Overwintering, cold tolerance and supercooling capacity comparison between *Liriomyza sativae* and *L. trifolii*, two invasive leafminers in China

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**Abstract**

*Liriomyza sativae* Blanchard and *Liriomyza trifolii* (Burgess) are two highly polyphagous pests that successively invaded China in the 1990s and 2000s, respectively, threatening vegetable and horticultural plants. Competitive displacement of *L. sativae* by *L. trifolii* occurred during the expansion process of the latter in southern China, while whether *L. trifolii* can expand their range to northern China remains unclear. Overwintering and cold tolerance capacity largely determine the species distribution range and can affect species displacement through overwintering and phenology. In this study, we compared the overwintering potential, cold tolerance and supercooling point (SCP) between these two leafminer species. Our results showed that *L. trifolii* can overwinter at higher altitudes than *L. sativae*. In addition, we found that they can both successfully overwinter in greenhouses in northern China, and the overwintering capacity of *L. trifolii* was higher than that of *L. sativae*. Moreover, the extreme low-temperature survival of *L. trifolii* was significantly higher than that of *L. sativae*, and the SCP of the former was lower than that of the latter. We thus conclude that the overwintering and cold tolerance capacity of *L. trifolii* is much better than that of *L. sativae*. Our findings indicate that *L. trifolii* has the potential to displace *L. sativae* and expand its range to northern China. Moreover, our results have important implications for predicting overwinter ranges and developing management strategies for invasive leafminers in China.

**Keywords** *Liriomyza* · Overwintering potential · Cold resistance · Distribution pattern · Species displacement

**Key message**

- Overwintering boundary of *L. trifolii* and *L. sativae* was 36.4° and 35.4°N, respectively.
- Overwintering capacity of *L. trifolii* was higher than that of *L. sativae*.
- The extreme low-temperature survival of *L. trifolii* was higher than that of *L. sativae*.
- The supercooling point of *L. trifolii* was lower than that of *L. sativae*.
- These advantages of *L. trifolii* would contribute to their range expanding and enhance their competitive displacement over *L. sativae*.

**Introduction**

Invasive alien species seriously threaten agricultural and natural ecosystems worldwide (Early et al. 2016; Han et al. 2019; Milosavljević et al. 2019; Rota-Stabelli et al. 2020; Zeng et al. 2020; Gugliuzzo et al. 2021). *Liriomyza sativae* and *L. trifolii* are among the most economically important invasive leafminers damaging a wide range of vegetable and ornamental plants (Kang et al. 2009). They both originated on American continents and have become cosmopolitan pests due to international global trade since...
the 1960s (Gao et al. 2017a). In China, L. sativae was first detected on Hainan Island in 1994, and L. trifolii was first detected in Guangdong Province in 2005 (Wen et al. 1996; Lei et al. 2007). Liriomyza sativae and L. trifolii are two very closely related species that have similar morphology and can even have hybrid offspring (Sakamaki et al. 2005; Tokumaru and Abe 2005). In addition, their host plant ranges are similar, and they share similar ecological niches in the same host plant (Xing et al. 2017). Therefore, plant ranges are similar, and they share similar ecological very closely related species that have similar morphol-

Lei et al. 2007).

detected in Guangdong Province in 2005 (Wen et al. 1996; detected on Hainan Island in 1994, and L. sativae was first
the 1960s (Gao et al. 2017a). In China, L. trifolii could overcome L. sativae when they invaded Hainan and Guangdong Prov-

inces (Gao et al. 2014). Whether L. trifolii can overcome L. sativae and expand its distribution to higher altitudes in northern China has still not been studied.

Climatic tolerances, including thermal tolerances, largely determine species ranges and can affect competitive displacement among insects (Kang et al. 2009; Reize and Trumble 2002). In addition, interacting species often differ in their thermal tolerances; for instance, a higher extreme high-temperature tolerance of L. trifolii over L. sativae was found in laboratory populations (Wang et al. 2014). In addition, the prerequisite for insects to establish in a new area is that adequate individuals can survive in low-temperature winter periods (Bale 1996; Huang et al. 2020; Li et al. 2021). Therefore, the low temperatures during winter in newly invaded areas were assumed to be able to prevent the establishment of invasive species (Kahrer et al. 2019). Consequently, low-temperature survival and overwintering ability largely determine the geographical distribution of invasive species. Low-temperature adapt-

ability can also affect competitive displacement between invasive and local insect species through temporal and phenological differences (Gao et al. 2017b).

