history of *H. axyridis* in the field. Cannibalism of larvae generally occurs at all stages (egg, larval, prepupal, and pupal) of *H. axyridis*. Osawa (1993) estimated that 50% of eggs are killed through cannibalism, with 20% preyed upon by non-siblings (egg cannibalism by larvae derived from different egg clusters) and 30% by siblings (egg cannibalism by sibling larvae in an egg cluster). At the pupal stage, 14.4% of all pupae are cannibalized (Osawa 1992a), mainly by the fourth instars.

Sibling cannibalism occurs in more than 90% of *H. axyridis* egg batches in its native area (Osawa 1989). The existence of unhatched eggs and hatching asynchrony are proximate factors affecting the intensity of sibling cannibalism (Kawai 1978; Osawa 1992b). In *H. axyridis*, possible costs and benefits in sibling cannibalism were considered from three kin-related points of view: the cannibal, the victim, and the mother (Osawa 1992b). The cannibalistic trait was clearly beneficial to the cannibal at low aphid density, whereas the cannibalized individual was beneficial only when the victim was cannibalized at low aphid density (Fig. 1) (Osawa 1992b). The mother attained almost equal fitness at low aphid density, regardless of the intensity of sibling cannibalism, suggesting that sibling cannibalism is, at least, not maladaptive for the mother at low aphid density (Osawa 1992b). Therefore, sibling cannibalism is adaptive for both the cannibal and the full sibling victim at low aphid density, and the mother attains equal fitness regardless of the intensity of sibling cannibalism (Osawa 1992b). Thus, through kin selection, sibling cannibalism at hatching plays an important role in the persistence of *H. axyridis* populations in nature (Osawa 1992b).

Non-sibling cannibalism was more intense in the middle and late in the oviposition periods and when the egg clusters were located closer to an aphid colony (Osawa 1989). Pupal cannibalism occurred more intensely on host plants of aphid colonies than at other pupal sites and near the aphid colony (Osawa 1992a). The higher rate of cannibalism near aphid colonies may be caused by intensive searching by *H. axyridis* larvae near aphid colonies (Osawa 1989, 1992a).

A few studies have quantitatively evaluated the intensity of cannibalism among *H. axyridis* larvae in nature (e.g., Takahashi 1989; Hironori and Katsuhiro 1997). However, in some cases, aphid populations have been found to collapse before the completion of *H. axyridis* larval development (Osawa 1992c). This circumstantial evidence strongly suggests that larval cannibalism, especially size-dependent cannibalism, i.e., larger larvae cannibalize smaller larvae, occurs intensively in some cases in *H. axyridis*. Intraguild predation may also occur along with larval and pupal cannibalism in field populations of *H. axyridis*.

Population dynamics and habitat characteristics

Larval mortality was found to be a key factor in *H. axyridis* life tables (Osawa 1993; Hironori and Katsuhiro 1997). Mortality at all stages tended to be density dependent, except for mortality observed at hatching due to sibling cannibalism (Osawa 1993). The R^2 values range from 0.468 to 0.624, indicating intense self-regulatory and stabilizing mechanisms in *H. axyridis* populations (Osawa 1993). Aphid predation by *H. axyridis* larvae and aphid migration may also play a certain role on the density dependence through the food shortage at local patches, although it is not confirmed. These stabilizing and persistent self-regulatory mechanisms, based on density-dependent mortality and unequal resource allocation of maternal investment through sibling cannibalism at hatching, promote survival in *H. axyridis* populations (Osawa 1993, 2000).

Population dynamics in animal are closely related to habitat structure. The habitats of *H. axyridis* can be categorized, according to the total number of beetles and eggs that occur in them, into those habitats suitable for survival and reproduction and those providing temporary refuge (i.e., those having a few adult arrivals and little oviposition) (Osawa 2000). Refuge habitats include elder, *Sambucus sieboldiana* (Caprifoliaceae), infected with the aphid *Aulacorthum magnoliae*, which is toxic to *H. axyridis* (Osawa 2000). *S. sieboldiana* is not lethal to *H. axyridis* adult but prevents the larval development (Okamoto 1978, Fukunaga and Akimoto 2007). *H. axyridis* moves

