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Six Species of Omnivorous Insects Feed on the Invasive Plant *Ageratina adenophora* in Kunming, Yunnan Province

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Abstract

In order to understand the feeding pressure of omnivorous insects on *Ageratina adenophora* Spreng., field surveys and laboratory experiments were carried out to confirm the feeding relationship between local herbivorous insects and *A. adenophora*. Six species of natural enemies of *A. adenophora* were confirmed for the first time. They were *Uroleucon gobonis* Matsumura (Hemiptera: Aphididae), *Atractomorpha lata* Motschoulsky (Orthoptera: Pyrgomorphidae), *Ourapteryx yerburii virescens* Matsumura (Lepidoptera: Geometridae), *Sclerogenia jessica* Butler (Lepidoptera: Noctuidae), *Argyrogramma agnata* Staudinger (Lepidoptera: Noctuidae), and *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *S. invicta* fed on the cuticle, cortex and phloem of *A. adenophora*, while the other insects mainly fed on the fresh leaves of *A. adenophora*. These findings will provide an important reference for the scientific management of *A. adenophora* in the future.

Keywords

Exotic Invasive Plant, Crofton Weed (*Ageratina adenophora* = *Eupatorium adenophorum*), Generalist Natural Enemy, Insect Herbivore, Omnivorous Insect

1. Introduction

Alien plant invasion caused by human activities has a serious impact on local biodiversity, ecological processes and ecosystem services [1]-[3]. After invading new habitats, alien plants inhibit the growth of native plants through various mechanisms, such as allelopathy [4], resource competition [5] [6], and soil microbial community mediation [7] [8]. The Enemy Release Hypothesis [9] proposed that escape from natural enemies allows exotic plants to grow vigorously. Blossey and Nötzold (1995) further hypothesized that release from natural enemies led exotic plants to undergo evolutionary changes that enhance competitive ability [10].

However, introducing co-evolved specialist natural enemies from their native ranges to control invasive alien plants has only been proven effective for a limited number of species [11] and remains controversial for many others [12], perhaps because the impacts of herbivorous insects on their hosts are highly variable and context-dependent [2]. For example, the stem-galling fly *Procecidochares utilis* Stone successfully controlled *Ageratina adenophora* Spreng. R. King & H. Robinson (Asteraceae; syn. *Eupatorium adenophorum* Spreng.) in Queensland, Australia and the Coromandel Peninsula, New Zealand [13]. However, its control efficacy is unsatisfactory in China. Yuan *et al.* [2] even found that galling caused by *P. utilis* can stimulate the production of lateral branches and capitula, which promotes the spread of *A. adenophora*.

A. adenophora is a composite weed native to Central America. At present, it has invaded more than 30 countries and regions with subtropical climates [1] [14]. It outcompetes native plants and causes severe ecological and economic damage [15]-[17]. To date, the invasion mechanism of *A. adenophora* has not been fully elucidated. Some studies indicated that *A. adenophora* faces increasing natural enemy pressure in invaded ranges [16] [18]-[21] and its invasiveness tends to decline [21]. Although there are different views on the role of herbivores in regulating *A. adenophora* [2], the present study supports that local herbivores play a positive role in controlling *A. adenophora*.

Biological control provides long-term, effective and ecologically safe management [2] [22] [23]. Since the control efficacy of the specialist natural enemy *P. utilis* on *A. adenophora* in China is limited, more attention should be paid to local generalist natural enemies. Here, we report six newly recorded insect herbivores of *A. adenophora* found in Kunming, Yunnan Province (**Table 1**).

Table 1. A brief summary of damage and ecological relationship of local omnivorous insects to *Ageratina adenophora.*

Names	Observation object	Feeding habit	Feeding site	Area consumed per day per day ($cm^2 \cdot day^{-1}$) (mean ± SE)	Ecological phenomena
Uroleucon gobonis Matsumura	group	Suck	Juice of stems and leaves	2.75 ± 0.48 (n = 4)	Feeding relationship
Atractomorpha lata Motschoulsky	individual	nibble	leaves	4.25 ± 0.47 (n = 4)	Feeding relationship
Ourapteryx yerburii virescens Matsumura	individual	nibble	leaves	5.5 ± 1.32 (n = 4)	Mimicry of color and shape
Sclerogenia jessica Butler	individual	nibble	leaves	2.75 ± 0.47 (n = 4)	Feeding relationship

