

# FLORAL SCENT AND POLLINATION OF THE INVASIVE PLANT *COREOPSIS LANCEOLATA* IN JAPAN

Muhammad Arifin<sup>1\*</sup> and Tomoko Okamoto<sup>1,2</sup>

<sup>1</sup>The United Graduate School of Agricultural Sciences, Gifu University, 501-1193, Gifu, Japan.

<sup>2</sup>Laboratory of Insect Ecology, Faculty of Applied Biological Sciences, Gifu University, 501-1193, Gifu, Japan.

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\*Corresponding author:  
[muh.arifin.1994@gmail.com](mailto:muh.arifin.1994@gmail.com)

**Abstract**—The invasive plant *Coreopsis lanceolata* threatens ecosystems in Japan by competing for resources with native plants. This species is self-incompatible and requires pollinator agents for seed production; however, it is known to produce many seeds. Here, we document the pollination biology and plant-pollinator interactions that facilitate seed production of *C. lanceolata* in the introduced range. Results revealed that *C. lanceolata* attracted a wide array of floral visitors comprising 60 species from 20 families. Although most floral visitors could be potential pollinators, the functional groups of halictid bees appeared to be the most important pollinators of *C. lanceolata* in terms of visitation frequency and the ability to carry pollen. The floral scent emission of *C. lanceolata* consists predominantly of monoterpenes, sesquiterpenes, and benzenoids. Furthermore, the mean seed set was nearly 30% of the ovule mean. Our study confirmed that in the introduced range in Japan, *C. lanceolata* is integrated into the local pollinator community, especially with the functional group of halictid bees involved in the reproductive success.

**Keywords**—Floral scent; plant-pollinator interaction; pollination success; reproductive biology; riparian ecosystem

## INTRODUCTION

*Coreopsis lanceolata* (Asteraceae) is one of Japan's 100 most noxious invasive plants (The Ecological Society of Japan 2002). This weed is native to North America and was introduced in 1880 as an ornamental plant that was later used for landscaping in Japan (Kaneko 2012). Currently, *C. lanceolata* has a scattered distribution and invades riparian areas and open spaces on the mainland and remote islands (Miyawaki & Washitani 2004; Koike et al. 2006; Inoue et al. 2020). Therefore, there is a concern that their presence may negatively influence nearby native species. Previous studies have reported that *C. lanceolata* limits the light availability to native riparian vegetation because of its coverage (Saito & Okubo 2011, 2013). Furthermore, serious ecological challenges from *C. lanceolata* have been reported in Australia (Randall 2007), China (Xu et al. 2012), South Africa (Moshobane et al. 2022), South Korea (Kil et al. 2004), and Zimbabwe (Maroyi 2012).

Reproduction is a key aspect of the life cycle of plants and plays a vital role in the establishment and colonization of alien plants in the introduced range (Barrett et al. 2008). Alien plants with restricted or low fitness reproductive potential may struggle in the introduced range and experience establishment failure. This is why successful reproduction is a critical factor in establishing and colonizing alien plants (van Kleunen et al. 2015). A report has revealed that a single *C. lanceolata* plant can produce approximately 12,000 seeds per flowering season (Zeng et al. 2014). The seeds are deposited in the soil, and a study on soil seed banks in the Kiso River area, central Japan, has reported that 460–865 seeds per 0.4 m<sup>2</sup> are deposited in the introduced range (Hatase et al. 2007). The seeds of *C. lanceolata* may survive for as long as 13 years in the seed bank (Banovetz & Scheiner 1994a), demonstrating the potential longevity of the soil seed banks. Due to its vigor and fertility, once *C. lanceolata* is established in the wild, it often forms large

communities, and there is a concern that it will negatively affect the habitat of native species.

Despite its massive seed production, studies in the native range of the United States have shown that *C. lanceolata* is self-incompatible, meaning it is unable to self-fertilize (Smith 1976). As a result, such self-incompatible species require cross-fertilization and are obligately dependent on vector-mediated pollination for seed production (da Santos et al. 2021). Previous studies have indicated that the self-incompatibility levels of alien plant species may vary between their native and introduced ranges, due to the evolutionary changes during invasion (Newbiggin & Uyenoyama 2005; Barrett et al. 2008). For instance, *Senecio inaequidens* (Asteraceae) has been reported to display self-incompatibility in its native range of South Africa, but several individuals were reported to be partially self-incompatible in the introduced range of France (López-García & Maillet 2005; Lafuma & Maurice 2007). However, recent research conducted on *C. lanceolata* in the introduced range of China has shown that it maintains self-incompatibility levels similar to those observed in its native range in the United States (Hao et al. 2011; Zeng et al. 2021). The self-incompatibility level of *C. lanceolata* in the introduced range of Japan is unknown. This study hypothesizes that, similar to the introduced range of China, the self-incompatibility level remains consistent in *C. lanceolata* in the introduced range of Japan.

Establishing mutualistic plant-pollinator interactions is crucial for ensuring seed production and maintaining population persistence for long-term invasion of self-incompatible species such as *C. lanceolata* (Liu et al. 2006; Vanparrys et al. 2008). Floral scents can play a role in attracting pollinators, as widely acknowledged in many studies (Solís-Montero et al. 2018; Wester et al. 2019; Grant et al. 2021). Moreover, the floral scent emitted by alien plant species could potentially facilitate the attraction of potential pollinators in the introduced range (Theis 2006; Castillo et al. 2014) and contribute, to some extent, to their invasiveness (Burkle & Runyon 2017). Despite its expected significant role in facilitating successful pollination, the floral scent of *C. lanceolata* remains unexplored.

The principal aims of this study were to determine the reproductive biology of *C. lanceolata*

in the introduced range of Japan. Specifically, we aimed to (i) determine the mutualistic plant-pollinator interactions that lead to successful seed production in *C. lanceolata*, (ii) characterize the floral scent emission that potentially contributes to pollinator attraction, and (iii) determine the level of self-incompatibility of *C. lanceolata* in the introduced range. To achieve these aims, we conducted pollinator observations, collected and analysed floral scent, and conducted a series of pollination treatments on the populations in central Japan.

## MATERIALS AND METHODS

### STUDY SPECIES AND SITES

*Coreopsis lanceolata* (Asteraceae) is an herbaceous perennial up to 70 cm in height, which produces a mass of flower heads at densities of approximately 30 capitula per 100 cm<sup>2</sup> (Zeng et al. 2021). Each capitulum comprises numerous ray and disk florets arranged into an entire inflorescence resembling a single flower (Fig. 1A). The capitula are bright yellow and 4–6 cm in diameter (Batianoff & Halford 2002). In Japan, the flowering period occurs between May and July.

This study was conducted from May to August 2021 across eight populations of *C. lanceolata* in southern Gifu Prefecture, Japan (Fig. 2; Tab. 1). The study sites have humid subtropical climates characterized by hot and humid summers and cool-to-mild winters. Six of the populations were at least 2 km apart; however, there were only ca. 600 m distance between Hirai1 and Hirai2. The population size of observed *C. lanceolata* varied across different populations from <10 to >100 individuals (for details see Tab. 1). Floral visitor observations were conducted in all populations; however, the collection of floral scents was only carried out in the Tsubaki Bora and Hirai2 populations. Additionally, the ovule analysis and pollination treatments were solely studied in the Tsubaki Bora population.

At the time of observation, co-flowering species, including two alien plants, namely *Erigeron annuus* and *Verbena brasiliensis*, were also in the anthesis period and inhabited all eight observation sites. In addition, an alien plant, *Trifolium repens*, co-flowered with *C. lanceolata* in Hirai1 and Hirai2.