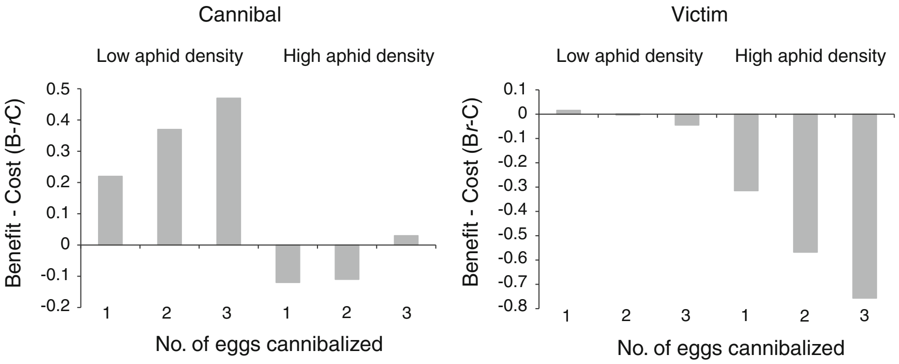

Fig. 1 The cost and benefit of sibling cannibalism to the cannibal and the victim in full sibling modified from Osawa (1992b). Benefit and cost (*Y* axis) are evaluated from the mean value of survival rate from the first to the second instar in full sibling ($r = 0.5$). This experiment was done by individual mark and recapture method distinguished for the larvae with different level of egg cannibalism (0, 1, 2, and 3 eggs) in a field. Low and high aphid density were controlled daily (added and/or removed by a fine brush) at 300 and 1200 aphid (*Apis spiraecola*) per host tree (*Citrus unshiu*, 50 cm in height), respectively

both short and long distances between these patchily distributed habitats, and reproduces at sites that are suitable in terms of prey quantity and quality (Osawa 2000). Thus, *H. axyridis* uses various types of habitats, including those with toxic aphids, in maintaining its populations.

The role of *H. axyridis* within aphidophagous guilds

Data from Osawa (1991) are used here to assess the role of *H. axyridis* in aphidophagous guilds. From early April to early August 1988, 20-min censuses were performed to collect all adult aphid predators, except ants and spiders, at 23 sites (these included seven species of plant with eight species of aphids), and all the individuals were identified to species. Individuals of *H. axyridis* were marked and released at the same site to evaluate the number of individuals of this species occurring in the habitats over the same period (Osawa 2000). Data for the five most common aphidophagous ladybird beetles; *H. axyridis* ($n =$ 505), *Coccinella septempunctata* ($n = 124$), *Propylea japonica* ($n = 30$), *Scymnus posticalis* ($n = 91$), and *Menochilus sexmaculatus* ($n = 125$), (92.97% of all coccinellids) were used for the analysis because they occur at the same habitats during the observed season. Morisita (1967) β was used to analyze the biodiversity of aphidophagous ladybird beetles. Regression analysis was performed between relative abundance of an individual species (e.g., *H. axyridis*) and the value of β at each site. Regression analysis was also performed between number of individuals in *H. axyridis* and number of an individual species, and between relative abundance of *H. axyridis* and number of an individual species. All statistical analyses were performed using SAS (SAS Institute 2007).

In total, 886 individuals were collected, and at 57.00% ($n = 505$), *H. axyridis* was the dominant species. The species-specific patterns of adult arrival to the habitats may be caused by (1) species-specific habitat preferences (e.g., Honek 1985) or (2) species-specific prey preferences (Okamoto 1978; see Hodek and Honek 1996) of the ladybird beetles.

Analysis of the relationship between relative abundance and biodiversity of aphidophagous ladybirds revealed that the only negative relationship was between the proportions of *H. axyridis* and the biodiversity of the five coexisting species of aphidophagous beetles (Fig. 2). Interestingly, a positive relationship was observed in the case of *S. posticalis*, while no relationship was observed in the cases of *C. septempunctata*, *P. japonica*, and *M. sexmaculatus* (Fig. 2). The negative relationship of *H. axyridis* is largely consistent with patterns obtained in areas invaded by *H. axyridis*, where the biodiversity of native aphidophagous communities has been found to decrease (e.g., Roy et al. 2008). However, it is pointed out that the ecological effects of introduced species on native organisms are difficult to quantify and many problems arise for the interpretation of empirical data (Kindlmann et al. 2011). The negative relationship of biodiversity between *H. axyridis* and the coexisting species in this study is also regarded as a typical pattern observed at dominant species with the wider range of habitats: dominant species with wider habitats tend to show a negative relationship between relative abundance and Morisita's index, the reverse is true for less dominant species with narrower habitats.

