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An Experimental Test of Trade-Offs Associated with the Adaptation to Alternate Host Plants in the Introduced Herbivorous Beetle, *Ophraella communa*

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Abstract

The adaptation to alternate host plants of introduced herbivorous insects can be vital to agriculture due to the emergence of crop pests. Historically, it is assumed that there are trade-offs associated with the adaptation to new host plants; a generalist genotype that adapts to an alternate host is expected to have a relatively lower fitness on the ancestral host than a specialist genotype (physiological cost) or a relatively lower host-searching ability for the ancestral host plant (behavioral cost). In this study, we tested the costs of adaptation to a new host plant in the introduced herbivorous insect, *Ophraella communa* LeSage (Coleoptera: Chrysomelidae). In its native range (United States), *O. communa* feeds mostly on *Ambrosia artemisiifolia* L. (Asterales: Asteraceae) and cannot utilize the related species, *Ambrosia trifida* L. (Asterales: Asteraceae), as a host plant. On the other hand, the introduced *O. communa* population in Japan utilizes *A. trifida* extensively, and is adapting to it, both physiologically and behaviorally. We compared larval performance on the ancestral and alternate plants and adult host-searching ability between the native and introduced beetle populations. The introduced *O. communa* showed higher larval survival and adult feeding preference for the alternate host plant *A. trifida* than did the native *O. communa*, indicating that the introduced *O. communa* has rapidly adapted to the alternate host plant. However, there are no differences in either larval performance on the ancestral host *A. artemisiifolia* or host-searching accuracy between the native and introduced *O. communa*.

Keywords Host shift · ecological specialization · *Ambrosia artemisiifolia* · *Ambrosia trifida*

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Introduction

An increasing number of studies have shown that introduced species can undergo rapid and adaptive evolution during the process of invasion (Cox 2004; Prentis et al. 2008; Colautti and Lau 2016). The rapid evolution of introduced species could amplify their impact on native ecosystems by increasing the expansion rate (Phillips et al. 2006; Williams et al. 2016), fertility, and competitive ability (Blossey and Nötzold 1995; Joshi and Vrieling 2005; Doorduin and Vrieling 2011). On the other hand, there may be trade-offs associated with adaptive evolution (cost of adaptation). To understand and to predict the eco-evolutionary consequences of the invasion of introduced species, we need to examine evolutionary trade-offs associated with their adaptation (Feng et al. 2009).

The adaptation to alternate host plants of introduced herbivorous insects can be vital to agriculture due to the emergence of crop pests and unintentional attacks on native plants by biological control agents (Louda et al. 2003; Agosta 2006), although there is little evidence that biocontrol agents have behaved in unexpected ways (van Klinken and Edwards 2002; Suckling and Sforza 2014). Historically, it is assumed that there is a physiological cost of adaptation to alternate host plants by herbivorous insects (the 'jack of all trades and master of none' principle; Futuyma and Moreno 1988; Futuyma, 2008; Forister et al. 2012). If the physiological cost was associated with the adaptation to alternate hosts, generalist genotypes that adapt to an alternate host would have a relatively lower performance on the ancestral host plants than the specialist genotype (owing to trade-offs in fitness). The physiological trade-off hypothesis has been supported by some studies (Fry 1990; Mackenzie 1996; Tilmon et al. 1998; Messina and Durham 2015; Gompert and Messina 2016), but several other studies have failed to find evidence for trade-offs (Futuyma 2008; Magalhães et al. 2009; Messina et al. 2009a, b; Laukkanen et al. 2013; Messina and Durham 2013).

Neural and information processing constraints have been recognized as another source of trade-offs in the process of adaptation to alternate host plants (Bernays and Funk 1999; Bernays 2001; Janz 2003). The information processing hypothesis assumes a behavioral cost of adaptation and states that specialist herbivores should make host-associated decisions more efficiently and accurately than generalists, owing to constraints on information processing during host-searching for feeding and oviposition (Janz and Nylin 1997; Egan and Funk 2006). Several studies have reported that specialist taxa show a higher efficiency or accuracy for host-searching than do generalist sister taxa (Janz 2003; Vargas et al. 2005; Egan and Funk 2006). However, the empirical evidence to support this hypothesis is still rather scarce (Liu et al. 2012), and a few studies found no association between host diet range and host-searching ability (Wee and Singer 2007; Liu et al. 2012).