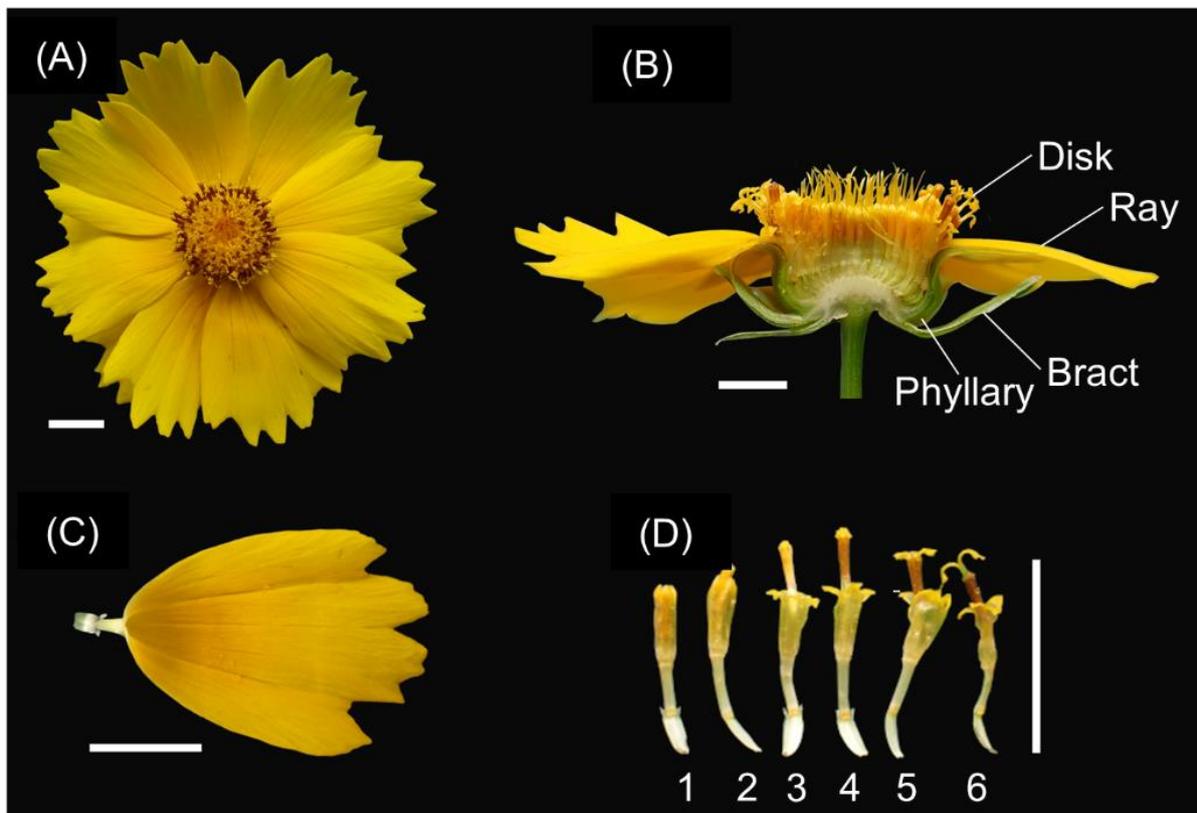


Figure 1. Flower head of *Coreopsis lanceolata*. (A) Fully bloomed flower; (B) Longitudinal section; (C) Ray floret; (D) Different developmental stages of disk floret. Scale bars = 10 mm.

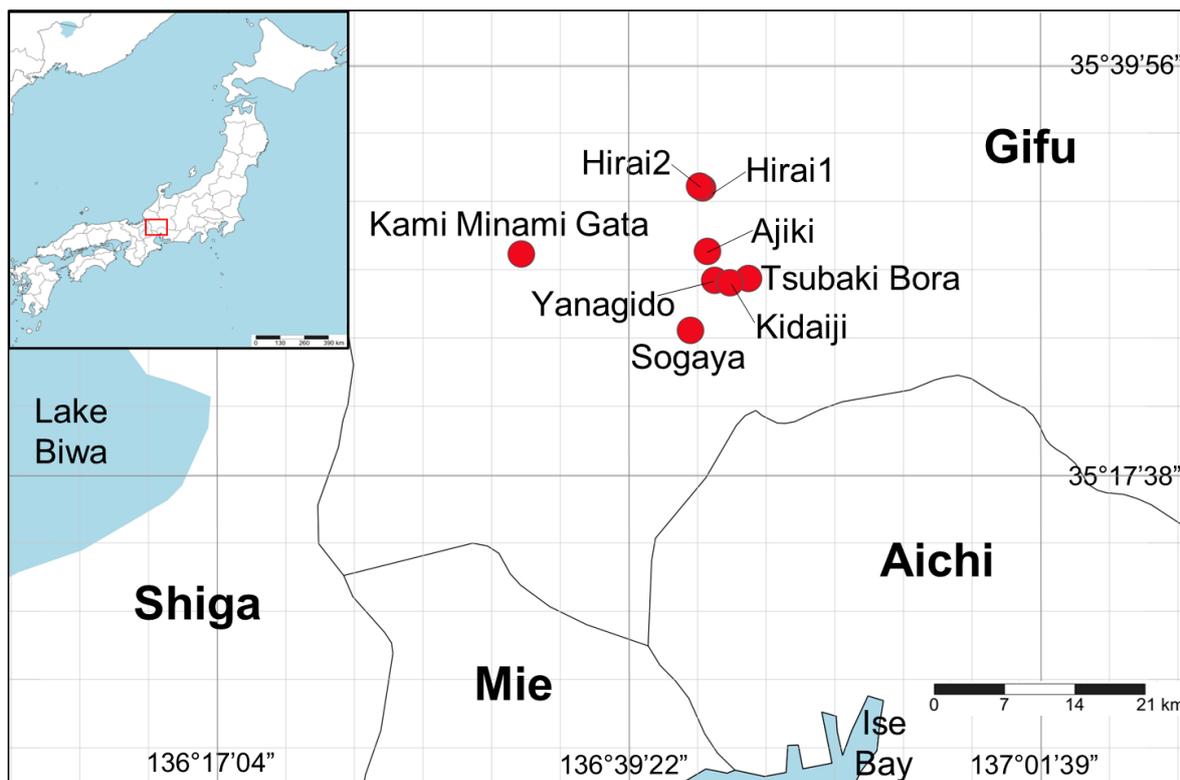


Figure 2. Map of the eight study populations of *Coreopsis lanceolata* (red circles). The maps were created using the software Simplemapp (Shorthouse 2010).

**Table 1. Details of the population observed in this study.**

City/ Municipality	Population	Coordinate	Elevation m. asl	Habitat Type	Population size#	Floral visitor observation (h)	Floral visitor	Floral scent	Fruit set
Gifu	Ajiki	35°29'47.0" N 136°43'37.1" E	26	Roadside adjacent to the residential area	30—50	14 June 2021 (5h)	✓		
	Kidaiji	35°28'04.5" N 136°44'50.1" E	13	Adjacent to paddy Fields	<30	9 June 2021 (4h)	✓		
	Sogaya	35°25'29.3" N 136°42'42.0" E	16	Open abandoned field	<20	11 July 2021 (2h)	✓		
	Tsubaki Bora	35°28'18.6" N 136°45'50.4" E	18	Roadside adjacent to the paddy field	30—50	20 June 2021 (7h); 13 July 2021 (2h)	✓	✓	✓
	Yanagido	35°28'12.6" N 136°44'00.6" E	13	Riverside adjacent to the paddy field	<10	9 June 2021 (1h)	✓		
Yamagata	Hirai1	35°33'14.0" N 136°43'21.1" E	70	Surrounded by residential area	>100	12 June 2021 (6h)	✓		
	Hirai2	35°33'20.0" N 136°43'11.6" E	73	Surrounded by residential area	>100	15 June 2021 (4h)	✓	✓	
Ibi	Kami Minami Gata	35°29'38.5" N 136°33'32.5" E	47	Riverside adjacent to paddy field	>100	26 June 2021 (4h)	✓		

#Population size refers to the total number of *C. lanceolata* individuals found in the population under study.

#### FLORAL VISITOR OBSERVATION AND ANALYSIS

Observations and collections of floral visitors were made diurnally on cloudy or sunny days between 07:00 and 18:30 (local time). The observations focused on pollinator behavior on the flower and the time spent foraging. Using a hand net, we collected only the floral visitors which made contact with the reproductive parts of the flowers. Most of the populations grew on a roadside approximately 300–800 m long (Fig. 4A; Tab. 1). However, the Sogaya population grew in an abandoned field in an area of approximately 10 m<sup>2</sup>. We clustered the population into four to seven sampling points (approximately 2 m<sup>2</sup> each) for observations. The researcher performed 10 min of observation and collection of floral visitors at one sampling point and then rotated to another sampling point. Subsequently, the collected floral visitors were deposited into 30 mL centrifuge tubes and stored at -20 °C until identification. A total of 35 h of observation was completed over 8 d in this study (the duration of observation time for each population is shown in Tab. 1).