In this study, a positive relationship was found between number of *H. axyridis* and that of *P. japonica*, and that of *C. septempunctata* (Fig. 3a). This suggests that (1) the habitat preference of *H. axyridis* largely overlapped at least that of *C. septempunctata* and *P. japonica*, and (2) habitats with high numbers of *H. axyridis* can still support the coexisting aphidophagous species at adult stage. Furthermore, no relationship was observed between the relative abundance of *H. axyridis* and the number of ladybird beetles in all four of the coexisting species (Fig. 3b). Therefore, relative and absolute high abundance of *H. axyridis* did not decrease the density of coexisting aphidophagous adult beetles *per se*. These results also suggest that decreased community biodiversity may be primarily caused by the wider range of habitats available to *H. axyridis* than to the coexisting species: the higher relative abundance of *H. axyridis* in unsuitable habitats less utilized by the coexisting species may result in the decreased aphidophagous biodiversity in relation to the increased relative abundance of *H. axyridis* (see Fig. 2). The species-specific habitat and prey preferences of the coexisting ladybird beetles may be strongly involved in producing this pattern in its native range. The quality and quantity of prey aphids affect the number of adult *H. axyridis* arriving and ovipositing, although the density of prey aphids is much higher than that of *H. axyridis* adults and eggs (Osawa 2000). Taken together, these results suggest that sufficient resources may still exist in a habitat for adult arrival and reproduction of coexisting species regardless of the number of arriving and reproducing *H. axyridis* in its native range.

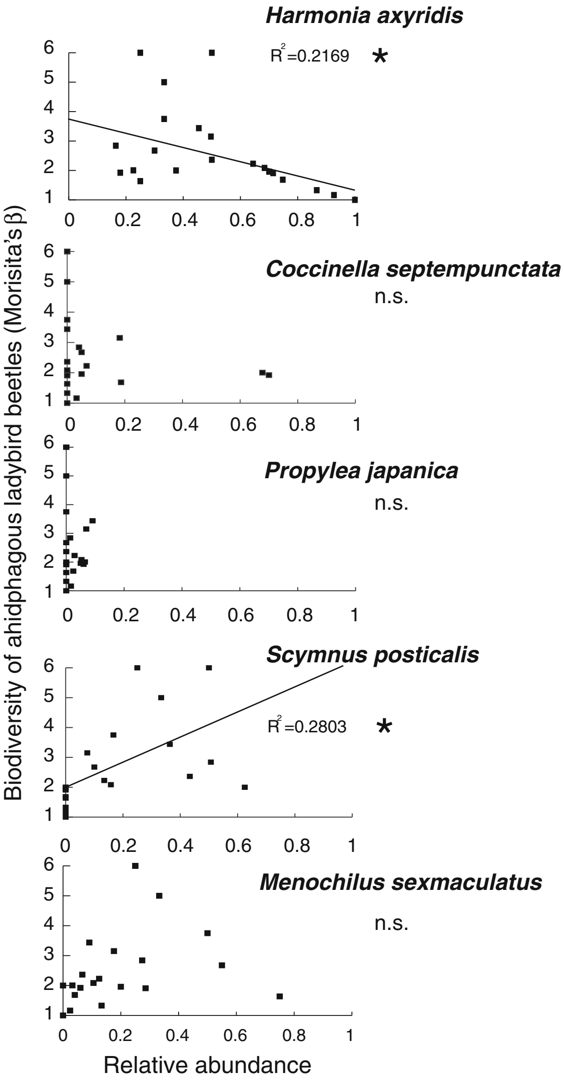

Fig. 2 The relationship between relative abundance and biodiversity of the aphidophagous ladybirds (Morisita's β) from field data (Osawa 1991). The data was collected through daily sampling from early April to early August in 1988 at 23 sites with seven species of plants with eight species of aphids at Botanical Garden, Kyoto University (35°02′ N 135°47′ E). Asterisks (*) and n.s. indicate statistical significance for the linear regressions from *F*-test at $P < 0.05$ and $P > 0.05$ level, respectively