In this study, we assessed the physiological and behavioral costs associated with adaptation to alternate hosts in the contemporary evolution of the introduced oligophagous herbivorous insect *Ophraella communa*. *Ophraella communa* and its potential host plants, *Ambrosia artemisiifolia* and *Ambrosia trifida*, are native to North America. The plants were accidentally introduced into Japan, *A. artemisiifolia* in the 1890s, and *A. trifida* in the 1950s; they are now considered invasive weeds in the country (Hisauchi 1950; Makino et al. 1997). *Ophraella communa* was also accidentally introduced into Japan in 1996. In its native range, *O. communa* mostly

feeds on *A. artemisiifolia* and does not use *A. trifida* as a host plant (Futuyma 1990; Funk et al. 1995a; Fukano and Doi 2013; Fukano et al. 2016), even though these plants are sympatrically distributed. However, *O. communa* populations in Japan started attacking the novel host, *A. trifida*, soon after their introduction in 1996 (Moriya and Shiyake 2001; Miyatake and Ohno 2010). Introduced *O. communa* feeds extensively on both *A. trifida* and *A. artemisiifolia* throughout the Japanese islands (Fukano and Doi 2013). The different host use pattern between native and introduced *O. communa* populations might be attributed to ecological (e.g. competition from other herbivores and natural enemies) and evolutionary changes (changes in plant quality and the herbivore's ability). In a previous study, we examined the effects of evolutionary changes in both the host plant and the herbivorous insect on the different patterns of host plant utilization. The results suggested that evolutionary change in both the host plant and the herbivorous insect are involved in the adaptation to the alternate host plant. Native *O. communa* cannot utilize native *A. trifida* as a host plant (very low survival rate and no oviposition) but they can utilize introduced *A. trifida* to a certain degree. On the other hand, introduced *O. communa* showed higher larval performance (higher survival rate and shorter time to pupation), adult feeding levels, and oviposition preference for both native and introduced *A. trifida*, compared with the native *O. communa* populations. These results suggested that (1) *A. trifida* is neither the fundamental nor the realized host range for *O. communa* in the native range, (2) after the introduction of *A. trifida* into Japan, introduced *A. trifida* reduced its resistance and fell within the fundamental host range for *O. communa*, and (3) after the introduction of *O. communa* into Japan, introduced *O. communa* populations rapidly evolved physiological and behavioral traits to adapt to the alternate host, *A. trifida* (Fukano et al. 2016).

Therefore, we can examine the physiological and behavioral costs associated with the adaptation to an alternate host by comparing larval performance and host-searching abilities between the ancestral, native *O. communa* (before adaptation) and the introduced *O. communa* (after adaptation). If there is a physiological cost associated with the adaptation to the alternate host plant, it is expected that the introduced *O. communa* would show a reduced performance on the ancestral host *A. artemisiifolia* compared with the native *O. communa*. If there is a behavioral cost associated with the adaptation to the alternate host, it is expected that introduced *O. communa* would show a higher inaccuracy in host-searching ability than native *O. communa*.

Materials and Methods

Sample Collection and Beetle Rearing

Seeds of *A. artemisiifolia* and *A. trifida* were collected in 2011 from a natural population located in Fuchu city, Tokyo, Japan (35° 65' N, 139° 50′ E). The collected seeds were stored at 4 °C. For germination, the seeds were placed on a wet paper and kept under dark conditions at 4 °C for 45 days. The germinated seedlings were transplanted to a field enclosure at the Tokyo University of Agriculture and Technology, to prevent insect damage. The plants were watered daily. For feeding and host-searching experiments, we used the leaves of plants that were at least 30 days old.

In 2014, about 25–40 adults of *O. communa* were collected from four *A. artemisiifolia* populations in their native range: near Harrisonburg, VA (US1, 38° 43' N, 78° 89' W), near Wilmington, NC (US2, 34° 12' N, 77° 81' W), near Atlanta, GA (US3, 33° 88' N, 84° 78' W), and near Petersburg, VA (US4, 37° 23' N, 77° 40' W), in addition to one *A. artemisiifolia* population in Japan: near Fuchu city, Tokyo (JPN1, 35° 65' N, 139° 50′ E). We used multiple native populations because the exact source location of the introduced *O. communa* populations is unknown (Nishide et al. 2015). On the other hand, we used only one introduced population because the introduced Japanese populations of *O. communa* show significantly lower genetic variation than the native populations, suggesting that the introduced Japanese populations can be traced back to a single major introduction (Nishide et al. 2015). Adult beetles from each population were reared on the leaves of experimentally grown *A. artemisiifolia* in a plastic container and egg clusters were collected from them. We used US1, US2, US3, US4, and JPN1 individuals for the experiments on larval performance, and US2, US3, and JPN1 for the experiments on adult searching ability. The rearing and all experiments were conducted in a quarantined incubator room (25 °C, 16 h light:8 h dark). The relative humidity inside and outside the containers was not controlled.

