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GENERALIZED POLLINATION SYSTEM PROVIDES PROTECTION FOR THE INVASION OF *SOLIDAGO CANADENSIS*

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Abstract

Sexual reproduction underlies plant invasion and spread, but the mechanism underlying reproductive success remains unclear. We tested the hypothesis that a plant's generalized pollination system promoted its invasion by using field experiments to investigate aspects of the pollination biology of *Solidago canadensis*, such as species, visit frequency and visit behaviour, in different populations in Xuzhou, Hefei, Nanchang and Ji'an. The field experiments supported the hypothesis that the plant's generalized pollination system is beneficial to its invasion. *S. canadensis* has a complex floral syndrome that facilitates the acceptance of different types of pollinators, strongly promoting its reproductive success. We found large numbers of visiting insects on *S. canadensis*, and the main pollinator species were relatively stable within habitats, although the main pollinator species differed among the geographical populations. In terms of time, insect visits were observed from morning to afternoon, mainly from 9:00 to 11:00. The pollination biology results showed that *S. canadensis* has a generalized pollination system that could ensure successful sexual reproduction by attracting insects in different habitats and provide a basis for reproduction after invasion.

Key words: *Solidago canadensis*; Pollination behaviour; Visiting insects; Invasion; Generalized pollination.

Introduction

Invasion biology has been the focus of ecological research since it was proposed in 1958 (Pino *et al*., 2005), and invasion is becoming a worldwide problem. Studies have shown that successful invasive plant species compete for local resources (e.g., ecological niches (Vanbergen *et al*., 2018), nutrients (Skurski *et al*., 2014), and pollinators (Anna & Richardson, 2006; Bjerknes *et al*., 2007)) and are more influential in invaded habitats than in their natural systems (Callaway & Aschehoug, 2000; Goodell & Parker, 2017). In fact, the ability of invasive plants to settle in new habitats depends on their fecundity, and the number and behaviour of pollinators can greatly affect the reproductive success of invasive plants (Baker, 1955; Baker, 1967). At the same time, large studies have indicated that invasive plants are dependent on pollinators for sexual reproduction (Gross *et al*., 2010; Hong *et al*., 2010; Yan *et al*., 2016), and a lack of pollinator services may limit the reproductive success and spread of invasive plants (Parker, 1997; Bufford & Daehler, 2014).

Pollination is an important part of sexual reproduction, providing an important opportunity for the cross-pollination and invasion of plants (Dong M *et al*., 2006). Approximately 87.5% of flowering plants rely on animals to carry pollen in order to reproduce sexually (Ollerton *et al*., 2011). The rich species diversity of plants and pollinators and their interrelationships lead to complex interactions in the ecosystem (Gong & Huang, 2007); for instance, insects act as a vehicle for cross-pollination and promote successful sexual reproduction, and the nectar, pollen and fruit of plants serve as food sources for insects to ensure their survival and reproduction (Chen *et al*., 2017). The mutually beneficial relationship between plants and insects is conducive to species diversity maintenance and ecosystem stability. In general, invasive plants may provide abundant nectar and pollen to attract pollinators (Chittka & Schürkens, 2001). Insufficient pollinators limit sexual reproduction (Ashman *et al*., 2004; Tiffany M *et al*., 2005) and population structure dynamics (Bascompte *et al*., 2006; Lundgren *et al*., 2015). However, invasive plants may disrupt the interaction between native plants and their pollinators by competing with the native plants for pollinators (Moragues & Traveset, 2005; Bjerknes *et al*., 2007; Mitchell *et al*., 2009; Yang *et al*., 2011; Shi-Guo *et al*., 2013), in turn affecting the reproduction of native species and thus the species diversity of the native habitat (Shi-Guo *et al*., 2013).

Pollination systems of plants are divided into specialized and generalized systems. Plants have gradually evolved generalized pollination systems in habitats rich in pollination resources (Qitao, 2019). According to the hypothesis of the most effective floral pollinator principle, plants will specialize on insects with the highest pollination efficiency or abundance when pollinators are abundant (Stebbins, 1974). However, flowering plants tend to generalized in pollination when pollination resources are scarce in the environment (Jocque *et al*., 2010), in which case the plants can reproduce only by attracting existing pollinating insects. Plants with generalized pollination systems may be more invasive than plants with specialized pollination systems (Rodger *et al*., 2010), as the former can "find" pollinators after invading new places to ensure sexual reproduction.