We used a stereo microscope and standard book references (The Japan Coleopterological Society 1956; Yasunaga et al. 1993; Komai et al. 2011; Japan Butterfly Conservation Society 2012; Tadauchi & Murao 2014; Terayama & Suda 2016) to properly identify the collected floral visitors. The morphological characteristics of the visitors were carefully examined and used as the basis for identification. The identification of flower visitors was attempted at the lowest possible taxonomic level, such as the genus or species level. However, in certain cases, identification was limited to the family level given the difficulty in identifying those species based on external morphology.

#### POLLEN LOAD ANALYSIS

Determination of potential pollinators among the collected floral visitors of *C. lanceolata* in all populations was done using a stereo microscope. Floral visitor carrying pollen grains of *C. lanceolata* were considered as potential pollinators. In addition, to distinguish the pollen grains of *C. lanceolata* from those of co-flowering plants, we collected flowers from both *C. lanceolata* and its co-flowering plants for identification. The pollen grains of *C.*

*lanceolata* were easily distinguished by their larger size and brighter yellow color under the stereo microscope in comparison to the smaller and less vibrant pollen grains of *E. annuus*, *T. repens*, and *V. brasiliensis*. Previous studies have reported that the size of pollen grains of *C. lanceolata* is approximately 35  $\mu\text{m}$ , while *E. annuus* and *T. repens* are both approximately 20  $\mu\text{m}$  (Malayeri et al. 2012; Sugita & Itamiya 2020).

Pollen load analysis was performed in all collected floral visitors ( $N = 476$ ). The count of pollen grains attached to each floral visitor's body was recorded, and the location of the pollen load on the body was also noted. We only measured pollen that can be efficiently transferred between flowers, not including the sticky and clumped pellets created by corbiculate bees, known as corbicular pollen, which is less effective in pollination (Parker et al. 2015; Quinet & Jacquemart 2020).

#### POLLINATOR IMPORTANCE ANALYSIS

We combined data on floral visitors across all populations to evaluate their potential role as pollinators. Using a modified version of the methods described in Lindsey (1984) and Youngsteadt et al. (2018), we conducted pollinator importance (PI) analysis at the family level. The PI calculation considers three parameters: (1) relative abundance (A); (2) proportion of individuals carrying pollen among the groups (P); (3) pollen load capacity (PL). To mitigate the impracticality of counting the exact number of pollen grains carried by each visitor, we elected to simplify the measurement of pollen load capacity by using four distinct categories: no pollen (0 pollen grain), few pollen (less than 20 pollen grains), moderate pollen (between 20 and 100 pollen grains), and abundant pollen (more than 100 pollen grains). The PI was calculated as follows:

$$PI_i = A_i \times P_i \times PL_i$$

where:

$PI_i$  = pollinator importance of the  $i$ th taxon,

$A_i$  = relative abundance of  $i$ th taxon, that is, the ratio of visits by a given taxon of floral visitor to all collected visitors, with values ranging from 0 to 1.

$P_i$  = proportion of individuals carrying pollen. Reflects the ability of an individual of the  $i$ th taxon

to carry the targeted pollen, with values ranging from 0 to 1, and

$PL_i$  = pollen load capacity, that is, the number of targeted pollen grains carried by the  $i$ th taxon. Values were classified based on capacity, where 0 = no pollen load, 1 = total number of pollen loads < 20, 2 = total number of pollen loads between  $\geq 20$  and <100, and 3 = total number of pollen loads  $\geq 100$ .

Higher PI values indicate greater potential for pollination as it implies that a certain taxon of floral visitor is more abundant and more likely to carry pollen when compared to another taxon. Moreover, PI values appear to be suitable for evaluating the relative importance of floral visitors in the reproduction of focal plant species that are the focus of our study. It allows for a systematic and objective evaluation of the contribution of different floral visitors to the pollination process of the focal plant species (Rogers et al. 2013; Stanley et al. 2013).

#### OVULE ANALYSIS AND POLLINATION TREATMENTS

To determine the mean and variation in the number of ovules in a capitulum, we randomly sampled 22 fully bloomed capitula from eight individuals in the Tsubaki Bora population and brought them to the laboratory for measurements. The number of ovules on the ray (Fig. 1C) and disk florets (Fig. 1D) was assessed using a stereo microscope.

Additionally, to test the hypothesis that seed production of *C. lanceolata* in the introduced range of Japan is obligately dependent upon pollinator visitation, we performed both bagged and open pollination treatments from early June to late August 2021 in the Tsubaki Bora population. In the bagged treatment, buds were enclosed prior to anthesis using fine-mesh nylon (bag size 10 cm  $\times$  10 cm;  $\leq 0.5$  mm mesh size) to block the access of floral visitors. In the open pollination treatment, the buds were left for anthesis and exposed to natural floral visitors, after which the capitula were enclosed 4 d after anthesis with a similar fine-mesh nylon bag to prevent seed fall before collection. In each treatment, we selected 26 capitula (two capitula each from 13 individuals). Mature seeds were collected at the end of August when the seeds were fully developed, as indicated by a completely dry peduncle.

The comparison of plant reproductive success was conducted by quantifying the number of seeds produced per flower head under each treatment. This assessment aimed to determine the impact of the treatments on seed development in single flower head. Developed and undeveloped seeds were morphologically distinguishable. The developed seed was characterized by an increase in size, hard and rough surface, and dark brown–black color. In contrast, the undeveloped seeds remained small in size, had a smooth surface, and were pale in color.

#### FLORAL SCENT COLLECTION AND ANALYSIS

To determine the similarity and variation in floral scent between geographically distinct populations, we employed the dynamic headspace technique (Raguso & Pellmyr 1998) to collect floral scent samples from intact flowers attached to their respective plants in two populations, Tsubaki Bora and Hirai2. We observed that the highest activity of floral visitors to *C. lanceolata* flowers was recorded between 10:00 and 14:00 local time. As a result, we carried out the collection of floral scent samples for 2 hours within this particular period. Specifically, we collected one scent sample per individual plant, which was obtained from two capitula of the same plant. In total, we collected nine scent samples from nine individuals (three and six samples from Tsubaki Bora and Hirai2, respectively). During scent collection, the capitula were enclosed in low-density polyethylene bags. The volatiles present in the headspace were adsorbed using an adsorbent cartridge made from Tenax TA (60 mg; 80/100 mesh; GL Science, Tokyo, Japan) that was positioned within glass tubes (inner diameter 4 mm; length 12 cm) and plugged with silanized glass wool. A mini pump (MP-Σ30N II, SIBATA, Tokyo, Japan) was utilized to generate a flow of air at a rate of 100 mL min<sup>-1</sup>, which was then directed out of the enclosed bag and passed through the adsorbent cartridge for a duration of two hours. As a control, we followed the same procedure to collect scents from unopened flower buds ( $N = 2$  per population), leaves ( $N = 2$  per population), and the ambient air from an empty bag ( $N = 1$  per population). Following collection, the adsorbent cartridges were sealed with polytetrafluoroethylene (PTFE) thread seal tape, wrapped in aluminum foil to prevent exposure to

direct sunlight, and stored at a temperature of -30°C for subsequent analysis.