Larval Performance on Different Hosts

To assess the physiological cost associated with the adaptation to an alternate host, we compared the larval performance of the native and introduced *O. communa* on *A. artemisiifolia* and *A. trifida*. After the hatching of collected egg clusters (eggs from the same cluster were treated as a family), the first instar larvae were assigned to feed on the leaves of *A. artemisiifolia* or *A. trifida*. The number of larvae used in the experiment were 37 (3 families), 137 (8 families), 86 (6 families), 60 (4 families), and 262 (15 families) for US1, US2, US3, US4, and JPN1, respectively. The numbers of first instar larvae assigned to *A. artemisiifolia* and *A. trifida* were 161 and 159, respectively, for the native beetles, and 131 and 131 for the introduced beetles. The larvae were reared in a plastic container (diameter: 20 cm, height: 15 cm). Every three to four days, the leaves were replaced with fresh ones and the number of surviving larvae was recorded. We reared the beetles until pupation and killed all individuals before adult eclosion, owing to quarantine considerations. The rearing experiments were performed on each family and thus, in total, 36 containers were used. We used the survival rate until pupation as an index of larval performance as it correlated with other fitness components, including pupation and adult weight (Fukano and Yahara 2012; Fukano et al. 2016).

Adult Searching Ability for Host Plants

To assess the behavioral cost associated with the adaptation to an alternate host, we compared the host-searching ability of adults between the native and introduced *O. communa*. We reared first instar larvae hatched from 10 egg clusters, which were obtained from wild individuals of each population, in a plastic container with several leaves of *A. artemisiifolia*. We used 3, 5, and 10 containers for rearing the larvae from US2, US3 and JPN1, respectively. After pupation, we collected the pupae and placed

them in small plastic containers until eclosion. The emerged adults were placed in individual plastic containers with *A. artemisiifolia.* We used adult beetles of age greater than five days (since eclosion) for the searching-ability experiment (13, 35, and 60 adults for US2, US3, and JPN1, respectively).

The searching ability of *O. communa* was quantified by conducting a four-choice experiment. The experiment was initiated by placing a single adult in the center of each experimental area (5.5 cm × 8.5 cm × 1.8 cm). We used a relatively small experimental arena for quantifying searching ability because we gave a high priority to the quarantine of the native genotypes. Four leaf squares (1 cm × 2 cm) on a wet filter paper were randomly placed in each of the four corners of the arena: two squares of *A. artemisiifolia* and *A. trifida* as potential host plants, and two squares of *Bidens frondosa*. We used *B. frondosa* as a non-host plant because it belongs to the Asteraceae family and is also native to North America. In total, we arranged four leaf squares, one in each corner. The leaves of *A. artemisiifolia* and *A. trifida* were collected from the experimentally grown plants, and *B. frondosa* leaves were collected from field-grown plants. We recorded the location of each test individual for 90 min, at 10 s intervals, using a digital camera (PENTAX WG-20), with a total of 540 pictures per trial. When a test individual was on a leaf square for at least two consecutive pictures, the individual was considered to be in contact with the leaf square. The searching ability experiments were performed on each individual, and thus, in total, 108 trials (with 432 leaf squares) were performed. The individuals were fasted for 12 h prior to the experiment.

We calculated the following indices from the recorded pictures: type of leaf square with which initial contact was made, time to contact with the leaf square of *A. artemisiifolia*, and time spent on each leaf square. Next, we defined the following behaviors as indicators of host-searching inaccuracy: (1) time spent on *A. trifida* was defined as an indicator of the degree of behavioral adaptation to *A. trifida*, (2) the proportion of individuals that initially came into contact with the leaf square of the non-host plant, *B. frondosa*, and (3) time spent on *B. frondosa* were both defined as indicators of host-searching inaccuracy.