Solidago canadensis is a perennial herb of Asteraceae that is native to North America and has become a weed worldwide, as it is widely distributed in Europe, Asia and Oceania (Weber, 2010). Since its introduction as an ornamental plant in 1935, *S. canadensis* has gradually escaped and become one of the most serious invasive plants in China, and it is now widely distributed in eastern China (Jianzhong *et al*., 2007). After its invasion, it quickly became the dominant species, inhibiting the growth of local species (Tang *et al*., 2012) and seriously affecting the local ecological environment. *S. canadensis* is mainly pollinated by insects (Hao *et al*., 2009), and a single plant can produce 6000~20000 seeds (Werner P A, 1980; Hua *et al*., 2007). It has a strong reproductive capacity and a wide diffusion range and can be found on both sides of rivers, in wastelands, and along roads and railways. With the passage of time since invasion and evolution, *S. canadensis* obtains genetic variations conducive to population establishment and propagation (Zhao *et al*., 2015), and artificial control of its invasion and spread consequently becomes more difficult. In recent years, a large number of studies on *S. canadensis* have been carried out. Dong *et al*., found that the sexual reproduction of *S. canadensis* is the main factor underlying its successful invasion (Dong *et al*., 2006), and pollination by insects was the key factor for successful sexual reproduction. Therefore, by analysing the pollination biological characteristics of *S. canadensis*, the reason for its strong invasion ability can be revealed. In this study, we focused on pollination biology to explain why *S. canadensis* has such an invasion ability and answered two questions: 1) What are the characteristics of the pollination of *S. canadensis* in different habitats? 2) What are the effects of generalized pollination on its invasiveness?

Material and Method

Location and study sites: This study was conducted from October 20 to November 24, 2018, at four sites along a latitudinal gradient in China: Xuzhou, Hefei, Nanchang, and Ji'an. At each site, a sampling quadrat with a total area of 200 m^2 was established (Table 1). The sample plot was guaranteed to be free from human interference during the investigation. Xuzhou has a temperate monsoon climate, with a mean annual rainfall of 88.66 mm and a mean annual temperature of 11.94 to 20.65°C from 2017 to 2018. Hefei, Nanchang, and Ji'an have a subtropical monsoon climate. The mean annual rainfall in these three areas was 155.73 mm, 116.64 mm and 135.48 mm and the mean annual temperature was 13.10 to 21.75°C, 16.22 to 23.15°C and 16.48 to 24.17°C from 2017 to 2018, respectively. Weather data were obtained from the China Meteorological Data Service Centre (www.data.cma.cn).

Pollinator surveys: In this experiment, the entire inflorescence of the composite was treated as a single flower. The experiment was carried out in the full-bloom stage (when 80% of the flowers were in bloom) of *S. canadensis*. Pollinators were investigated on an hourly basis (from 8:00 to 16:00) and on two consecutive days of observation. The pollination frequency of pollinators was observed directly, and the insect starts from touching the flower and ends after flying away. This process is recorded as a visit to the flower; that is, the number of all insect species visiting each 30 flower per unit time (20 min) at each site was observed and recorded from 8:00 to 16:00 on sunny days, and then the frequency was calculated (Yan *et al*., 2016). The pollinators were caught in insect nets and placed in 75% alcohol for laboratory identification (Zeng *et al*., 2021), and the number of pollinators was recorded.

Pollinator behaviour: We sought to observe and record the single-flower residence time and the visiting behaviour of pollinators. When an insect touched the flower, the residence period began, and when it flew away, the residence time ended. This period of time was considered the single-flower residence time. Pollinator behaviour was also recorded.

Results

Pollinators: Field investigation of the four sites revealed concentrated areas of *S. canadensis* invasion in China. Here, 94 different species of visiting insects of *S. canadensis* were recorded along the four transects, including insects from 7 orders and 34 families (Fig. 1 and Table S1). We analysed flower-visiting insects in China and found that the dominant pollinator group was Diptera, accounting for 45.89% of the total pollinators, mainly including *Stomorhina obsoleta*, *Eristalinus aeneus* and *Chrysomya megacephala*. Hymenoptera, mainly Apidae, accounted for 22.6%. Lepidoptera, mainly butterflies, accounted for 20.55% of all pollinating insects. *Celastrina argiola* (Tongeia) and *Polygonia c-aureum* (Nymphalidae) were the most commonly observed insects, but the number of individual insects was relatively small. True bugs (Hemiptera) and Coleoptera (primarily ladybugs) accounted for only 6.16% and 4.79% of the total pollinators, respectively (Table 2). As shown in Table S1, *S. obsoleta*, *E. aeneus*, *C. megacephala*, *Eristalis cerealis, Apis cerana* and *P. c*-aureus were the main pollinators of *S. canadensis*.

Comparison of flower-visiting insects among geographic populations: The insects visiting *S. canadensis* differed among areas (Table S1). Along the latitudinal gradient, we investigated the pollinators of *S. canadensis* in four cities. The main pollinators of *S. canadensis* in different areas were Diptera, Hymenoptera and Lepidoptera (Fig. 2), but the main pollinators varied among the populations. As shown in (Table 3), *S. obsoleta* was the most abundant in all populations except that in Hefei. *C. megacephala* was observed at every location, with Nanchang having the largest share. However, *E. aeneus* mainly appeared in Xuzhou, with a few individuals in southern Xuzhou and none in Nanchang and Ji'an. The observed species of bees differed among locations; Xuzhou, Nanchang, and Ji'an had only *A. cerana*, and Hefei was dominated by *Apis mellifera*. Among butterflies, *P. c-aureum* was found in all geographic populations except that in Ji'an. Although the number of individuals differed among areas, the proportions of pollinators were not different. This shows that *S. canadensis* can adapt to different regions, and even if there are differences between pollinators, it can attract enough pollinators to be pollinated. In summary, the main pollinators of *S. canadensis* differ among geographic populations, with flies as the main pollinators at high and low latitudes and bees as the main pollinators at middle latitudes.