The collected scent samples were eluted from the adsorbent with n-hexane (1.5 mL) and carefully evaporated under N<sub>2</sub> flow until they reached 20 µL at about 25°C room temperature. Then, 1 µL sample was used for gas chromatography-mass spectrometry (GC-MS) analysis. An aliquot of 1 µL of the sample was taken using a microsyringe, and 1 µL of n-eicosane (10 ng µL<sup>-1</sup> concentration) was added to the sample as an internal standard. The GC-MS analysis was performed using an Rtx-5sil MS capillary column (30 m × 0.25 mm; 250-µm film thickness; Restek Corporation, USA) operated on a Shimadzu GC-2010 instrument (Tokyo, Japan). Helium (rate flux 48.2 cm s<sup>-1</sup>) was used as the carrier gas. The injector was set in the splitless mode for 1 min. Electron ionization mass spectra were acquired with 70-eV ionization voltage and a source temperature of 250°C. After 5-min incubation at 40°C, the oven temperature was raised to 5 °C min<sup>-1</sup> to 200 °C, and 10 °C min<sup>-1</sup> to 280 °C and then maintained for 5 min. To identify the floral scent compounds, we compared the volatiles emitted by flowers with those emitted by the control (unbloomed flower buds, leaves and ambient air). We focused on analyzing the compounds emitted by the flowers and not emitted in the control samples. In cases where a compound was detected in both the floral and control samples, we eliminated those compounds from our further analysis. The compounds were identified by matching the fragmentation pattern at least 90% with those in the National Institute of Standards and Technology (NIST 05 and NIST 05s) libraries. We also estimated the retention indices for all compounds using n-alkane standards and compared them to those reported in prior researchs in the NIST chemistry webbook (<https://webbook.nist.gov/chemistry/>) and Pherobase, which is a database for pheromones and semiochemicals (<https://www.pherobase.com/>). In addition, the majority of the identified compounds were validated by comparing the retention time and mass spectra to those of standard compounds. Ultimately, we measured the emission rate of each floral scent sample in ng h<sup>-1</sup> capitulum<sup>-1</sup> based on the internal standard method (Svensson et al. 2005). The relative quantity of each compound was calculated as the percentage of its peak area relative to the

total peak area in the chromatogram of each sample.

#### STATISTICAL ANALYSIS

Prior to analysis, all raw data were checked for a fit to the normal distribution using the Shapiro-Wilk test. Data on developed seeds were tested for significant differences between bagged and open pollination treatments using the Mann-Whitney *U*-test (non-normally distributed data). The total emission rate of floral scents in the Tsubaki Bora and Hirai2 populations was also compared using the Mann-Whitney *U*-test. Moreover, to assess differences in floral scent composition between populations, we generated Bray-Curtis dissimilarity matrices based on the relative quantity of each compound found in the GC-MS analysis.

To visualize the distribution of scent profiles between the two populations, we used NMDS based on Bray-Curtis dissimilarity indices. A permutational multivariate analysis of variance (PERMANOVA) of the Bray-Curtis index with 999 permutations was performed to test for differences in scent composition between populations. R version 4.2.1 coupled with the “stats” and “vegan” packages (Oksanen et al. 2022; R Core Team 2022) were used to perform the statistical analysis.

## RESULTS

#### FLORAL VISITOR ASSEMBLAGES AND POLLINATOR IMPORTANCE

Our observation of floral visitor assemblages of *C. lanceolata* in eight distinct populations over a single flowering season indicated that the greatest activity of *C. lanceolata* visitors occurred between 10:00 and 14:00 (local time). The *C. lanceolata* flowers were visited by a wide array of insect species, with a total of 476 visiting individuals from 60 arthropod species across 20 families and six orders (see Appendix 1). The floral visitor assemblages of *C. lanceolata* were diverse, and their relative abundance varied across populations, as shown in Fig. 3. Notably, the functional group of halictid bees (Fig. 4B), specifically native species of genus *Halictus* and *Lasioglossum*, were the most frequent visitors across all populations, as indicated by their legitimate visits (Fig. 3). However, the prevalence of these halictid bees varied among different populations, ranging from 5–68% of the collected visitors within the same population. In six populations, halictid bees were the most dominant visitors in terms of the number of visitations, but this pattern was not observed in the Kidaiji and Yanagido populations, where lepidopterans and syrphid flies were predominant, respectively.

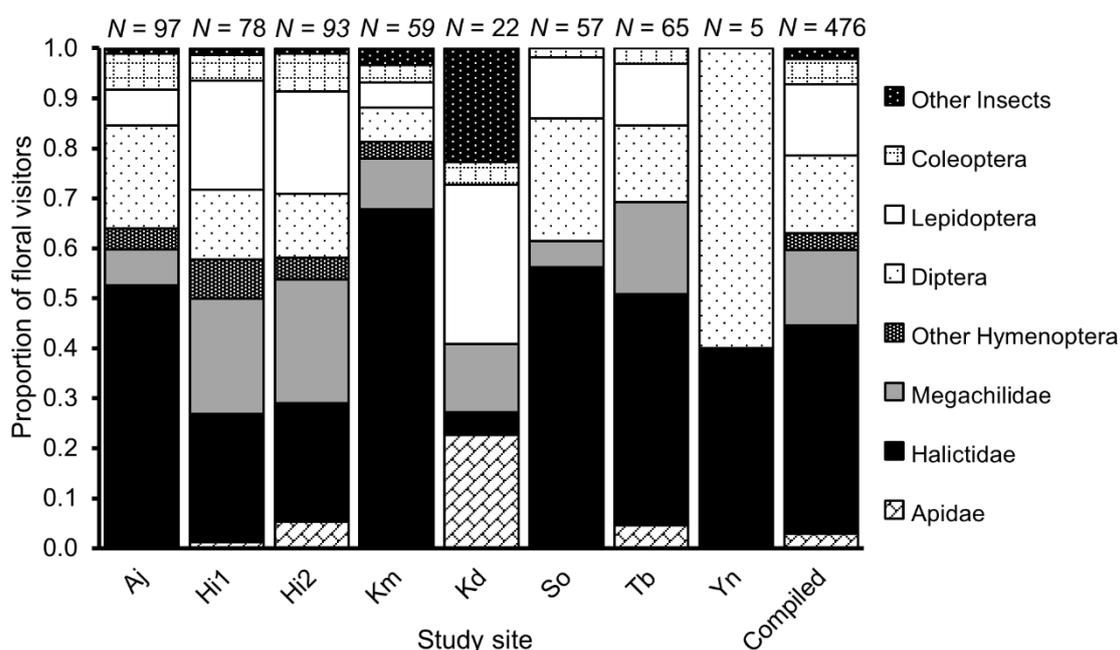
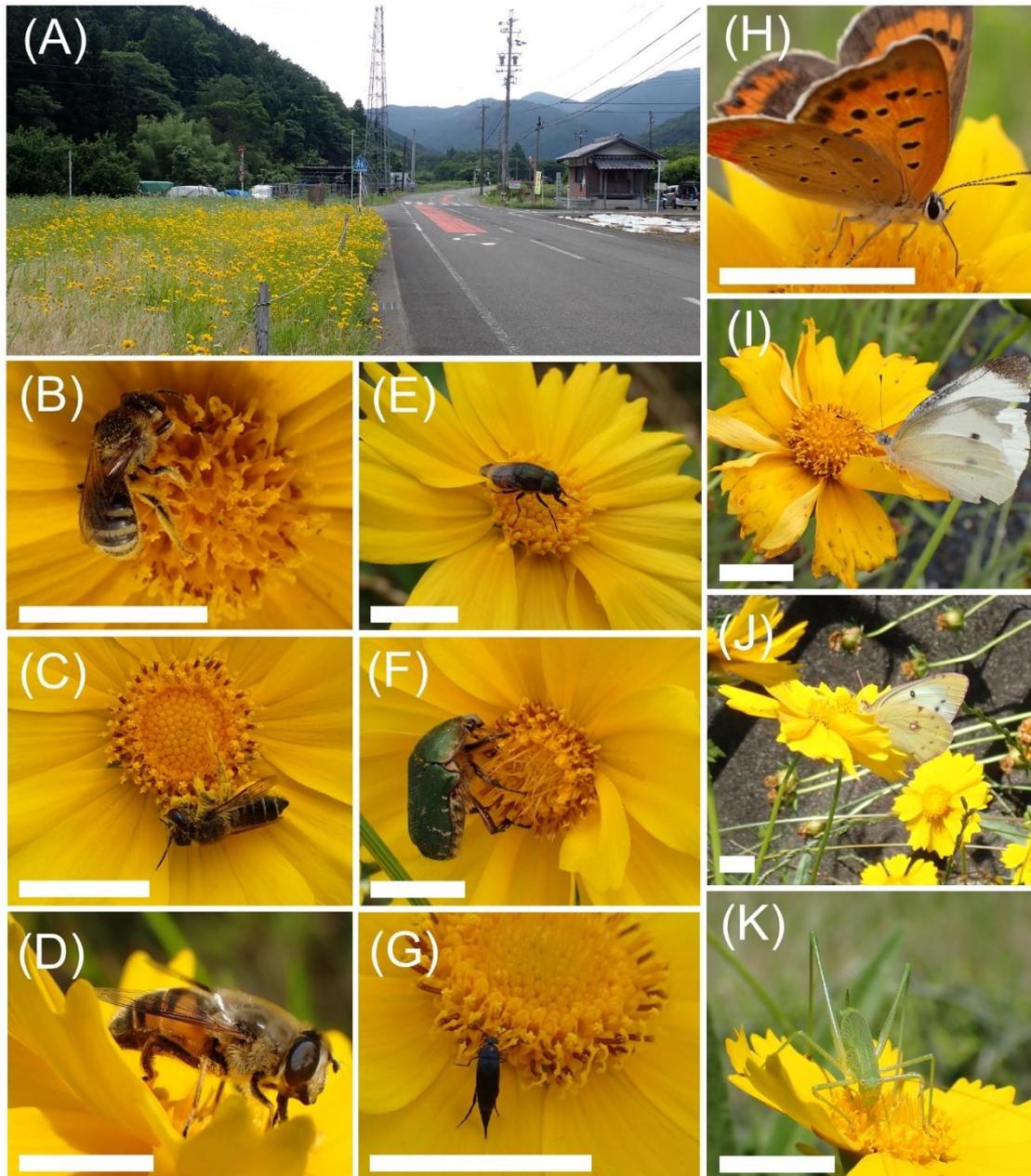