Statistical Analyses

To evaluate the physiological cost of adaptation, we compared the survival rates of native and introduced *O. communa* on *A. artemisiifolia* and *A. trifida*. Generalized linear mixed models (GLMMs) were fitted with the individual survival rate until pupation as the response variable; the feeding plant, beetle origin (native or introduced range), and population (nested in the origins) as the explanatory variables; and beetle family as a random effect. For this analysis, we used the binomial distribution and the logit link.

To evaluate the behavioral cost of adaptation, we compared the degree of behavioral adaptation (the time spent on *A. artemisiifolia* and *A. trifida*) and host-searching inaccuracy (proportion of individuals that came into contact with *B. frondosa* and the time spent on *B. frondosa*) between the native and introduced *O. communa*, using GLMMs with beetle origin (native or introduced range), populations (nested in the origins) and sex as explanatory variables. For the time to contact with *A. artemisiifolia* and the time spent on *A. artemisiifolia* and *A. trifida*, we applied a

quasi-distribution and identity link functions, because the response variable had unequal variance. For the data comprising the proportion of initial contact, we applied multinomial logit models using the multinom function in the nnet package of R (Venables and Ripley 2002). Likelihood ratio tests were used to evaluate the significance of the explanatory variables. For all statistical analyses, the software R 3.0.1 (R Development Core Team 2010) was used.

Results

Larval Performance on Different Hosts

There was no significant difference between the native and the introduced *O. communa* for the survival rate on *A. artemisiifolia* (Deviance = 3.47, d.f. = 1, $P = 0.06$, Fig. 1a). The introduced *O. communa* showed a significantly higher survival rate on *A. trifida* than the native *O. communa* (Deviance = 30.20, d.f. = 1, $P < 0.01$, Fig. 1a). Source populations of native *O. communa* had a significant effect on survival rate on *A. artemisiifolia* (Deviance = 8.94, d.f. = 3, $P = 0.03$) but not on survival rate on *A. trifida* (Deviance = 1.87, d.f. = 3, $P = 0.60$). In the native *O. communa*, the survival rate on *A. artemisiifolia* was significantly higher than that on *A. trifida* (Deviance = 32.34, d.f. = 1, $P < 0.01$, Fig. 1a). On the other hand, in the introduced *O. communa*, there was no significant difference between the survival rates on *A. artemisiifolia* and *A. trifida* (Deviance = 0.15, d.f. = 1, $P < 0.90$, Fig. 1a). The survival rates on
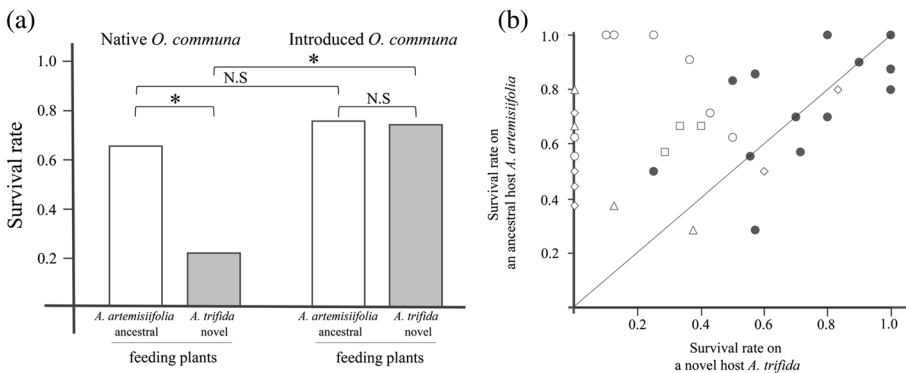

Fig. 1 Comparison of the physiological abilities of native and introduced *Ophraella communa*. **a** Survival rate, from egg hatching to pupation, of native *O. communa* (left bars) and introduced *O. communa* (right bars), on the ancestral host *Ambrosia artemisiifolia* (white bars) and on the alternate host *A. trifida* (grey bars). The asterisks indicate statistically significant differences between the experimental groups. **b** The relationship between sibling survival rates of *O. communa* larvae feeding on *A. artemisiifolia* and those on *A. trifida*. Black circles indicate the siblings of the JPN1 population. White squares, circles, triangles, and diamonds indicate the siblings of the US1, US2, US3, and US4 populations, respectively. The diagonal line indicates the line of equality