Liriomyza sativae and L. huidobrensis, which both invaded China in the 1990s, were found to be largely differ-
in their cold tolerances, which thus resulted in their specific geographic and overwinter ranges (Kang et al. 2009). They can survive above 0 °C for long-term exposure but can survive for several minutes to several days below 0 °C, and the low-temperature survival of L. sativae is lower than that of L. huidobrensis (Chen and Kang 2002, 2005). Moreover, the supercooling point (SCP) of L. huidobrensis was significantly lower than that of L. sativae (Chen and Kang 2004, 2005). Consequently, the distinct range distributions of L. sativae and L. huidobrensis were formed during their invasion and expansion in China (Kang et al. 2009). Liriomyza trifolii emerged and damaged earlier than L. sativae in the upcoming year after winter (Chang et al. 2016). No research was available for their cold tolerance and overwinter abilities (Gao et al. 2011; Abe 2017).

We want to address two questions in this study: (1) Does the latter invasive L. trifolii have overwintering advantages over the previously invasive L. sativae? (2) What is the cold tolerance differences between them? We used L. sativae and L. trifolii pupae to answer these questions because they usually overwinter in the puparial stage (Parrella 1987). To examine their overwintering potential, we first conducted overwinter experiments at 16 local sites along latitude gra-
dients. The greenhouse and field overwinter potentials of L. sativae and L. trifolii were also compared in northern China. To compare their cold tolerances, their survival rates under different extremly low temperatures (5, 0, –10, –20 °C) at different exposure durations were estimated in the laboratory. In addition, the SCP of L. sativae and L. trifolii was determined.

Materials and methods

Insect rearing and pupae preparation

Populations of L. trifolii and L. sativae were collected from field vegetable plants in Sanya, Hainan Province, China (18°14′52″N; 109°30′29″E). They were subsequently cul-
tured on kidney bean plants (Phaseolus vulgaris L.) at 26 ± 1 °C, humidity at 75% with a 14:10 light: dark photo-
to-period. The two species were reared for more than 3 genera-
tions to ensure the homogeneity of each population before the two species were used in the experiments.

We used pupae to investigate the overwinter potential and cold tolerance of these two leafminer species. One-day-old pupae were used in the following experiments because this stage was developmentally mature and most sensitive to thermal stress (Parrella 1987; Zhao and Kang 2000).

Overwintering capacity along latitudinal gradients

To determine the overwintering capacity and overwintering boundary of the two leafminer species in China, we con-
ducted overwintering experiments from November 2019 to April 2020 at 16 locations spanning 7 degrees of latitude from 30.23° to 37.43°N in Central and North China (Fig. 1, Table S1). We used a specialized bottle (Fig. 2) to perform the overwintering experiments: we put the bottles into the topsoil (ca. 2 cm in depth) (Fig. 2) of each location (Linden 1993). We also put shelters on each bottle to keep out rain-
water, snow and predators. Each bottle contained 100 pupae and was treated as one replicate. Each location was repli-
cated 5 times. We started the experiments in the northernmost location (Dezhou, Shandong Province) in early Novem-
ber 2019 and ended in the southernmost location (Ningbo, Zhejiang Province) in late November 2019. In April 2020, we collected pupae from north to south and placed them into
a climate chamber at 26 ± 1 °C and humidity: 75% with a 14:10 light: dark photoperiod. We checked the survival rate of each replicate by observing adult emergence (including emerged leafminer flies in the field).