Figure 3. The proportion of floral visitors of *Coreopsis lanceolata*. *n* above the bar refers to the total number of floral visitors collected for each population. Abbreviation: Aj = Ajiki; Hir1 = Hirai1; Hir2 = Hirai2; Km = Kami Minami Gata; Kd = Kidaiji; So = Sogaya; Tb = Tsubaki Bora; Yn = Yanagido. “Compiled” refers to the compilation of data of floral visitors collected across all populations.



**Figure 4.** Habitat and floral visitor of *Coreopsis lanceolata*. (A) Habitat *C. lanceolata* of Hirai2 population colonies along the roadside; (B) *Halictus* spp.; (C) *Megachile* spp.; (D) Syrphid fly *Eristalinae* spp.; (E) *Stomorhina* spp.; (F) *Cetonia pirifera*; (G) *Mordellidae* spp.; (H) *Lycaena phlaeas*; (I) *Pieris rapae*; (J) *Colias erate*; (K) *Tettigoniidae* spp. Scale bars = 10 mm.

Upon analyzing the compiled data of all populations together, we found that halictid bees represented the majority of visitor assemblages, comprising 41.6% of all collections, followed by megachilid bees (15.1%; Fig. 4C) and syrphid flies from the subfamilies *Eristalinae* (Fig. 4D) and *Syrphinae* (13.0%). Furthermore, in most populations we observed lepidopterans of family Pieridae, particularly the species *Colias erate* (Fig. 4J) and *Pieris rapae* (Fig. 4I) and family Lycaenidae

such as *Lycaena phlaeas* (Fig. 4H). Scarab beetles, specifically *Cetonia pirifera*, were occasionally found visiting the capitula of *C. lanceolata* in five populations (Fig. 4F; Appendix 1). Visitation by other insect families, such as *Tettigoniidae* (Fig. 4K) and *Lygaeidae*, was rarely observed in the four and three populations, respectively.

The analysis of the pollen-carrying capacity of floral visitors of *C. lanceolata* revealed that approximately 96.6% of them were capable of

carrying pollen. The pollen grains of *C. lanceolata* were exposed in large, open flowers; thus, most of the pollen grains became easily attached to the legs and undersides of the thoraxes and abdomens of the floral visitors. For instance, in lepidopterans, more than twice the number of pollen grains were found on the legs than that found on the proboscis.

Further analysis of the importance of pollinators revealed that the PI value of the halictid bee family was the highest among the pollinators,

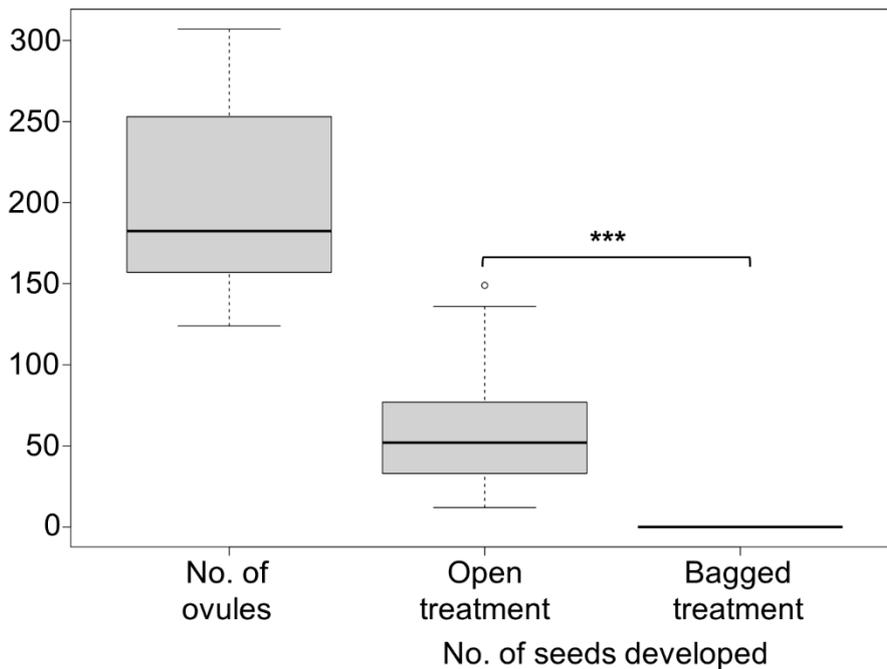
followed by megachilid bees, syrphid flies, and pierid butterflies (Tab. 2). The high PI value of halictid bees indicates that they have strong potential to play a significant role in the pollination services of *C. lanceolata*. Halictid bees usually visit many blossoms per capitulum and forage on multiple nearby capitula before departing. On average, a single halictid bee spends more than 30 seconds per visit foraging for nectar and pollen from flowers. In comparison, other floral visitors

**Table 2. The importance of different families of the floral visitor as a pollinator for *Coreopsis lanceolata*.**

Order/Family	Abundance (A)	Carrying pollen (P)	Pollen load (PL)‡	Pollinator importance (PI)
<b>HYMENOPTERA</b>				
Apidae	0.030	1.000	3.000	0.090
Halictidae	0.416	1.000	3.000	1.248
Megacilidae	0.152	1.000	3.000	0.456
Scoliidae	0.021	1.000	2.000	0.042
Vespidae	0.008	1.000	2.000	0.016
Other Hymenoptera	0.004	1.000	2.000	0.008
<b>DIPTERA</b>				
Calliphoridae	0.002	1.000	1.000	0.002
Rhiniidae	0.017	0.875	2.000	0.030
Syrphidae	0.133	0.933	2.000	0.248
Other Diptera	0.006	1.000	1.000	0.006
<b>LEPIDOPTERA</b>				
Crambidae	0.002	1.000	2.000	0.004
Hesperiidae	0.002	1.000	2.000	0.004
Lycaenidae	0.035	0.667	1.000	0.023
Nymphalidae	0.014	0.667	2.000	0.019
Papilionidae	0.002	0.000	0.000	0.000
Pieridae	0.086	0.841	2.000	0.145
<b>COLEOPTERA</b>				
Chrysomelidae	0.019	1.000	2.000	0.038
Curculionidae	0.004	1.000	3.000	0.012
Mordellidae	0.008	1.000	2.000	0.016
Oedemeridae	0.002	1.000	3.000	0.006
Scarabaeidae	0.017	1.000	2.000	0.034
<b>ORTHOPTERA</b>				
Tettigoniidae	0.008	1.000	1.000	0.008
<b>HEMIPTERA</b>				
Lygaeidae	0.012	1.000	3.000	0.036

**Note:** Data on floral visitation across all populations were compiled. The information in this table is limited to the specimens that were collected.