A. artemisiifolia and *A. trifida* of each family of native and introduced *O. communa* are shown in Fig. 1b.

Adult Host-Searching Ability

While native *O. communa* spent more time on the leaf square of *A. artemisiifolia* than that of *A. trifida* (Deviance = 15.17, d.f. = 1, $P < 0.01$, Fig. 2a), introduced *O. communa* did not show a significant difference in the time spent on *A. artemisiifolia* and *A. trifida* (Deviance = 0.26, d.f. = 1, $P = 0.61$, Fig. 2a). There were no significant differences in the time spent on the leaf square of *A. artemisiifolia* between native and introduced *O. communa* (Deviance = 1.41, d.f. = 1, $P = 0.23$, Fig. 2a). Introduced *O. communa* spent significantly more time on the leaf square of *A. trifida* than did native *O. communa* (Deviance = 5.90, d.f. = 1, $P = 0.02$, Fig. 2a).

There were no significant differences between native and introduced *O. communa* with respect to the proportion of leaf types with which initial contact was made (Deviance = 0.29, d.f. = 1, $P = 0.86$, Fig. 2b) and the time spent on the leaf squares of *B. frondosa* (Deviance = 0.61, d.f. = 1, $P = 0.433$, Fig. 2c). There were no effects of the source populations of native *O. communa* on the proportion of the leaf types with which initial contact was made (Deviance = 0.79, d.f. = 1, $P = 0.67$), and the time spent on *B. frondosa* (Deviance = 2.97, d.f. = 1, $P = 0.07$), *A. artemisiifolia* (Deviance = 0.52, d.f. = 1, $P = 0.47$), and *A. trifida* (Deviance = 0.82, d.f. = 1, $P = 0.36$).

Discussion

In this study, we investigated the physiological and behavioral costs associated with the contemporary adaptation of an introduced population of *O. communa* to an alternate host, *A. trifida*. The larval feeding experiments showed that the larval survival of the introduced *O. communa* on the alternate host *A. trifida* is higher than that of the native *O. communa*, and is not statistically different from the survival on the ancestral host, *A. artemisiifolia* (Fig. 1). These results suggest that introduced *O. communa* beetles have physiologically adapted to *A. trifida* during the 18 years since the species' introduction into Japan, consistent with the results of a previous study (Fukano et al. 2016). On the other hand, the larval survival of introduced *O. communa* on the ancestral host *A. artemisiifolia* was not different from (or marginally higher than, $P = 0.06$) that of native *O. communa*. These results suggest that the introduced *O. communa* beetles have physiologically adapted to the alternate host plant *A. trifida* without any apparent physiological cost to the ancestral host plant. It should be noticed that maternal environments may influence the different host use patterns of native and introduced *O. communa*. All adult beetles were collected from *A. artemisiifolia* plants in both the native and introduced ranges. However, the beetles collected in the

Fig. 2 Comparisons of the adult searching abilities of native and introduced *Ophraella communa*. **a** Box plot of the time spent on the leaf squares of *Ambrosia artemisiifolia* and *A. trifida* by native and introduced *O. communa*. **b** Proportions of the plant species with which initial contact was made. **c** Box plot of the time spent on the non-host plant *Bidens frondosa*. The asterisks indicate statistically significant differences between experimental groups. The diagonal line indicates the line of equality

(a)

(b)