Table 1. Basic characteristics of the experimental site.

Site	Longitude and Latitude	Habitat	Other flower plant
Xuzhou	34°14'24" N, 117 °26'20" E	Lakeside	*Lagedium sibiricum*, *Inula japonica*, *Kalimeris indica*, *Conyza canadensis*, *Bidens frondosa* and *Phragmites communis*
Hefei	31° 47' 42" N, 117°17' 7" E	Abandoned land	*Bidens pilosa*, *Humulus scandens*, *Lagedium sibiricum*, *Mosla scabra* and *Bidens frondosa*
Nanchang	28° 45' 34" N, 115° 49' 32" E	Abandoned land	*Lagedium sibiricum*, *Dendranthema indicum*, *Bidensalba*, *Aster tataricus*, *Solanum nigrum* and *Ageratum conyzoides*
Ji'an	27° 6' 61" N, 115° 1'15" E	Abandoned land	*Polygonum hydropiper*, *Hibiscus mutabilis* and *Camellia* sp.

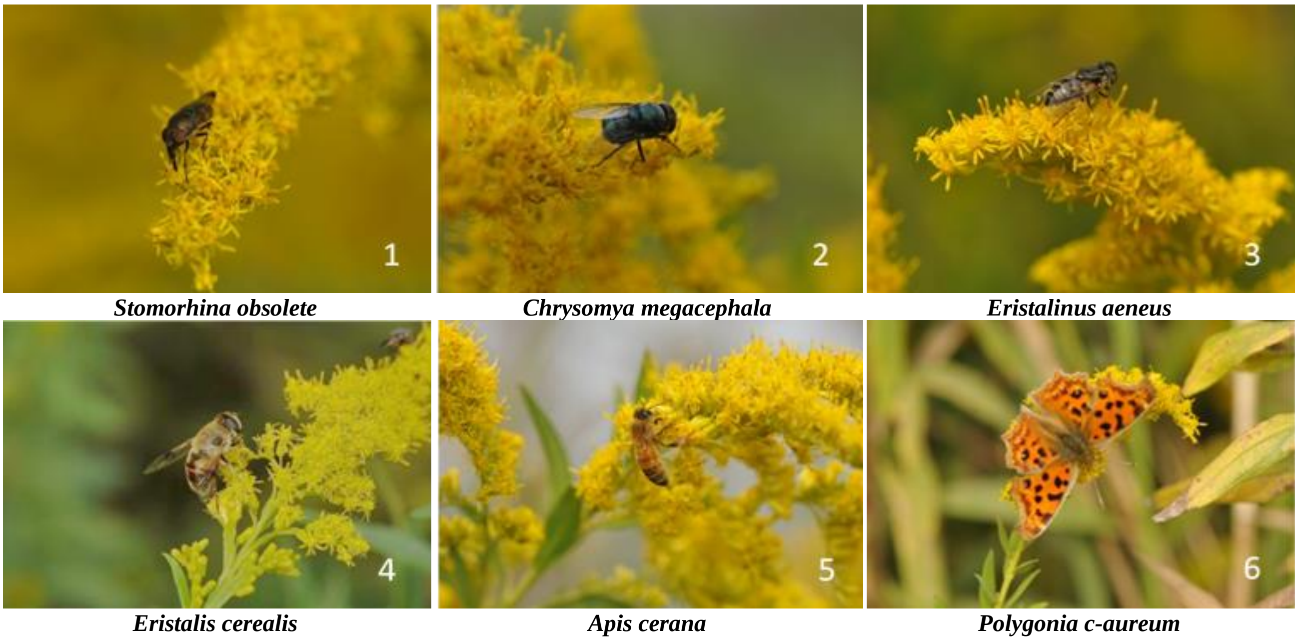

Fig. 1. Main flower-visiting insects of *S. canadensis*.

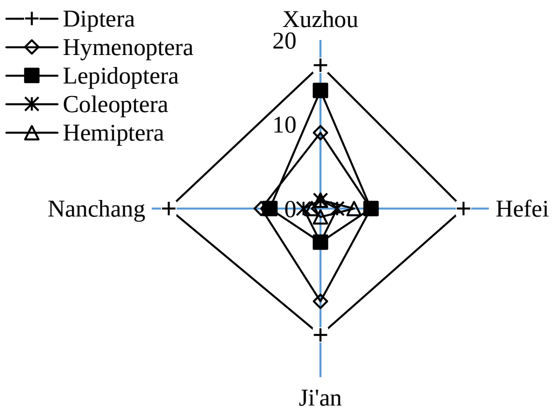

Fig. 2. Composition of flower-visiting insects of *S. canadensis* in the different population. (The value of the axis represents the number of insect species).