‡ The value for pollen load capacity was classified based on the number of targeted pollen grains carried by each species of floral visitor, where: 0= no pollen load; 1= total number of pollen loads <20; 2= total number of pollen loads between 20 and <100; 3= total number of pollen loads ≥100.



**Figure 5.** Number of ovules ( $N = 22$ ) and seeds developed in open ( $N = 26$ ) and bagged treatment ( $N = 26$ ) at Tsubaki Bora population. \*\*\* indicates  $P < 0.001$ .

spend less than 20 seconds per visit. Moreover, because of their small size, the halictids could insert their heads almost completely into the florets to collect nectar from the base. Consequently, as they crawl across the florets to obtain nectar, they effortlessly cover their entire bodies with pollen grains. Upon visiting other flowers, halictid bees repeat these actions, leading to successful pollination as the deposited pollen is transferred to the stigma.

#### OVULES AND SEED SET

The mean ( $\pm$  SD) number of ovules of *C. lanceolata* at the anthesis stage in the Tsubaki Bora population was  $201.6 \pm 61.5$  ( $N = 22$ ; Fig. 5). Moreover, we conducted an evaluation of the role of pollinator visitation in the pollination and seed development of *C. lanceolata* by using bagged and open pollination treatments. Our aim was to test the hypothesis that the seed production of this species is obligately dependent on pollinator visitation. The open pollination treatment yielded considerably more seeds than the bagged treatment (Fig. 5; Mann–Whitney  $U = 676$ ,  $P < 0.001$ ). The open pollination treatment resulted in a mean number of seeds of  $60.8 \pm 35.9$  ( $N = 26$ ; Fig. 5). By contrast, the bagged treatment yielded no seeds ( $N = 26$ ; Fig. 5). These results were consistent with the hypothesis that *C. lanceolata* in the introduced range of Japan is obligately dependent on pollinators for seed production. Ultimately,

comparison of the mean number of seeds produced by open pollination with the mean number of ovules at the anthesis stage revealed that approximately 30% of the seeds were generated from the initial ovules.

#### EMISSION OF FLORAL SCENTS

A total of 16 compounds were identified in the floral scent samples of *C. lanceolata* in the Tsubaki Bora and Hirai2 populations (Tab. 3). They consisted of three benzenoids (2.3–13.4% of relative peak area), five monoterpenes (9.1–29.2%), four sesquiterpenes (27.8–74.9%), and four unidentified compounds (2.1–14.2%).  $\beta$ -Bisabolene,  $\beta$ -Bourbonene, and (*Z*)-Verbenol were consistently present and abundant in the samples from both populations. Limonene was detected in the Hirai2 population samples but was absent in the Tsubaki Bora samples. Additionally, the scent composition of the two populations was significantly different (PERMANOVA; degrees of freedom [ $DF$ ] = 1, pseudo- $F = 3.03$ ,  $P = 0.04$ ). These differences contributed to the clear separation of clusters in the Tsubaki Bora and Hirai2 samples in the two-dimensional non-metric multidimensional scaling (NMDS) representation (Fig. 6). Ultimately, the mean scent emission rate per capitulum in Tsubaki Bora was significantly higher than in Hirai2, which was  $4.4 \pm 3.0$  and  $1.1 \pm 0.7$  ng h<sup>-1</sup>, respectively (Tab. 3; Mann–Whitney  $U = 18$ ,  $P = 0.02$ ).

**Table 3. Average relative amounts (%) of floral scent compounds of *Coreopsis lanceolata* in Tsubaki Bora and Hiraiz population. Compounds are listed in order of increasing retention time within each compound class. N in parenthesis refers to the number of floral scents samples.**

Compounds	Retention indices <sup>a</sup>	Tsubaki Bora (N = 3)		Hiraiz (N = 6)	
		Relative amount <sup>e</sup>	Absolute amount <sup>f</sup>	Relative amount <sup>e</sup>	Absolute amount <sup>f</sup>
<i>Benzenoids</i>					
Phenylacetaldehyde <sup>c</sup>	1045	7.64 ± 2.83	0.35 ± 0.26	2.66 ± 4.90	0.03 ± 0.04
Methyl phenylacetate <sup>b</sup>	1176	0.61 ± 0.65	0.03 ± 0.02	–	–
Methyl salicylate <sup>c</sup>	1195	0.43 ± 0.41	0.02 ± 0.02	0.33 ± 0.74	0.01 ± 0.02
<i>Monoterpenes</i>					
o-Cymene <sup>b</sup>	1026	1.62 ± 1.31	0.05 ± 0.01	7.22 ± 16.15	0.02 ± 0.06
Limonene <sup>c</sup>	1031	–	–	22.61 ± 17.14	0.29 ± 0.31
Eucalyptol <sup>c</sup>	1033	–	–	1.85 ± 4.15	0.03 ± 0.08
(E)-Linalool oxide, furanoid <sup>c</sup>	1087	0.75 ± 0.70	0.03 ± 0.03	–	–
(Z)-Verbenol <sup>b</sup>	1165	15.37 ± 6.85	0.55 ± 0.16	31.65 ± 15.57	0.30 ± 0.19
<i>Sesquiterpene</i>					
β-Bourbonene <sup>b</sup>	1391	17.90 ± 8.19	0.85 ± 0.83	12.01 ± 12.90	0.16 ± 0.24
β-Elemene <sup>c</sup>	1394	4.43 ± 1.13	0.22 ± 0.20	0.31 ± 0.69	0.01 ± 0.02
β-Cedrene <sup>b</sup>	1427	18.05 ± 4.48	0.79 ± 0.49	8.32 ± 7.51	0.10 ± 0.14
β-Bisabolene <sup>b</sup>	1512	25.01 ± 3.95	1.18 ± 0.98	7.24 ± 9.43	0.08 ± 0.10
<i>Unidentified<sup>d</sup></i>					
I: m/z [43, 119, 41, 109, 81]	1259	1.23 ± 1.08	0.03 ± 0.03	1.14 ± 1.65	0.02 ± 0.03
II: m/z [119, 132, 105, 41]	1485	2.54 ± 1.65	0.14 ± 0.17	1.05 ± 2.34	0.02 ± 0.05
III: m/z [41, 69, 132, 134, 119]	1682	2.35 ± 0.80	0.09 ± 0.04	0.36 ± 0.80	<0.01
IV: m/z [43, 58, 71, 57, 59, 41]	1842	2.08 ± 1.11	0.07 ± 0.01	3.25 ± 5.04	0.03 ± 0.04
Number of compounds recorded (mean ± SD)		12.67 ± 0.58		5.67 ± 3.01	
Emission rate (mean ± SD; ng h <sup>-1</sup> capitulum <sup>-1</sup> )		4.42 ± 2.99		1.10 ± 0.66	

<sup>a</sup> Retention indices calculated by n-alkane standards.

<sup>b</sup> Identification of compounds was performed by comparing the similarity of mass spectrum to those in libraries and previously published Kovats retention index in NIST Chemistry WebBook.

<sup>c</sup> Identification of compounds based on mass spectrum and Kovats retention index of the standard compound.

<sup>d</sup> Ion fragments for unidentified compounds are listed from the stronger, with the ion having the highest intensity listed first, followed by ions with lower intensities.

<sup>e</sup> The mean (± SD) relative amount (%) of floral scent compounds was calculated by dividing the number of a specific floral scent compound emitted by the overall number of floral scents emitted.

<sup>f</sup> Mean (± SD) of absolute amount (ng) of floral scent per hour per capitulum.