(c)
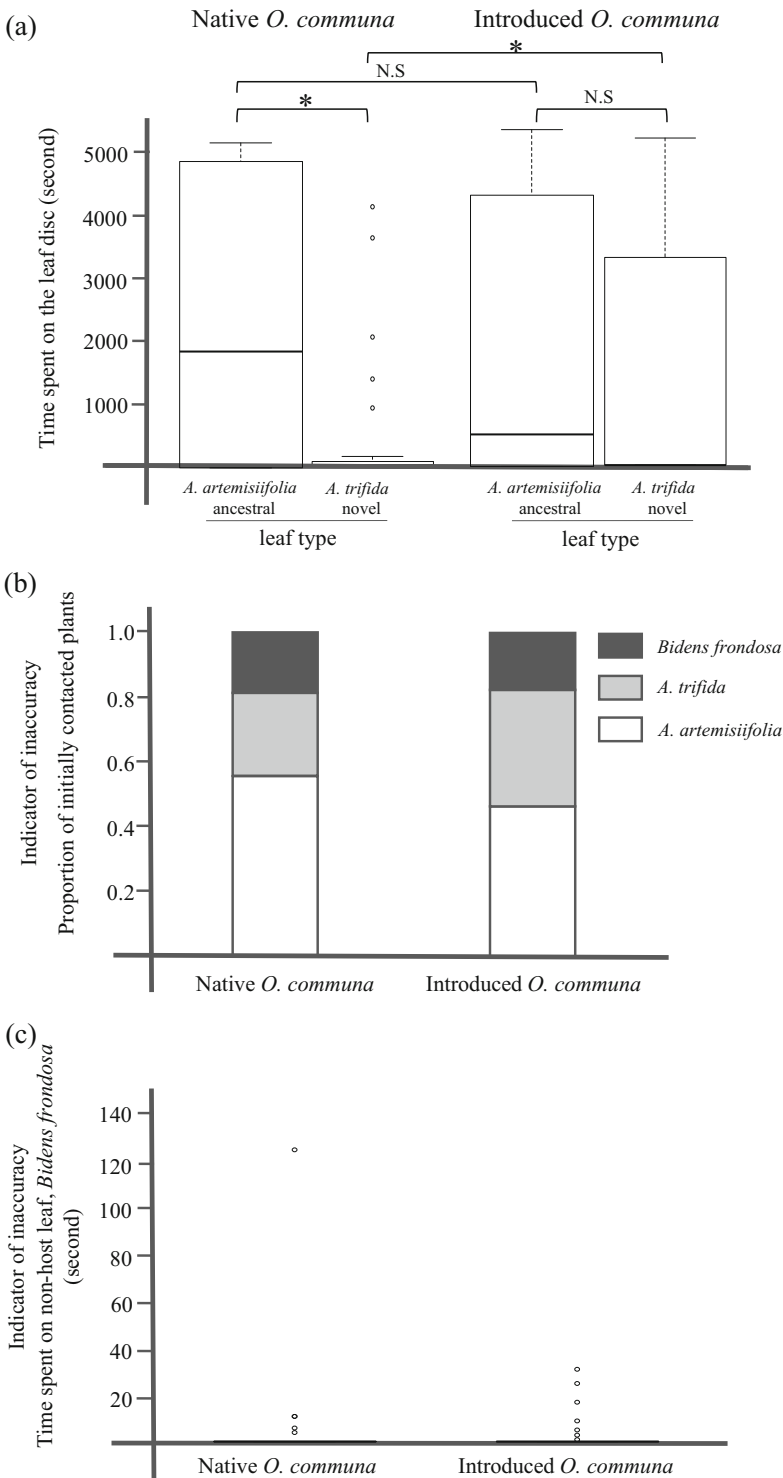
introduced range may have fed on *A. trifida* before being collected from *A. artemisiifolia*. The potential difference in maternal feeding experience might change the performance and preference of the offspring. Further study needs to be conducted on the maternal and developmental experiences influencing the adaptation to alternate host plants. Rearing on a common host would remove the maternal effects and facilitate elucidation of non-genetic effects.

These results are consistent with those of previous studies on host associations in *Ophraella* beetles (Futuyma and McCafferty 1990; Funk et al. 1995b; Gassmann et al. 2006). For example, Gassmann et al. (2006) pointed out that *Ophraella notula*, which has switched to using *Iva* species, performs similar to *O. slobodkini*, which remains specialized on *A. artemisiifolia*. They suggested that alternate host associations arise from behavioral adaptations and that physiological adaptations may be a secondary result.

Two ecological factors may explain why a physiological trade-off was not detected in the introduced *O. communa*. First, alternate host *A. trifida* is a close relative of the ancestral host *A. artemisiifolia* (Hodgins et al. 2015), and these species might share many of their secondary defense compounds. Thus, the physiological changes sufficient to adapt to *A. trifida* might not be enough to reduce the larval performance on *A. artemisiifolia*. Second, introduced *O. communa* utilizes not only *A. trifida* but also *A. artemisiifolia* to some extent. Under this situation, natural selection may favor physiological adaption to *A. trifida* without reducing performance on *A. artemisiifolia.* The lack of genetic trade-offs between larval performance on the ancestral host plant and the alternate host plant is consistent with earlier studies that used quasi-natural selection experiments (Futuyma 2008; Magalhães et al. 2009; Messina et al. 2009a, b; Laukkanen et al. 2013; Messina and Durham 2013). Therefore, physiological trade-offs might not be tightly linked to the adaptation to an alternate host plant, at least in the short term, and thus, might not be a trigger for the ecological specialization of herbivorous insects.