**Overwintering capacity in common garden experiments**

To compare the overwintering ability of the two species in northern China, we carried out common garden experiments under greenhouse and field conditions at the

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**Fig. 1** Schematic diagram of locations of overwinter experiments along latitudinal gradient

**Fig. 2** Schematic diagram of overwintering experiments
Langfang Experimental Station, Institute of Plant Protection (IPP), Chinese Academy of Agricultural Science (CAAS) (39°30′38″N; 116°36′2″E). We put bottles (Fig. 2) into the topsoil (ca. 2 cm in depth) of experimental fields and greenhouses (Linden 1993). Each bottle contained 100 pupae and was treated as one replicate. We started the experiments at late December 2019. We collected the pupae of each replicate in fields and greenhouses every 10 days, and we ended the experiments after 100 days of exposure (early April 2020). Survival rate of each sampling was checked in laboratory. The combination of each species and duration of exposure was considered one treatment. Each treatment was replicated 5 times.

**Cold tolerance capacity**

To determine the cold tolerance capacities of the two leafminer species, their pupae were exposed to 5 °C and 0 °C for 1, 2, 3, 4, 5 and 6 days and exposed to −10 °C and −20 °C for 10, 20, 30, 40, 50 and 60 min. We considered the combination of each temperature and duration of exposure as one treatment. There were 5 replicates of each treatment, and each replicate contained 100 pupae. We checked the survival rate of each treatment by observing adult emergence under laboratory conditions.

**Supercooling point determination**

The supercooling points (SCPs) of the pupae of the two leafminer species were determined following the method described by Zhao and Kang (2000). We used a thermocouple (Testo, model 177-T4, Germany) to determine their SCPs. The individuals of the two species were fixed to the end of the sensor (nickel worm) of the thermocouple by white petrolatum. Individuals were cooled at a rate of 0.5 °C per minute in a programmable refrigerated test chamber. Any decrease in the temperature was recorded. The SCPs were defined as the lowest temperature before an exothermic reaction, as indicated by a sudden temperature increase. Each species was tested for 50 pupae. The SCP data were read using Comsoft3 Software.

**Statistical analysis**

We fitted a linear mixed model (LMM) with the lme function from the lme4 package (Bates et al. 2015) to compare the survival rate of overwintering pupae in the field and common garden experiments. To evaluate the overwintering capacity along latitudinal gradients, we fitted a linear mixed model with the survival rate as the response variable, species as a fixed factor and duration of exposure as a random factor. In addition, we fitted linear mixed models with the survival rate as the response variable and latitude as the explanatory variable. To evaluate their cold tolerance capacities, we fitted linear mixed models with the survival rate as the response variable, species as a fixed factor and duration of exposure as a random factor. All linear mixed model results were summarized with ANOVA. The SCP data were read using Comsoft3 Software. The independent-sample Student’s t-test was used for comparison of SCPs and for comparison of the survival rate of each experiment between *L. trifolii* and *L. sativae*.

All statistical analyses were conducted using R (version 3.6.3). We performed a normality test and residual test for all linear mixed models in R (package ‘DHARMa’, Hartig 2019). The results showed that all the data met the conditions for fitting the models. We also checked the SCP data for normality and equality of variances prior to statistical analysis.

**Results**

**Overwintering capacity along latitudinal gradients**

The overwintering survival of *L. trifolii* pupae was significantly higher than that of *L. sativae* pupae (*F* = 51.704, *P* < 0.001; Fig. 3a). The pupae of both species showed the same types of latitudinal patterns between ranges, as their overwintering survival decreased linearly with increasing latitude (*L. trifolii*: survival rate = −5.98 + 220.61 * lat, *R*² = 0.7453; *L. sativae*: survival rate = −4.15 + 150.70 * lat, *R*² = 0.7323) (Fig. 3b). The *L. trifolii* pupae successfully overwintered at 36.4°N, while *L. sativae* pupae successfully overwintered at 35.4°N (Fig. 3b).