Continued

Argyrogramma agnata Staudinger	individual	nibble	leaves	3.25 ± 0.85 (n = 4)	Feeding relationship
Solenopsis invicta Buren	group	nibble	Non-lignified tissue of stem	3.5 ± 0.65 (n = 4)	Food web relationship; competitive feeding

2. Materials and Methods

From 2012 to 2015, field investigations on insect natural enemies of *A. adenophora* were conducted in Kunming, Yunnan Province (25˚02'11"N, 102˚42'31"E; ca. 1891 m a.s.l.). Feeding evidence of local natural enemies on *A. adenophora* was recorded through observation, photography and field notes. Systematic survey routes were established within a 10 km radius of densely populated areas (cities, villages, markets and parks). Surveys focused on areas within 10 m of highways. Sampling plots (≥100 m^2) were established at intervals of ≥1 km. In each plot, at least five 2 m × 3 m quadrats were set up for insect collection.

When insects could not be directly observed, a plastic sheet was placed on the ground approximately 50 cm from the base to the canopy of *A. adenophora* plants. The plants were gently tapped from bottom to top with bamboo sticks to dislodge insects onto the sheet. Collected insects were placed in rearing containers and transported to the laboratory for further observation. Field data included habitat type, insect morphology, putative feeding behavior, feeding habit, feeding site and related ecological factors. Live insects were transferred to the laboratory for feeding trials.

Ageratina adenophora plants were cultivated in plastic pots (15 cm diameter × 10 cm depth) in a greenhouse to rear field-collected insects. To ensure accurate assessment, only *A. adenophora* was retained in pots; seedlings of other weeds were removed regularly. Plants were grown in raw red soil, with a 5 cm space from the soil surface to the pot rim for water retention. Insects difficult to rear indoors were enclosed on potted *A. adenophora* using transparent nylon mesh cages. Only one insect species was placed per plant, with no supplementary food.

Insects unsuitable for observation on whole plants were reared in Petri dishes or rearing boxes and provided daily with fresh *A. adenophora* leaves or stems. Humidity was maintained using moist absorbent cotton. Old dry leaves and frass were not removed to minimize disturbance. Feeding behavior was recorded at 08:00, 11:00, 15:00 and 19:00 daily, with each observation period lasting at least 30 minutes. For *U. gobonis* (Hemiptera: Aphidoidea), leaf area reduction was measured by comparison with undamaged leaves on the same plant. For other insects, stem and leaf area loss was quantified by image analysis of photographed tissues.

3. Results and Analysis

This study verified that six insect species can feed on *A. adenophora*. They are described below.

(1) *Uroleucon gobonis* Matsumura (Hemiptera: Aphidoidea) (**Figure 1**)

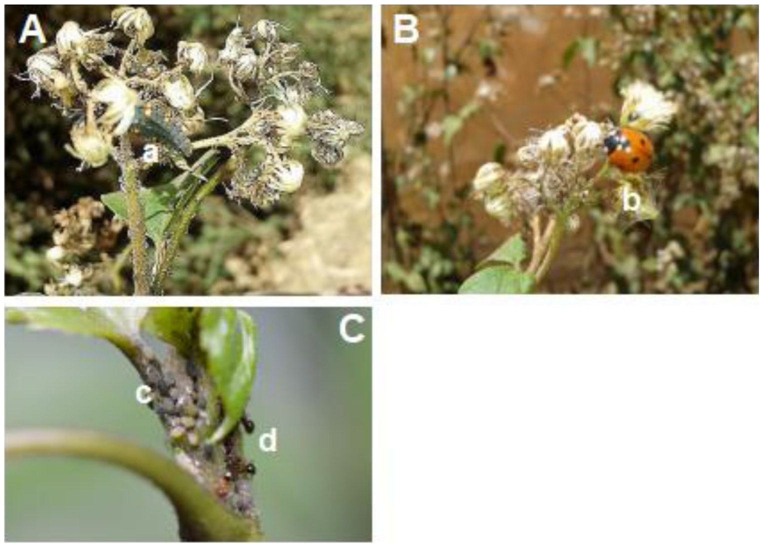

Figure 1. *Uroleucon gobonis* Matsumura (Homoptera: Aphididae) parasitized on the stems and leaves of *Ageratina adenophora* Sprengel, and abstracted larva and adult of *Coccinella septempunctata* L. and *Solenopsis invicta Buren*. Aa: Larva of *C. septempunctata* L.; Bb: Adult of *C. septempunctata* L.; Cc: larva of *U. gobonis* on the stem of *A. adenophora Spreng*; Cd: *Solenopsis invicta Buren* on the stem of *A. adenophora*.