Table 2. Number of species in each order and their percentages of total number of *S. canadensis* in China.

Order	Species	Percent
Diptera	16.75 ± 1.09^{aA}	45.89%
Hymenoptera	8.25 ± 1.92^{bB}	22.6%
Lepidoptera	7.5 ± 3.84^{bBC}	20.55%
Hemiptera	2.25 ± 1.09^{cC}	6.16%
Coleoptera	1.75 ± 1.3^{cC}	4.79%

(abc represents $p \leq 0.05$, ABC represents $p \leq 0.01$; Value mean ± SD)

The duration of each visit and visit frequency: During the peak flower stage of *S. canadensis*, the residence time of visiting insects on each flower was determined (Table 4). The longest residence time of 18~300 s was observed for *S. obsoleta* of Calliphoridae (Diptera), and the average residence time was 98.11±97.25 s. The residence time of *C. megacephala* was 6~120 s, with an average of 42±32.78 s. The residence time of *E. aeneus* of Syrphidae was 3~103 s, with an average of 30±24.96 s. The visit time of *A. cerana* of order Hymenoptera was between 3 and 16 s, with an average of 7.25±3.24 s. The single-flower residence time of *S. obsoleta* on *S. canadensis* was significantly longer than that of *C. megacephala* and *E. aeneus* and much longer than that of *A. cerana*, while there were no significant differences among *C. megacephala*, *E. aeneus* and *A. cerana*.

For insect-pollinated plants, the visit frequency of insects directly affects pollination efficiency, while the activities of pollinators are affected by environmental factors, such as temperature, humidity, and wind speed. The frequency of flower-visiting insects on *S. canadensis* was continuously observed and recorded from 8:00 to 16:00 (Fig. 3). Only a few insects were active between 8:00 and 9:00 due to the low temperature and high humidity. After 9:00, the temperature rose and the humidity decreased, and most insects began to visit the flowers. The visit frequency peaked between 10:00 and 11:00. At 12:00, the temperature was higher, which affected the visiting behaviour of flies and bees, and the visit frequency decreased. From 9:00 to 13:00, the pollination frequency of *E. aeneus* was the highest, followed by that of *O. obsoleta*, and *C. megacephala* and *A. cerana* showed the same pollination frequencies. Although there were twice as many *S. obsoleta* as *E. aeneus*, the visit frequency of *S. obsoleta* was lower due to its longer residence time on a single inflorescence. From 8:00 to 16:00, *S. canadensis* showed stable insect visitation, which facilitated its reproduction.

Table 3. The number of main flower-visiting insects of *S. canadensis* in each experimental sample.

Main flower-visiting insects	Xuzhou	Hefei	Nanchang	Ji'an
Stomorhina obsoleta	55 ± 3.5^{aA}	8.5 ± 4.5^{ab}	65.5 ± 9.5^{aA}	63.5 ± 1.5^{aA}
Chrysomya megacephala	9 ± 0^{cC}	10.5 ± 6.5^{ab}	22.5 ± 11.5^{bB}	11 ± 4^{bB}
Eristalinus aeneus	26.5 ± 1.5^{bB}	1.5 ± 0.5^{b}	0	1 ± 1^{bB}
Apis cerana	5.5 ± 1.5^{cC}	1 ± 1^{b}	$3 \pm 0b^{B}$	2.5 ± 1.5^{bB}
Apis mellifera	0	19 ± 7^{a}	0	0
Polygonia c-aureum	4.5 ± 0.5^{cC}	6.5 ± 3^{b}	1.5 ± 0.5^{bB}	0

(abc represents $p \leq 0.05$, ABC represents $p \leq 0.01$; Value: mean ± SD)

Table 4. The visiting times of main insects of *Solidago canadensis* single flower.

Main insects	Visiting times of single flower/s
Stomorhina obsoleta	98.11 ± 97.25^{aA}
Chrysomya megacephala	$42 \pm 32.78b^{AB}$
Eristalinus aeneus	$30 \pm 24.96b^{AB}$
Apis cerana	7.25 ± 3.24^{bB}

(ab represents $p \leq 0.05$, AB represents $p \leq 0.01$; Value: mean ± SD)

The visit frequencies of insects on *S. canadensis* differed among the geographic populations (Figs. 4 & 5) shows that the frequency of flower-visiting insects was significantly higher in Xuzhou than in the other three regions. The visit frequency of *S. bsolete* in Xuzhou was significantly higher than that in Nanchang, and its visit frequency in Ji'an was significantly higher than that in Hefei and Nanchang. The number of flower visits of *C. megacephala* did not differ significantly from that of *A. cerana* or *A. mellifera* among the four samples.