**Overwintering potential in common garden experiments**

In the field, we found that the pupae of both *L. trifolii* and *L. sativae* did not successfully overwinter, but they showed different survival rates for different exposure durations (*F* = 16.101, *P* < 0.001). The survival rate of *L. trifolii* pupae was significantly higher than that of *L. sativae* pupae when the exposure durations were 30 (*L. trifolii*, 7.2 ± 1.16%; *L. sativae*, 2.0 ± 0.55%), 40 (*L. trifolii*, 8.0 ± 1.92%; *L. sativae*, 0%), 50 (*L. trifolii*, 2.4 ± 0.93%; *L. sativae*, 0%) and 60 (*L. trifolii*, 2.2 ± 0.86%; *L. sativae*, 0%) days (Fig. 4a).

In the greenhouse, we found that the pupae of both *L. trifolii* and *L. sativae* could successfully overwinter; however, the overwintering survival of *L. trifolii* pupae was significantly higher than that of *L. sativae* pupae (*L. trifolii*, 39.2 ± 3.61%; *L. sativae*, 9.6 ± 1.03%; *F* = 342.14, *P* < 0.001).
The survival rate of *L. trifolii* pupae was significantly higher than that of *L. sativae* pupae when the exposure durations were 20 (*L. trifolii*, 44.8 ± 2.04%; *L. sativae*, 27.8 ± 2.06%), 30 (*L. trifolii*, 45.4 ± 3.03%; *L. sativae*, 25.0 ± 3.05%), 40 (*L. trifolii*, 40.2 ± 3.61%; *L. sativae*, 12.4 ± 2.06%), 50 (*L. trifolii*, 40.6 ± 2.66%; *L. sativae*, 14.4 ± 2.91%), 60 (*L. trifolii*, 40.0 ± 2.83%; *L. sativae*, 11.8 ± 1.56%), 70 (*L. trifolii*, 38.0 ± 2.43%; *L. sativae*, 11.6 ± 1.72%), 80 (*L. trifolii*, 38.4 ± 1.44%; *L. sativae*, 12.4 ± 2.50%), 90 (*L. trifolii*, 37.6 ± 1.72%; *L. sativae*, 10.8 ± 1.36%) and 100 (*L. trifolii*, 39.2 ± 3.61%; *L. sativae*, 9.6 ± 1.03%) days (Fig. 4b).

**Cold tolerance capacity**

Extreme low-temperature survival results showed that when exposed to 5 °C for different durations, no significant differences were found between the survival rates of *L. trifolii* pupae and *L. sativae* pupae (*F* = 0.1339, *P* = 0.7083; Fig. 5a). Nonetheless, when they were exposed to 0, -10 and -20 °C, the survival rate of *L. trifolii* pupae was significantly higher than that of *L. sativae* pupae at different exposure durations (0 °C: *F* = 177.82, *P* < 0.001; - 10 °C: *F* = 87.5, *P* < 0.001; - 20 °C: *F* = 69.646, *P* < 0.001) (Fig. 5b-d). The pupae of both species did survive more than 6 days at 5 °C (Fig. 5a). The *L. sativae* pupae did not survive when they were exposed to 0 °C for more than 4 days, while *L. trifolii* pupae survived at 0 °C for more than 6 days (Fig. 5b). The survival rate of *L. trifolii* pupae was significantly higher than that of *L. sativae* pupae when the exposure duration was more than 30 min at -10 °C (Fig. 5c). The *L. trifolii* pupae can survive at -20 °C for more than 40 min, while for *L. sativae* pupae, the survival rate is lower than 10% when exposed to -20 °C for 30 min (Fig. 5d).

**Supercooling point**

The SCP of *L. trifolii* was significantly lower than that of *L. sativae* (*t* = 32.172, *P* < 0.001; Fig. 6). The mean
SCP of *L. trifolii* was $-22.56 \pm 0.24 \, ^\circ C$ (ranging from $-17.10$ to $-25.16 \, ^\circ C$). The mean SCP of *L. sativae* was $-11.79 \pm 0.22 \, ^\circ C$ (ranging from $-9.20$ to $-18.09 \, ^\circ C$).