Theoretical study has suggested that intraguild predation, in a simple three-species system where one of the competitors is also a predator and the other is its prey, provides a rich array of possible outcomes, including exclusions, coexistence, priority effects (i.e., negative/positive impact on ecological community development due to prior arrival at a site), alternative stable states, and increases in resource levels (Fig. 4a) (Polis and Holt 1992). Intraguild predation has been paid much an attention to explain the negative impact of *H. axyridis* on native aphidophagous communities in invaded areas, especially at

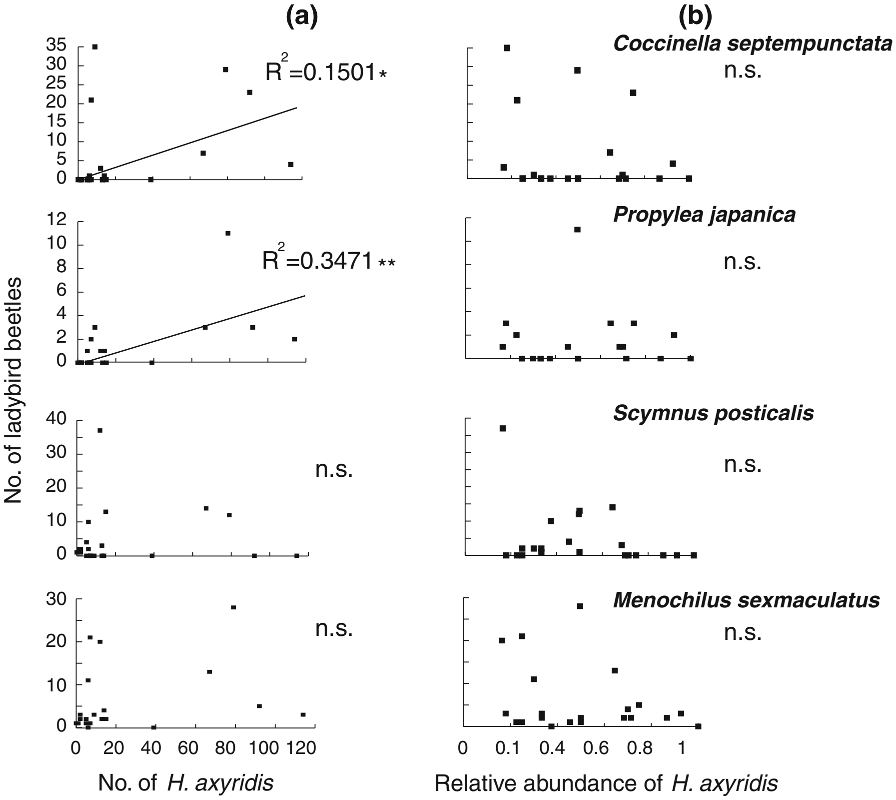

Fig. 3 The relationship between number of *H. axyridis* and number of the ladybird beetles (**a**) and that between relative abundance of *H. axyridis* and number of the ladybird beetles (**b**) from the field data (Osawa 1991). A asterisk (*), a double asterisk (**), and n.s. indicate statistical significance for the linear regressions from *F*-test at $P < 0.08$, $P = 0.01$ and $P > 0.1$ level, respectively