Flower-visiting insects' behaviour: On *S. canadensis* flowers, flies mainly use their mouthparts to lick nectar. As they move up the inflorescence, their sternum and abdomen touch the pollen of a single flower in the inflorescence, thus helping the plant complete pollination. When visiting flowers, *S. obsoleta* usually holds the pistil with its forefoot and licks the stigma or the nectar of the flower with its mouthparts. During this period, it stays for a long time, which helps extend the pollination time. During a visit, *C. megacephala* usually visits a small flower in the middle part of the inflorescence and then visits the whole inflorescence by moving counter clockwise along the edge. When visiting *S. canadensis*, *E. aeneus* supports its body with its middle feet, using its hind feet to lick the nectar. A large amount of pollen adheres to hairs on the sternum, completing the pollination process as the insect moves on the inflorescence.

The hymenopteran flower-visiting insects include more efficient pollinators, such as bees. *A. cerana* is usually selective when visiting *S. canadensis*, visiting the whole inflorescence only once and rarely visiting the same inflorescence repeatedly. The mouthpiece of *A. cerana* is used to suck nectar from the flower. After a short stay, the bee flies to the next flower. During this time, the head, sternum and abdomen of the bee is in constant contact with the pollen on the inflorescence. In addition, its pollen bask*et al*so collects pollen, which plays a role in pollination.

The pollination efficiency of butterflies is lower than that of flies and bees. Most butterflies did not appear until approximately 10:00. During flower visits, they usually visit the top of the inflorescence and suck nectar with their mouthparts from bottom to top, as observed in *Graphium sarpedon*. However, hemipterans, coleopterans and other insects are rare; they generally visit flowers occasionally and may have low pollination efficiency.

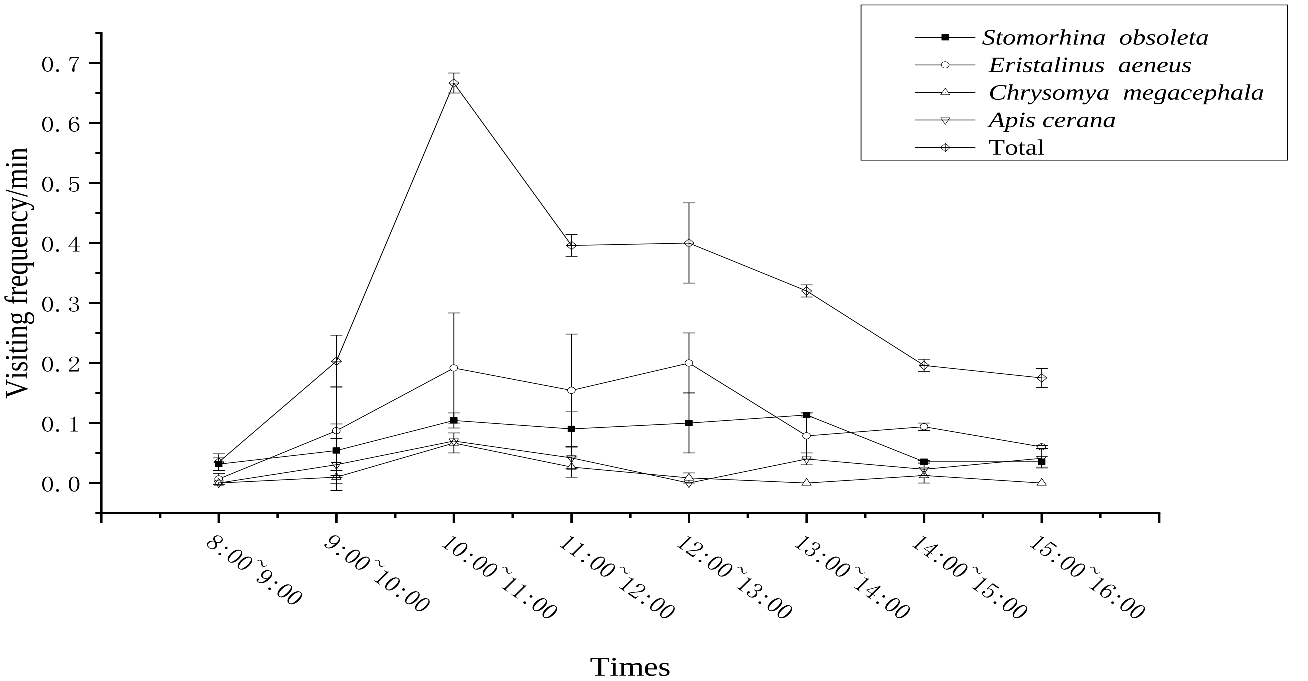

Fig. 3. The frequency of main flower-visiting insects of *S. canadensis* in Xuzhou.

Table S1. The flower-visiting insects of *S. canadensis* in China.