## DISCUSSION

### FLORAL VISITATION

*Coreopsis lanceolata* in the introduced range in Japan was visited by floral visitor assemblages comprising 60 species from several families and orders, suggesting a generalized pollination system for this plant. Species with generalized

pollination systems are able to attract a diversity of pollinator assemblages from various taxonomic groups, facilitating the provision of pollination services (Waser et al. 1996; Johnson & Steiner 2000; Fleming et al. 2001). The generalized pollination system is commonly adopted by flowers of the family Asteraceae (e.g., observed in studies of *Aspilia jolyana*, *Chromolaena odorata*, *Conyza sumatrensis*, and *Espeletia grandiflora* (Fagua &

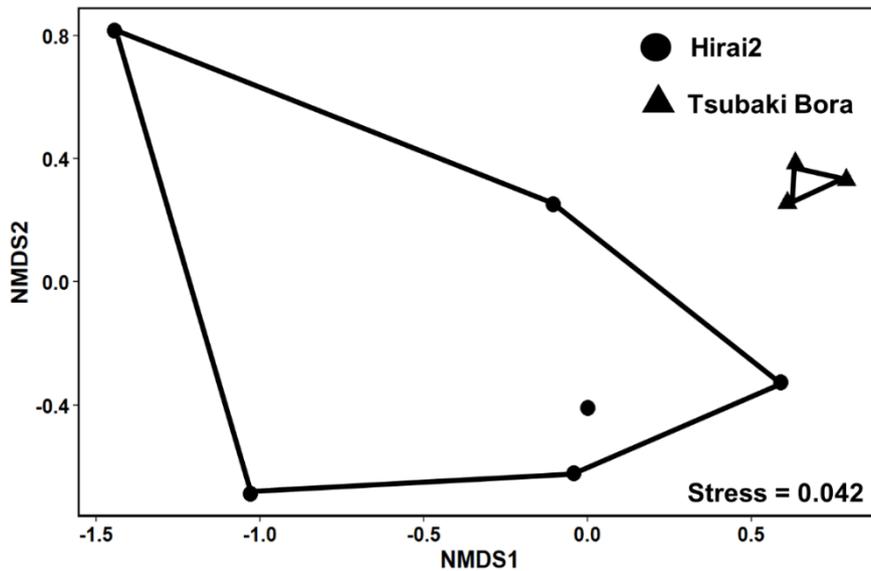


Figure 6. Two-dimensional representation based on nonmetric multidimensional scaling (NMDS) of floral scent composition of *Coreopsis lanceolata* in Hirai2 ( $N = 3$ ) and Tsubaki Bora ( $N = 6$ ) population.

Gonzalez 2007; Hao et al. 2009; Maruyama et al. 2018; Layek et al. 2022)). In *C. lanceolata*, this generalized pollination system is likely provided by the structure of the *C. lanceolata* flower head, which presents the pollen and nectar (approximately  $0.5 \mu\text{L flower head}^{-1} 24 \text{ h}^{-1}$ ) in a way that it can be utilized by various floral visitors (Wojcik et al. 2008; Kalamani et al. 2022).

Examining pollinator data from the native range is necessary to understand the pollination biology of alien plant species in the introduced ranges and assess whether the lack of pollinators or their displacement by local visitors affects the reproduction and invasiveness of alien plant species (Montero-Castaño et al. 2014; Issaly et al. 2020). We did not conduct a direct observation of *C. lanceolata* in its native range in the United States; however, a comparison of the present study and the literature reviews in earlier studies of *C. lanceolata* and congeners in their native range (Hilty 2020; Appendix 2) suggested that the functional group at the family taxa level in the present study [i.e., bees [apid, halictid, and megachilid], scoliid wasp, syrphid flies, butterflies [nymphalid, lycaenid, and pierid], and beetles] are in line with those in the native range. Our findings, to a certain extent, adds evidence to the previous studies that alien plants in the introduced range probably attract pollinators from similar functional groups in their native range (Ollerton et al. 2012; Montero-Castaño et al. 2014; Petanidou et

al. 2018). Nevertheless, we documented visits from eight insect families that had not previously been reported in the native range (Appendix 1 & 2), demonstrating that potential pollinators associated with this species are more diverse in the introduced range in Japan. Moreover, our study provides valuable insights into the diversity and prevalence of floral visitors to *C. lanceolata* in different populations, highlighting the importance of considering population-specific factors in studies of plant-pollinator interactions.

In general, the present study indicates that halictid bees were the most frequently observed visitors of *C. lanceolata*. However, we also observed spatial variation in the composition of floral visitor assemblages, particularly in small populations, as depicted in Fig. 3, where the Yanagido and Kidaiji populations showed different predominant visitors. One potential explanation for the differences in the structure of plant-pollinator communities is variation in population size and floral density, which have been reported in some studies to affect the composition of visitor species (Sowig 1989; Bernhardt et al. 2008; Courtice et al. 2020). Additionally, population size and floral density often increase pollinator abundance and per-flower visitation rates in large populations as compared to small ones.

The generalized pollination system of *C. lanceolata* allowed this species to attract various insects to facilitate pollination (Zeng et al. 2021).

However, when comparing the number of visits and the load capacity for carrying pollen grains, the important pollinators were the halictid bees (Tab. 2). Based on data collected during a single flowering season, our study highlighted early evidence that *C. lanceolata* may exhibit functional group specialization toward halictid bees in the introduced range of Japan. Functional group specialization is observed in plant species that rely on multiple functionally similar pollinators belonging to a single taxonomic group for pollination services (Ollerton et al. 2007; Dalsgaard et al. 2008; Armbruster 2017). The functional group specialization on halictid bees in Asteraceae is not reported here for the first time. In a previous study, functional specialization for halictid and collectid bees was reported in *Heterotheca subaxillaris* (Asteraceae), a perennial yellow-flowered plant species in Texas, USA (Olsen 1997). Other studies have also documented functional group specialization for various insect groups of bees and wasps in several plant families, including Cactaceae, Rutaceae, Vitaceae, and Zingiberaceae (Sakai et al. 1999; Kishore et al. 2012; Pauw & Stanway 2015; Fisogni et al. 2016; Martins & Freitas 2018; Nagasaki 2021). These findings suggest that functional group specialization within plants with generalized pollination systems is likely to occur in many more plant families than have been studied so far. However, due to the limited duration of our study, the conclusion regarding the functional specialization of halictid bees in *C. lanceolata* is preliminary. Previous studies in other plant species have shown that plant-pollinator interactions networks can exhibit temporal variation dynamics within and between flowering seasons (Traveset & Sáez 1997; Olesen et al. 2008; Souza et al. 2018; C ezar et al. 2022). Therefore, further multi-year studies of *C. lanceolata* in its introduced range in Japan are necessary to assess the consistency and persistence of the observed plant-pollinator interactions.

Moreover, the results of the present study are in contrast to an earlier study in the introduced range of China, where no species of halictid bees had been observed (Zeng et al. 2021). In China, *Apis cerana* (Apidae family) is the most important visitor of *C. lanceolata* (Zeng et al. 2021). *Apis cerana* is also a native species in Japan (Takahashi et al. 2007); therefore, we expected similar results for our study. However, we found no *A. cerana* visiting *C.*