On 5 May 2012, large numbers of *U. gobonis* were found on stems of *A. adenophora* along a sidewalk near Heilongtan Park, northern Kunming. Larval density reached 3 - 7 individuals per cm^2 on stems and 10 - 20 per cm^2 on leaf undersides. Infested leaves were 0.5 - 1 cm smaller and wrinkled compared with healthy leaves. *Solenopsis invicta* and larvae of *Coccinella septempunctata* preyed on *U. gobonis*, indicating a tri-trophic food chain (*A. Adenophora*-*U. gobonis*-*S. invicta*/*C. septempunctata*) in the field. When infested branches were placed on potted *A. adenophora* in the laboratory, *U. gobonis* successfully colonized stems and leaves within two weeks.

(2) *Atractomorpha lata* Motschoulsky (Orthoptera: Pyrgomorphidae) (**Figure 2**)

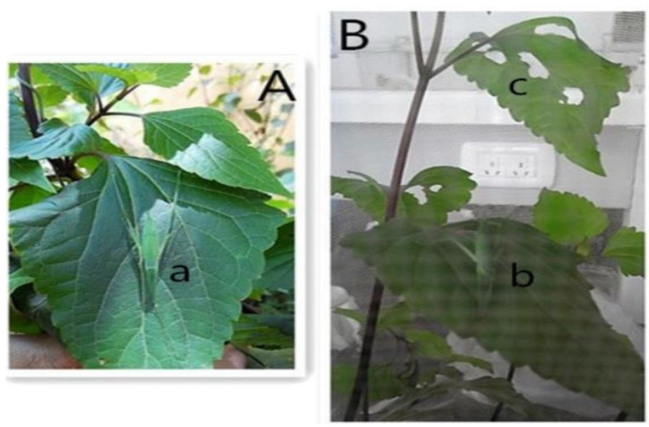

Figure 2. *Atractomorpha lata Motschoulsky* (Orthoptera: *Conocephalidae*) can eat leaves of *Ageratina adenophora* Sprengel when there were not other foods. Aa, an *A. lata* on the leaves of *A. adenophora*; Bb, Bc, holes left by *A. lata* eating.

On 10 August 2012, an individual of *A. lata* was found feeding on leaves of *A. adenophora* in a *Cunninghamia lanceolata* forest near Heilongtan Park. After being caged on potted *A. adenophora* in the laboratory, the insect produced irregular holes (0.5 - 2 cm diameter) in leaves, and the number of holes increased over time (**Figure 2(b)-(c)**). After 30 days, *A. lata* escaped, but the results confirmed that *A. lata* can feed and survive on *A. adenophora* as the sole food source.

(3) *Ourapteryx yerburii virescens* Matsumura (Lepidoptera: Geometridae) (**Figure 3**)