Order	Family	Species	Xuzhou	Hefei	Nanchang	Ji'an
Diptera	Calliphoridae	*Stomorhina obsoleta*	59	13	56	65
		Stomorhina sp.1	9			11
		Stomorhina sp.2				3
		Lucilia sericata			3	2
		Lucilia sp.1			3	
		Chrysomya megacephala	9	17	34	15
	Sarcophagidae	*Sarcophaga* sp.	4	1	3	3
		Boettcherisca peregrina		2		
		Sarcophaga sp.1		3		1
		Sarcophaga sp.2		1	4	
		Sarcophaga sp.3	2		4	6
		Sarcophaga sp.4				4
	Tachinidae	*Peletina* sp.		1		
		Carcelia sp.1		1	1	
		Carcelia sp.2		2		
	Syrphidae	*Syritta orientalis*			1	
		Eristalinus aeneus	25	2	1	
		Helophilus affinis	2	3		
		Melanostoma		1	2	1
		Phytomia zonata	3	4	3	
		Eristalis cerealis	7	1		
		Eristalinus arvorum	2		2	2
		Eristalinus sp.1	1		1	2
		Sphaerophoria sp.		1		
		Ischiodon scutellaris	1		1	
		Eristalinus sp. 2			1	
		Zyistrophe balteata	2	2	8	10
		Syrphidae sp. 1		1		
		Syrphidae sp. 2				1
	Tabanidae	*Tabanus* sp.	1			
	Tipulidae	*Limonia*	1			
		Tipulidae sp.1	1			
	Keroplatidae	*Macrocera* sp.				1
	Oestridae	*Gymnosoma* sp.	2		1	
Hymenoptera	Apidae	*Nomia chalybeata*			1	
		Apis mellifera		26	3	1
		Apis cerana	7			
	Tenthredinidae	*Arge xanthogaster*				1
	Megachilidae	*Megachilidae remota*		1		
		Megachile dinura		1		
	Polistinae	*Polistes gallicus*	1			
		Potistes hebraeus				1
	Halictidae	*Halictus simplex*				1
		Halictidae sp. 1				
		Sphecodes sp.	2			1
	Scoliidae	*Campsomeris grossa*	2			
		Scolia sp. 1	3		4	7
	Chalcidoidea	*Dirhinus bakeri*			1	
		Chalcidoidea sp.1		1		4
		Chalcidoidea sp. 2	2			1
		Chalcidoidea sp. 3				2
		Chalcidoidea sp. 4				5
		Chalcidoidea sp. 5	1			
		Chalcidoidea sp. 6			8	
	Vespoidea	*Vespa velutina nigrithorax*	1	2	5	
		Ropalidia sp. 2			1	
		Vespula flaviceps	1			
		Rhynchium sp.				1
	Formicidae	*Camponotus selene*		2		

Table S1. (Cont'd.).

Order	Family	Species	Xuzhou	Hefei	Nanchang	Ji'an
		Plebeiinae sp.	2		3	
		Lycaena phlaeas				
		Lampides boeticus		4	6	
		Tongeia fischeri	1			
	Tongeia	*Tongeia* sp. 1	1			
		Tongeia sp. 2	1			
		Tongeia sp. 3	1			
		Tongeia sp. 4	1			
		Celastrina argiola	5		2	
Lepidoptera		*Aricia agestis*	2			
	Papilionidae	*Graphium sarpedon*		1		
	Pieridae	*Pieris canidia*	2	4	6	1
		Eurema blanda		2	2	2
	Hesperiidae	*Parnara guttata*	1	1		
	Nymphalidae	*Polygonia c-aureum*	4	10	1	
		Vanessa indica	1			
	Sphingidae	*Haemorrhagia radians*	1			
	Noctuidae	*Noctuidae* sp. 1				1
	Crambidae	*Palpita inusitata*	1			
		Hymenia recurvalis				1
	Coccinellidae	*Oenopia sauzeti*				1
		Hyperaspis sp.		2	2	1
Coleoptera		*Harmonia axyridis*	1	1		
	Chrysomelidae	*Aulacophora* sp. 1				1
		Colaphellus bowvingi				5
	Cercopidae	*Aphrophora costalis*		1		
		Clovia sp.		1		
Hemiptera	Reduviidae	*Epidaus sexpinus*				2
	Lygaeidae	*Nysius ericae*		1	1	
		Tropidothorax elegans		2		
	Urostylidae	*Urostylis spectabilis*	1			
Araneae	Thomisidae	*Misumena* sp. 1				1
	Salticidae	*Salticidae* sp. 1				1
		Salticidae sp. 2				
Orthoptera	Tettigoniidae	*Tettigoniidae* sp. 1		2		