larval stages, as clarified by several authors in laboratory experiments (e.g., Yasuda and Ohnuma 1999; Yasuda et al. 2004; Ware and Majerus 2008, see also Koch 2003; Kindlmann and Houdková 2006; Pell et al. 2008). However, intraguild predation may be rare in communities because the intermediate predators in such configurations face a double jeopardy of competition and predation from the top predators and are therefore vulnerable to exclusion (Pimm and Lowton 1978). In aphidophagaous ladybird beetles, habitat spatial variation and predation timing may play an important role on reducing the occurrence of intraguild predation from the several empirical studies (e.g., Takahashi and Naito 1984; Schellhorn and Andow 2005; see also Sloggett 2008). Furthemore, habitat segregation and heterogeneity are generally believed to weaken the intensity of intraguild predation because they reduce the speed of energy flow (i.e., predation) and competition, resulting in a higher chance of survival of coexisting consumers in the system (Fig. 4a). Especially in aphidophagous communities, it is suggested that habitat segregation and heterogeneity increase the survival chance of the coexisting consumers by escaping from predation (Pell et al. 2008). In addition to the resources distribution pattern, timing of prey predation, size of habitat, and quality and quantity of prey requirements of the coexisting species also may play important roles in the intensity of intraguild predation by predators. Therefore, I hypothesize that stabilizing and persistent self-regulatory mechanisms of *H. axyridis* in its native range prevent this species from becoming numerous enough to reduce the diversity of aphidophagous predators through intraguild predation (Fig. 4b). Cannibalism, in particular, plays an important role in maintaining the system at all stages of *H. axyridis* development because cannibalism directly decelerates the amount and speed of energy flow from resources and consumers toward *H. axyridis* (Fig. 4b). Indeed, habitat heterogeneity is likely important also. For example, temporal and spatial habitat variation in habitat suitability were shown to play an important role in the coexistence of the recent invader *Adalia bipunctata* and native species such as *H. axyridis* or *C. septempunctata* within aphidophagous guilds in Japan (Toda and

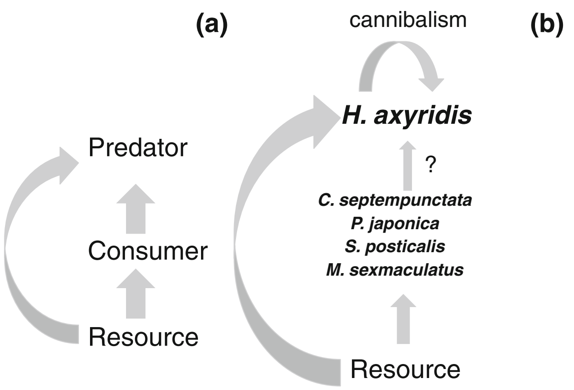

Fig. 4 Intraguild predation occurs when one consumer of a resource also eats another consumer (Pim and Lowton 1978; Polis and Holt 1992) (**a**) and intraguild predation of other ladybird beetles by the predator *H. axyridis* is hypothesized to occur in its native range, with *H. axyridis* also subject to significant cannibalism (**b**). Arrows indicate direction of energy flow

Sakuratani 2006). The finding suggests a vacant niche for *A. bipunctata* in Japan. Considered together, studies conducted on *H. axyridis* in its native range provide some evidence that increased habitat heterogeneity may enhance the potential for the coexistence of the exotic *H. axyridis* and native aphidophagous predators in invaded areas.

In nature, adults of *H. axyridis* concentrate on the arrival and oviposition at the favorable habitats with high aphid density (Osawa 2000), indicating that *H. axyridis* mainly targets these habitats to maintain the populations and cannot recognize a habitat and maintain its population at low aphid density. This suggests that *H. axyridis* is not a suitable agent for classical biological control where the object is to maintain aphid densities at low levels through the areas. These problems with the use of the generalist predator *H. axyridis* for biological control should be seen as a warning that intensive research, especially on the ecology of the native habitat, is needed before using and releasing organisms into novel environments (see Snyder and Evans 2006). Moreover, artificial selection through the mass rearing of the released *H. axyridis*, together with natural selection in invaded areas and small source populations, may lead to modifications of the genetic traits of *H. axyridis*. These selective forces may have favored aggressive traits associated with inter- and intra-specific competition, i.e., cannibalism and intraguild predation. In fact, Roy et al. (2008) clarified that intraguild predation toward infected aphids by *Pandora neoaphidis* by *H. axyridis* collected at invaded area was more intense than those collected at its native range. Further ecological and genetic monitoring of populations of *H. axyridis* in invaded areas is required.

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