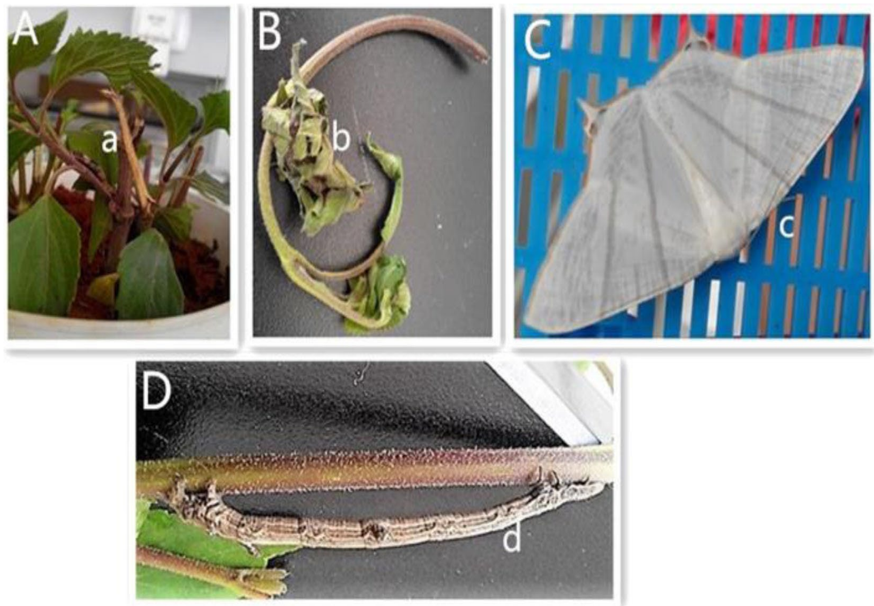

Figure 3. *Ourapteryx yerburii virescens* Matsumura (*Lepidoptera: Geometridae*). It experienced three development stages of larva, pupa, adult when only fed on *Ageratina adenophora* Sprengel *in the laboratory*. Aa: a younger larva of *O. yerburii virescens* on *A. adenophora* ; Bb: a pupa of *O. yerburii virescens* in; Cc: adult of *O. yerburii* virescе; Dd: an elder larva of *O. yerburii* virescens.

On 9 July 2013, two larvae of *O. yerburii virescens* were found feeding on leaves of *A. adenophora* in a monoculture stand at Kunming University. After being caged on potted plants, the older larva pupated two days later. Pupae were transferred to rearing boxes for adult emergence and oviposition. On 29 July, the pupa eclosed into a female adult that lived for 3 days and laid 11 eggs on the box wall. The younger larva pupated on 29 July and emerged one week later, but did not oviposit and died after 3 days.

O. yerburii virescens exhibits morphological mimicry of *A. adenophora*. The body shape and color of late instar larvae **resembled dry stems** of *A. adenophora* (**Figure 3(Dd)**), whereas young larvae resembled purple tender stems (**Figure 3(Aa)**). Larvae are highly sedentary, maintaining a single posture for at least 3 hours, which is an adaptive strategy to avoid natural enemies.

(4) *Sclerogenia jessica* Butler (Lepidoptera: Noctuidae) (**Figure 4**)

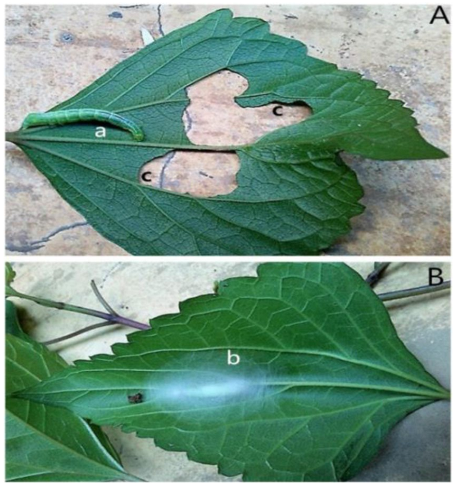

Figure 4. *Sclerogenia jessica* Butl (*Lepidoptera: Noctuidae*) experienced three development stages of larva, pupa, adult on condition that only fed on leaves of *Ageratina adenophora* Sprengel in the laboratory. Aa: Larva of *S. Jessica*; Bb: Pupa of *S. Jessica*; Ac: holes left by *A. lata* eating.

On 6 March 2014, six larvae and four pupae of *S. jessica* were found on leaves of *A. adenophora* in a shaded, minimally disturbed site behind Kunming University Library. When confined on *A. adenophora*, *S. jessica* successfully completed larval, pupal and adult development on a pure diet of this weed. The pupal and adult durations were 7 ± 2 d (n = 6) and 3 ± 1 d (n = 4), respectively. In subsequent surveys in Qujing, Kunming and Honghe Prefecture, Yunnan Province, larvae of *S. jessica* were also found feeding on leaves of *A. adenophora*. Host plants were consistently located in shaded habitats.