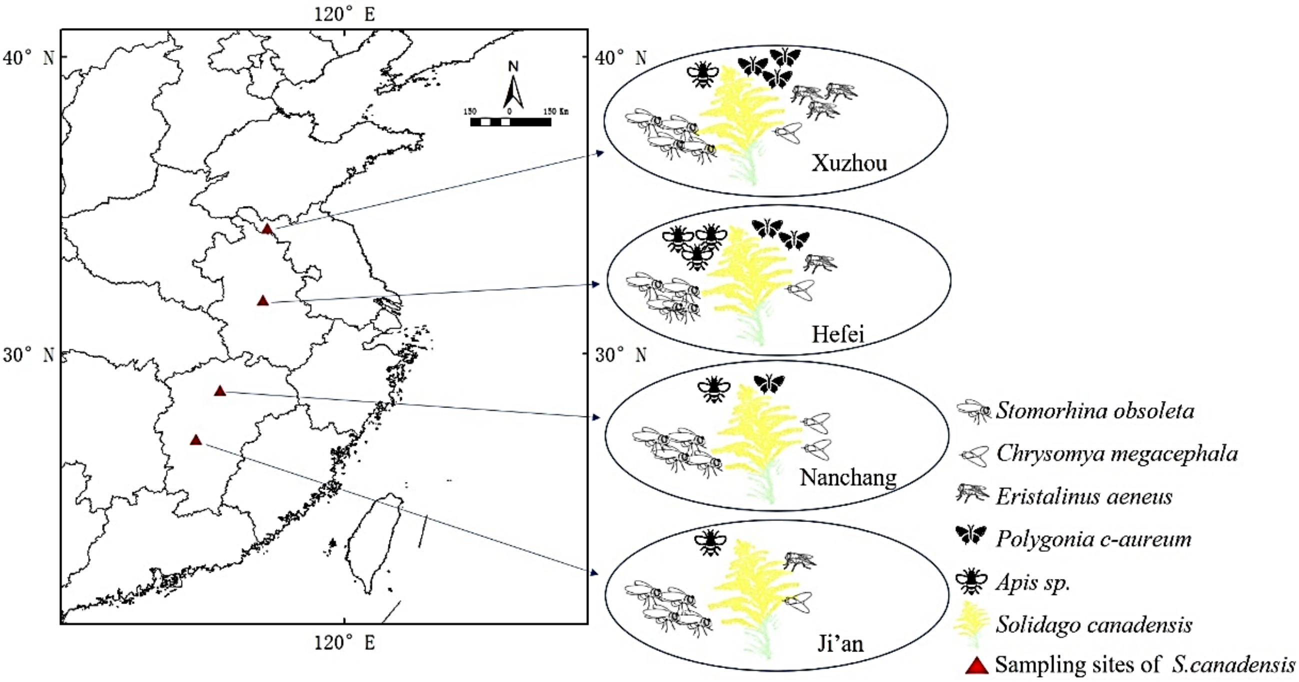

Fig. 4. Differences of pollinators in different geographic populations of *S. canadensis*.