Our previous study suggested that native *O. communa* could not adapt to native *A. trifida* but they could adapt to introduced *A. trifida*, probably because introduced *A. trifida* reduce its resistance after introduction to Japan (Fukano et al. 2016). It seems that there are large variations among the families of native *O. communa* in their ability to use introduced *A. trifida* as a host plant (Fig. 1). These variations in host use pattern in the native *O. communa* populations may play an important role in the process of adaptation to introduced *A. trifida*. When *O. communa* was introduced into Japan and came in contact with introduced *A. trifida*, individuals with a high ability to use the introduced *A. trifida* (pre-adapted individuals) might have changed their host use pattern. Thus, they could have achieved rapid evolutionary adaptation for the behavioral and physiological traits necessary to utilize the introduced *A. trifida*.

Another key explanation for the cost of generalization is the neural constraint (or information-processing) hypothesis, which proposes a behavioral cost of adaptation. Several studies have supported the hypothesis that relative generalists have a lower efficiency and/or accuracy for host-searching ability than relative specialists (Janz 2003; Vargas et al. 2005; Egan and Funk 2006). The host-searching experiment showed that introduced *O. communa* has a greater behavioral preference for *A. trifida* than native *O. communa* (Fig. 2a), indicating behavioral adaptation by introduced *O. communa*. However, we could not detect any behavioral cost associated with this

adaptation to the alternate host plant. Adult *O. communa* beetles in the introduced population showed no increase in inaccuracy (Fig. 2b, c), compared with *O. communa* from native populations. These results imply that introduced *O. communa* does not pay any neural or cognitive cost for the host-associated decisions, even though it acquired an additional plant source for its diet. However, we must also consider the limitations of our experimental design. We used a relatively small experimental arena due to the quarantine space constraint, and there has been no fitness measurements on the beetle. In addition, we used only one species as the non-host plant. In natural conditions, *O. communa* might sometimes disperse over long distances from the natal host plant (Watanabe and Hirai 2004) and might come in contact with several non-host plants. In such situations, introduced *O. communa* might pay a cost of generalization in terms of host-searching efficiency and accuracy, compared with the native, specialist *O. communa*, because they have to process more complex information. To examine the cost associated with the adaptation to *A. trifida* in more detail, we might need to experiment with a larger setting simulating natural conditions, as well as more detailed behavioral experiments, such as experiments with a Y-tube olfactometer.

After the introduction of *O. communa* into Japan, there seems to have been an increase in its population density and abundance, compared with its native range (Fukano and Doi 2013). This increase in abundance of introduced *O. communa* can be attributed to the adaptation to *A. trifida* without the costs of generalization, as well as other ecological and evolutionary factors, including rapid local adaptation to abiotic conditions (Tanaka et al. 2015; Tanaka and Murata 2016), release from native parasites and predators (Moriya et al. 2002), and defense reduction in the introduced populations of *A. artemisiifolia* and *A. trifida* (Fukano and Yahara 2012; Fukano et al. 2016). *Ambrosia trifida* plants have high biomass productivity and dominate several patches of riparian vegetation in Japan. Therefore, adaptation to *A. trifida* could drastically increase the amount of available food resources. *Ambrosia trifida* is an important food resource, especially in the late summer, for introduced *O. communa*, because *O. communa* sometimes completely defoliates *A. artemisiifolia* plants. Physiological adaptation to *A. trifida*, without any apparent cost to the ancestral host plant, might be essential for the seasonal changes in host-use patterns of introduced *O. communa*. Generally, introduced herbivores using alternative host plants in the introduced range should be an ecological risk. However, *O. communa* is an important biocontrol agent of *A. artemisiifolia* in several countries, such as China and Australia (Zhou et al. 2011, 2014). Thus, the adaptation to *A. trifida* without any apparent cost may be beneficial for the management of invasive plants in Japan.

Ophraella communa was also introduced into Europe in 2013 and is now expanding its geographical range (Bosio et al. 2014; Müller-Schärer et al. 2014). Rapid evolutionary change and evolutionary trade-offs might be important for predicting the impact of the invasion of *O. communa* on native ecosystems and agricultural crops in Europe.

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