*lanceolata* in our study sites; yet we observed that the alien congener European honeybee *A. mellifera* visited the species in Hirai2 and Kidaiji populations, representing approximately 4% and 5% of the observed visitors within those populations, respectively (Appendix 1). These variations in pollinator communities are usually related to variation in floral traits, such as floral size (Inoue & Amano 1986; Rech et al. 2018). However, a comparison of the floral display size of *C. lanceolata* in the introduced ranges of Japan and China (Zeng et al. 2021) suggested no differences (Appendix 3). The corolla diameter, tubular flower diameter, and length of disk floret are  $52.2 \pm 4.4$  mm,  $11.4 \pm 0.9$  mm, and  $8.9 \pm 0.7$  cm, respectively, for the China population, and  $54.3 \pm 5.1$  mm,  $10.6 \pm 1.6$  mm and  $8.5 \pm 2.9$  mm, respectively, for the Japan population. Other possible explanation is that in the sympatric condition in Japan, where *C. lanceolata* co-flowered with plant species with more rewards, in terms of quantity and quality, members of the genus *Apis* were less attracted to *C. lanceolata* and preferred to visit the co-flowering plant species. The lack of visitation of *Apis* species to *C. lanceolata* at our study sites was not caused by the scarcity of *Apis* assemblages. Our personal observations showed that *Apis* were commonly present in our study sites and actively visited co-flowering species, such as *Verbena brasiliensis*, *Erigeron annuus*, and *Trifolium repens* (Appendix 4 & 5). For instance, in the Kami Minami Gata population, *A. mellifera* was observed to account for 65% of visitations to *V. brassiliensis*, and 3% of visitations to *E. annuus*, however, no single visitation was recorded for *C. lanceolata* (Appendix 1 & 4). Plants with co-flowering neighbors may influence plant-pollinator interactions by modifying pollinator composition, availability, or behavior in the community (L azaro et al. 2009). As a social insect, collective decision-making among honeybee *A. mellifera* has been observed in regards to adjusting foraging behavior based on profitability factors, such as the distance from the hive and availability and quality of food sources (Seeley et al. 1991; Bose et al. 2017; Lemanski et al. 2021). We argue that collective decision-making may impacts the foraging patterns of honeybees within our study sites. When presented with multiple food sources that have varying levels of profitability, the honeybees are likely to allocate a majority of their foraging efforts towards the more

profitable option. Further research on the non-sympatric area of *C. lanceolata* in the introduced range of Japan is needed to understand this plant–insect interaction completely.

#### POSSIBLE ASSOCIATION BETWEEN FLORAL VOLATILES AND POLLINATORS

The analysis of floral scents allowed us to characterize the scent chemistry of *C. lanceolata* for the first time. In most studies, floral scents have been reported to play a crucial role as attractants for insects and mammals (Heiduk et al. 2010; Wester et al. 2019; Wang et al. 2021). The floral scents of *C. lanceolata* were distinctive to the human nose. The chemical analysis of the headspace revealed that the floral scents were characterized by significant concentrations of the sesquiterpene and monoterpene compound classes. The majority of compounds identified in the floral scent samples have also been found in the bouquet of floral scents in other angiosperms (Knudsen 1993). Most of the identified compounds were emitted in modest quantities. Only five of the 16 identified compounds were found at relatively high levels ( $\geq 15\%$ ) in at least one population (Tab. 3). Among these, (*Z*)-Verbenol was the most abundant chemical in the volatile bouquets of *C. lanceolata* populations. This compound has been identified in the volatile profile of many orchids (Kaiser 1993) and in other Asteracea species such as *Tanacetum vulgare* (Gabel et al. 1992) and is recognized as a potential insect attractant for moths. In addition, other primary compounds found in *C. lanceolata*, such as (*E*)-linalool oxide, furanoid,  $\beta$ -bourbonene, and  $\beta$ -elemene, are known to be released by flowers visited by the halictid bee *Lasioglossum* spp. (Theis 2006; Giuliani et al. 2018; Braunschmid et al. 2021). This suggests that, to some extent, these compounds might play a role in the attraction of halictid bees. Furthermore, the flowers of *C. lanceolata* were found to release compounds such as phenylacetaldehyde and methyl salicylate, which have been found to be attractive to a wide variety of insect visitors, e.g. in orchid *Disa fragrans* (Johnson & Hobbhahn 2010), orchid *Gymnadenia* (Huber et al. 2005), and cactus *Echinopsis chiloensis* ssp. *Chiloensis* (Lemaitre et al. 2014), suggesting that these compounds may also play a role in the generalized pollination system of *C. lanceolata*. The significant prevalence of these compounds across the studied populations raises the possibility that they may be essential compounds with a variety of

roles that warrant further study, particularly in determining which specific compounds within the fragrance are responsible for physiological and behavioral effects on insect visitors.

Our study shows variation in the emitted compounds between the Tsubaki Bora and Hirai2 populations. Twelve compounds were emitted in both populations, but limonene and eucalyptol were only emitted in the Hirai2 population. The NMDS analysis (Fig. 6) indicated distinct variations in floral scent profiles between the two populations studied. Numerous studies have been conducted on intraspecific diversity in floral odor chemistry across populations of diverse plant families, including *Magnolia kobus*, several species of *Lithophragma*, and *Geonoma macrostachys* (Azuma et al. 2001; Knudsen 2002; Friberg et al. 2019). Variation in floral scents across populations may occur because of adaptations to different local pollinator species (Burkle & Runyon 2017). However, in the present study, there was minimal variation in the functional groups of pollinators visiting *C. lanceolata* (Appendix 1) in those two populations. Therefore, factors other than pollinator-mediated selection are expected to be responsible for variations in the floral scents of *C. lanceolata*. Genetic drift, biochemical, and/or environmental variation among the study sites may be additional factors explaining the variation in floral scent (Suinyuy et al. 2012; Delle-Vedove et al. 2017). However, it is important to acknowledge that the number of floral scent samples analyzed in our study was small, which may limit the robustness of our findings. Thus, additional investigations are warranted to better understand the extent of variation in floral scent profiles of *C. lanceolata* across populations.

#### BREEDING SYSTEM AND SEED PRODUCTION

This study confirmed our hypothesis, at least at our study site, that *C. lanceolata* in the introduced range of Japan is self-incompatible and relies solely on pollinators for seed production. This result is similar to that of a previous study in the native range of the United States and the introduced range of China, in which *C. lanceolata* was not capable of self-pollination and relied on pollen transfer agents (Banovetz & Scheiner 1994b; Zeng et al. 2021). This implies that the self-incompatibility system did not evolve when the plant was established or during colonization in

Japan. Ultimately, the results of our open pollination treatment suggested that *C. lanceolata* did not suffer from pollination failure, wherein the seed set was approximately 30%, and the mean number of seeds produced per capitulum was  $60.7 \pm 35.8$  seeds ( $N = 26$ ). This result is not different from that reported in the Kiso River, Japan (Hatase et al. 2007) and Jianxi Province, China (Zeng et al. 2021); the mean seed production was  $98.0 \pm 27.8$  and  $120.1 \pm 11.2$ , respectively. However, the result of the present study is about 1.5 times higher than those previously reported in the native range (Banovetz & Scheiner 1994a), wherein the mean seed production ranges from  $41.4 \pm 3.3$  to  $50.8 \pm 2.6$ . This difference could be linked to various complex climatic and edaphic factors (e.g., the physical, chemical, and biological properties of soils) in the native and introduced ranges (Coffin & Lauenroth 1992; Mencuccini et al. 1995; Pearse et al. 2017).

#### CONCLUSIONS

This study revealed that seed production of *C. lanceolata* in its introduced range in Japan is entirely dependent on pollinators. The plant species of *C. lanceolata* exhibited a generalized pollination system, in which pollinator assemblages were comprised of a wide variety of insects from the local community, ensuring successful dispersal through diverse mating opportunities with various pollinators. The present study has provided preliminary evidence that *C. lanceolata* exhibits some trend of functional specialization towards halictid bees. In addition, diurnal floral scent emissions were characterized by significant concentrations of sesquiterpene and monoterpene compounds, which are common in other plant species with generalized pollination systems. Furthermore, some specific compounds were emitted that are also commonly emitted in other plant species pollinated by halictid bees.

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#### DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

#### DATA AVAILABILITY STATEMENT

The data used to write this article are available as appendices.

#### APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix 1. List and distribution of floral visitors of *Coreopsis lanceolata*.

Appendix 2. List of previous studies recording floral visitors of the genus *Coreopsis*.

Appendix 3. A comparison of floral morphology between the Tsubaki Bora population in Japan during the 2021 flowering season ( $N = 22$ ) and the Jiangxi population in China during the 2018 flowering season ( $N = 30$ ).

Appendix 4. Composition of floral visitors of *Verbena brassiliensis* ( $N = 26$ ,  $N$  refers to the total number of collected specimens) and *Erigeron annuus* ( $N = 30$ ), the co-flowering species nearby *Coreopsis lanceolata* in Kami Minami Gata population.

Appendix 5. *Apis mellifera* visited the co-flowering species nearby *Coreopsis lanceolata* such as (a) *Verbena brassiliensis*; (b) *Erigeron annuus*; (c) *Trifolium repens*.

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