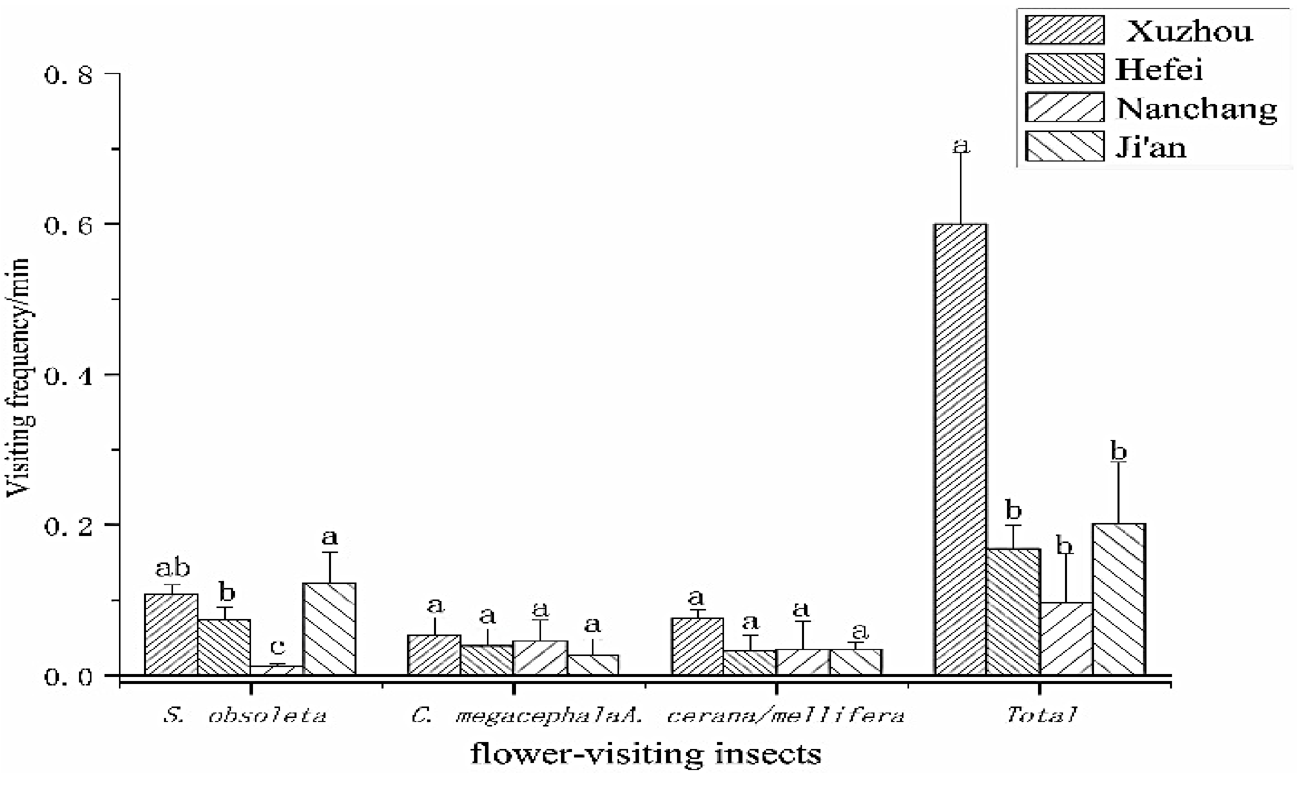

Fig. 5. The frequency of main flower-visiting insects of *S. canadensis.*

Discussion

S. canadensis is a self-incompatible plant that requires insects for pollination (Zhang *et al*., 2015). We recorded more than 94 species of flower-visiting insects along the four transects, and each site had more than 33 species, mainly belonging to Diptera (*S. obsoleta* was prominent), Hymenoptera and Lepidoptera, which shows that *S. canadensis* is essentially a generalist species in terms of pollination. Its floral syndrome conforms to a generalized pollination syndrome, showing typical characteristics such as yellow flowers, rich nectar (Wang *et al*., 2009), a capitulum and conical inflorescences that are favourable for attracting visiting insects. *S. canadensis* may provide rich nectar as a rich food source for flower visitors. Ward, M. and Johnson, S.D. found that three alpine species of milkweed attract pollinators by rich nectar in Australia (Ward *et al*., 2013). Large areas of yellow flowers help attract bees that are sensitive to yellow (Corbet & Sarah, 1989; Pereira *et al*., 2011). The characteristic capitulum of *S. canadensis* attracts at least 25 species (Johnson, 2000), and inflorescences consisting of small flowers are single-sided, forming a conical shape with peripheral inflorescences and expanding the surface area of the inflorescences, while bright yellow, clustered pollen (Wang *et al*., 2009) increases the number and frequency of visitors. The generalized pollination of *S. canadensis* might be conducive to overcoming competition for insects with local plants and might be helpful in ensuring sexual reproduction success. The findings of recent studies also supported this hypothesis (Vanparys *et al*., 2008; Yan *et al*., 2016).

The main pollinators differed among the geographical populations studied. We found that the *S. canadensis* pollinators in different regions were mainly Diptera, Hymenoptera and Lepidoptera, but there were differences in the main pollinators among regions. Flies were the main flower-visiting insects in the *S. canadensis* populations at high and low latitudes. Flies may appear at temperatures greater than 13°C (Ye & Liu, 2005); they feed on nectar and move around the inflorescence, and their body parts move between different flowers, greatly increasing pollen transmission. Bees (*A. mellifera*) occupied a dominant position at the middle latitudes. *A. mellifera* is mainly farmed, with few wild populations in China, and there may be a high proportion of bees in the middle-latitude area due to the relatively well-developed beekeeping industry. This finding of differences among geographic populations is consistent with those of some previous studies, such as a study on *Changnienia amoena* (Sun, 2005). In addition, spatial differences in pollinators have been reported (Duan 2006; Arnold *et al*., 2009; Qitao, 2019), and as altitude increases, pollinators tend to shift from bees to flies (Arnold *et al*., 2009). On the Qinghai-Tibet Plateau, flies were the main pollinators in high-altitude areas, while ants were the main pollinators in low-altitude areas (Duan, 2006). Temperature conditions have similar regularity under altitude gradient and latitude gradient (Dimri *et al*., 2022; Finnegan & Miller, 2022), and also affect the spatial distribution of insects. *S. canadensis* blooms in autumn, when the ambient temperature is low, and generalized pollination ensures enough pollinators in different geographical areas, which is beneficial for sexual propagation and increases the invasion capability of *S. canadensis*.

The pollination biology results for *S. canadensis* show that it has a generalized pollination system and that there are enough pollinators in different geographic areas, which helps reduce the limitation of pollinating resources. We found that *S. canadensis* attracted dozens of insects, and the visit frequencies of different insects varied. Xuzhou had more *E. aeneus* than other places, so the total flower visit frequency of this species was higher. Despite differences in the visit frequencies of pollinators, the similar visiting behaviours of pollinators among different geographical locations of *S. canadensis* may favour adaptive generalization (Nadia *et al*., 2013), which is conducive to adaptation to the new environment and increases invasiveness. In addition, the same floral structure bears different attractions for different insects (Gegear & Laverty, 2005). For example, in *Trollius ranunculoides*, stamens and sepals can increase the visit frequency of bees but have no obvious attraction effect on ants (Liu *et al*., 2013). In *S. canadensis*, butterflies mainly visit the top of the inflorescence, while other lepidopterans and hymenopterans mainly visit other parts, which reduces competition among different insects.

In summary, the invasion of *S. canadensis* has become a global problem, and thus far, effective solutions have not been found. In this paper, we found that *S. canadensis* has a generalized pollination system that attracts a large number of insects, and populations in different areas have different visiting insects. This guarantees its sexual reproduction after invasion, is conducive to its dispersal in the natural state and increases its adaptability to invasion sites.

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