(5) *Argyrogramma agnata* Staudinger (Lepidoptera: Noctuidae) (**Figure 5**)

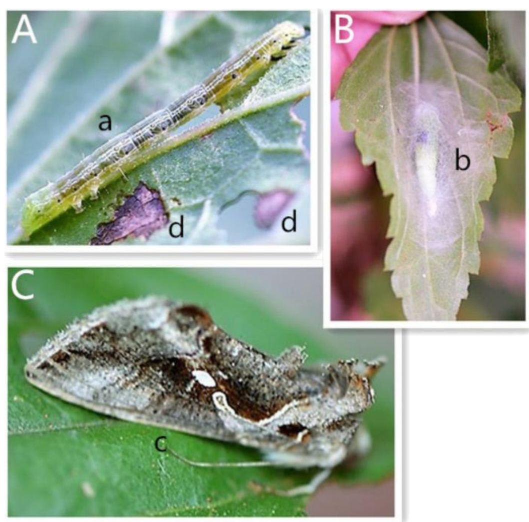

Figure 5. *Argyrogramma agnata* Staudinger (*Lepidoptera*: *Noctuidae*) experienced three development stages of larva, pupa, adult on condition that only fed on *Ageratina adenophora* Sprengel in the greenhouse. Aa: larva of *A. agnata*; Bb: pupa of *A. agnata*; Cc: adult of *A. agnate*; d: Necrotic spots in the leaf eaten by *A. agnata.*

From August 2012 to March 2015, 50 individuals of *A. agnata* were released in a Kunming University greenhouse adjacent to a flue-cured tobacco experimental plot. On 10 September 2014, four larvae of *A. agnata* were found feeding on tobacco leaves. On 26 October 2014, five larvae were found on nearby *A. adenophora* leaves. Larvae were caged on *A. adenophora* in situ. All larvae completed larval-pupal-adult development between 21 October and 14 November 2014. Pupal durations were 10, 13, 12 and 14 days; adult lifespans were 4, 5, 3 and 3 days, respectively. Similar observations were recorded in Qujing, Honghe and Wuding Prefecture, Yunnan Province.

(6) *Solenopsis invicta* Buren (Hymenoptera: Formicidae) (**Figure 6**)

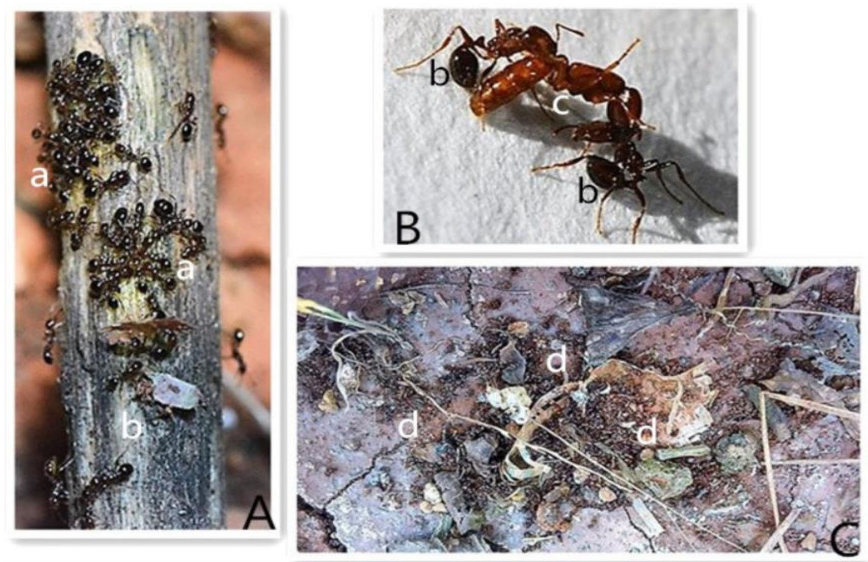

Figure 6. *Solenopsis invicta* (*Buren*) (Hymenoptera: Formicidae) fed on roots, stems, leaves of living *Ageratina adenophora* Sprengel and fought against *Dorylus orientalis.* Aa, *S. invicta* is attacking epidermis and cortex tissue of stems of *A. adenophora*; B, *S. invicta* (b) and *D. orientalis* (c) is fighting; Cd, corpses of *D. orientalis* moved by *S. invicta* to the ground around *A. adenophora*; Ab, imprints left by *S. invicta* eating on the stems of *A. adenophora*.