**Discussion**

Climatic stresses, including overwintering and cold tolerance capacity, largely determine the species distribution of leafminers (Chen and Kang 2005; Kang et al. 2009; Kirichenko et al. 2019; de Campos et al. 2021). *Liriomyza sativae* and *L. trifolii* are two devastating leafminers that invaded China in the 1990s and 2000s, respectively (Gao et al. 2015; Xing et al. 2017). *Liriomyza sativae* are now distributed in most provinces of China, while *L. trifolii* is found in only 10 provinces (Gao et al. 2017a). Interestingly, in contrast with their distribution ranges, we found that the overwintering potential and cold tolerance capacities of *L. trifolii* were both higher than those of *L. sativae*.

*Liriomyza trifolii* was reported to be able to overwinter safely in the field of Maryland (39°N), USA (Larew et al. 1986); however, we found here that only 2% *L. trifolii* pupae can successfully overwinter at 36.4°N in China. For *L. sativae*, it was proposed that they could not overwinter outside as far north as latitude 34°N in China (Zhao and Kang 2000). Here, we found that 2.4% of *L. sativae* pupae can successfully overwinter at 35.4°N. Prior work has suggested that many species are likely to move poleward in latitude as warming starts (Jepsen, et al. 2008; Estay et al. 2009;
Although leafminers cannot overwinter in the fields of northern China, they may overwinter in greenhouses that are widespread at higher latitudes (Chen and Kang 2005). We tested this hypothesis at Hebei, China (39.5°N). The results showed that the two leafminers can both overwinter in the greenhouse at the experimental site, but they cannot overwinter in the field (Fig. 4). In addition, the survival rate of overwintering pupae of *L. trifolii* was significantly higher than that of *L. sativae* in the greenhouse, indicating that the former is likely to possess larger overwintering populations in the upcoming year. This result was consistent with a previous report that *L. trifolii* emerged earlier than *L. sativae* in spring in Jiangsu Province, China (Chang et al. 2016).

Cold tolerance largely determines the overwintering capacities of leafminers (Chen and Kang 2005). Here, we found that the low-temperature tolerance of *L. trifolii* was higher than that of *L. sativae* (Fig. 5). Leafminers are freeze susceptible or freeze avoiding, and they can tolerate sub-zero temperatures by supercooling (Bale 1996; Chen and Kang 2002). In addition, the SCPs of leafminer pupae have been reported as an index of cold tolerance (Zhao and Kang 2000). Our results showed that the SCP of *L. trifolii* pupae (−22.56 °C) was significantly lower than that of *L. sativae* (−11.79 °C), indicating a lower crystallization temperature for *L. trifolii* pupae. The geographical distribution differences between leafminers were related to their distinct cold resistance abilities (Chen and Kang 2002; Kang et al. 2009). Accordingly, the higher cold tolerance abilities of *L. trifolii* over *L. sativae* would contribute advantages to the former in species abundance, distribution range and competitive interaction when they experienced low temperatures.

In contrast with the overwintering and cold tolerance advantages of *L. trifolii*, the distribution range of *L. trifolii* was obviously smaller than that of *L. sativae* according to our previous investigations (Gao et al. 2017). We considered that biotic resistance to species invasion and expansion could explain this contradictory phenomenon. The invasion and expansion of *L. sativae* occurred earlier than that of *L. trifolii* by more than 10 years (Gao et al. 2015). Given that *L. sativae* and *L. trifolii* share similar host plants and ecological niches (Xing et al. 2017), *L. trifolii* should compete and displace *L. sativae* during their invasion and expansion. Although *L. trifolii* has many competitive advantages over *L. sativae*, the displacement of *L. sativae* by *L. trifolii* was difficult and even reversed (Wang et al. 2014; Gao et al. 2015; Gao et al. 2017; Xing et al. 2017). In conclusion, we compared the overwintering ability and cold tolerance of two successively invasive leafminers in China in this study. Our results suggested that the overwintering and cold tolerance capacities of *L. trifolii* were both higher than that of *L. sativae*, which implies that *L. trifolii* has the potential to displace *L. sativae* and colonize higher latitude regions in China. Thus, this study provides information for predicting the distribution patterns of the two widespread invasive leafminers in China. Moreover, knowledge of the cold hardiness and overwintering regions of *L. trifolii* and *L. sativae* can help develop management strategies for them. Future studies should clarify the discrepancy between their cold tolerance and current distribution pattern through common garden experiments and long-term field monitoring of their population dynamics. In addition, the underlying metabolic and molecular mechanism involved in this phenomenon needs to be further investigated.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10340-021-01420-0.