From August 2012 to March 2015, *A. adenophora* plants were cultivated in a Kunming University greenhouse. On 3 March 2015, numerous *Dorylus orientalis* Westwood were observed feeding on succulent stem tissues and epidermis of *A. adenophora*. In May 2015, dead or dying *D. orientalis* individuals were found around two *A. adenophora* plants, while large numbers of *S. invicta* were feeding on stem epidermis and cortex. The ants fed on 1 - 2 cm^2 patches before moving to new sites, with each feeding zone covering less than half the stem circumference. Feeding progressed upward from the stem base, leaving mottled lesions (3 - 5 cm long × ca. 1 cm wide) on stems.

Solenopsis invicta periodically removed dead *D. orientalis* from soil cavities at the base of *A. adenophora* and deposited them on the surrounding ground. Petri dish trials revealed intense interspecific aggression between similarly sized workers of *S. invicta* and *D. orientalis*, with *D. orientalis* consistently defeated. *S. invicta* attacked all body parts of *D. orientalis*, **frequently severing the petiole** and causing rapid mortality. On host plants favored by *D. orientalis* (e.g., *Conyza canadensis*, *Galinsoga parviflora*, *Bidens pilosa*), *D. orientalis* was rarely present if *S. invicta* occurred nearby. These results indicate that both ant species are natural enemies of *A. adenophora* and compete intensely for this host plant.

4. Discussion and Conclusion

The observation that local omnivorous insects feed on *A. adenophora* suggests that adaptive evolution has occurred between this invasive plant and local insect natural enemies. Yunnan Province harbors exceptionally high biodiversity due to its unique geological history, geographic location, topography and climate [24]. High insect diversity facilitates the formation of feeding associations between native insects and *A. adenophora*. Together with previously reported natural enemies (*Procecidochares utilis* [25]-[27], *Dorylus orientalis* [21], Orthezia quadrua [20]), the six newly recorded herbivores indicate that *A. adenophora* in Yunnan experiences strong natural enemy pressure.

Native herbivorous insects adapt to invasive plants via behavioral, physiological and biochemical evolution, thereby increasing feeding pressure on these plants [28]. For example, *Uroleucon ambrosiae* feeds exclusively on *Ambrosia trifida* in eastern North America (its native range) but evolved oligophagy in arid western North America, where it feeds on several composite weeds [29]. The stem borer *Apagomerella versicolor* (Coleoptera: Cerambycidae) feeds only on *Pluchea sagittalis* in northern Argentina but utilizes seven Asteraceae species in central and southern Argentina [30]. Similarly, co-evolution between *A. adenophora* and its native enemies will gradually increase enemy pressure.

Wang *et al.* [31] reported higher herbivore species richness and abundance in severely invaded *A. adenophora* habitats than in moderately or lightly invaded sites. Jiang *et al.* [32] found greater natural enemy diversity in heavily invaded stands than in moderately invaded or uninvaded communities. These patterns suggest that natural enemy pressure increases with invasion time, consistent with the Behavior Constraint Hypothesis and the New Weapon Hypothesis [28]. Once native omnivorous insects adapt to *A. adenophora* behaviorally, physiologically and biochemically, they will utilize this invader as a suitable host plant. The morphological mimicry of *O. yerburii virescens*, competitive feeding between *D. orientalis* and *S. invicta*, and the tri-trophic food chain of *A. Adenophora*-*U. gobonis*-*C. septempunctata* collectively demonstrate that stable feeding associations have formed between some native omnivores and *A. adenophora*.

Due to economic and ecological concerns, physical, chemical and manual control methods are not widely applied for *A. adenophora* management. In contrast, biological control holds great potential and has been extensively explored [33] [34]. Successful control of invasive plants by specialist natural enemies remains rare, likely because the efficacy of single species is limited. Furthermore, climate warming may reduce the effectiveness of specialist enemies by enhancing plant resistance [35]. Invasive plants typically possess physical and chemical defenses against native generalist enemies [36] [37], which can only be overcome by adaptive evolution. Since *A. adenophora* invaded China in the 1940s, sufficient time has elapsed for native natural enemies to adapt to this invader, leading to an increasing number of recorded insect herbivores [20] [21].

Although this study could not fully quantify the control potential of the six polyphagous insects due to limitations in observation duration and scope, our results show that their feeding damage lacks habitat specificity and multiple species often co-occur in the same habitats. We therefore infer that the combined biological control impact of these insect species on *A. adenophora* is considerable and should not be underestimated.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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