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Author contributions ZX and ZL designed the research. QZ and ZX conducted experiments. QZ, ZX, SW, and HW analyzed data. QZ and ZX wrote the manuscript. All authors read and approved the manuscript.

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Declarations

Conflict of interest There is no conflict of interests.

References

Abe Y (2017) Invasion of Japan by exotic leafminers *Liriomyza spp.* (Diptera: Agromyzidae) and its consequences. Appl Entomol Zool 52:175–182. https://doi.org/10.1007/s13355-017-0486-z

Bale JS (1996) Insect hardiness: a matter of life and death. Eur J Entomol 93:369–382. https://doi.org/10.1007/BF02765804

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Chang Y, Shen Y, Dong CS, Geng WR, Tian ZH, Du YZ (2016) Population dynamics of *Liriomyza trifolii* and *Liriomyza sativae* in Jiangsu. Chin J Appl Entomol 53:884–891

Chen B, Kang L (2002) Cold hardiness and supercooling capacity for *Liriomyza huidobrensis* (Diptera: Agromyzidae) along latitudinal gradients. Environ Entomol 33:155–164. https://doi.org/10.1603/0046-225X-33.2.155

Chen B, Kang L (2004) Variation in cold hardiness of *Liriomyza sativae* pupae. In: Abou-Khaled M, Sibbald M (eds) Cold hardiness, supercooling and life cycle of arthropods. Kluwer Academic, Dordrecht, pp 297–305

Chen B, Kang L (2005) Variation in cold hardiness of *Liriomyza sativae* pupae. In: Abou-Khaled M, Sibbald M (eds) Cold hardiness, supercooling and life cycle of arthropods. Kluwer Academic, Dordrecht, pp 297–305

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Bale JS (1996) Insect hardiness: a matter of life and death. Eur J Entomol 93:369–382. https://doi.org/10.1007/BF02765804

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Chang Y, Shen Y, Dong CS, Geng WR, Tian ZH, Du YZ (2016) Population dynamics of *Liriomyza trifolii* and *Liriomyza sativae* in Jiangsu. Chin J Appl Entomol 53:884–891

Chen B, Kang L (2002) Cold hardiness and supercooling capacity for *Liriomyza huidobrensis* (Diptera: Agromyzidae) along latitudinal gradients. Environ Entomol 33:155–164. https://doi.org/10.1603/0046-225X-33.2.155

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Chen B, Kang L (2005) Implication of pupal cold tolerance for the northern over-wintering range limit of the leafminer *Liriomyza sativae* (Diptera: Agromyzidae) in China. Appl Entomol Zool 40:437–446. https://doi.org/10.1303/aer.2005.437

De Campos MR, Béarez P, Amiens-Denexue E et al (2021) Thermal biology of *Tuta absoluta*: demographic parameters and facultative diapause. J Pest Sci 94:829–842. https://doi.org/10.1007/s10071-020-01286-8

Early R, Bradley BA, Dukes JS et al (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Commun 7:1–9. https://doi.org/10.1038/ncomms12485

Estay SA, Lima M, Labra FA (2009) Predicting insect pest status under climate change scenarios: combining experimental data and population dynamics modelling. J Appl Entomol 133:491–499. https://doi.org/10.1111/j.1439-0418.2008.01380.x

Gao YL, Reitz SR (2017b) Emerging themes in our understanding of species displacements. Annu Rev Entomol 62:165–183. https://doi.org/10.1146/annurev-ento-031616-035425

Gao YL, Lei ZR, Abe Y, Reitz SR (2011) Species displacements are toward the sustainable management of invasive alien species in the twenty-first century and national response capacities. Nat Commun 7:1–9. https://doi.org/10.1038/ncomms12485

Hartig F (2019) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.3. https://CRAN.R-project.org/package=DHARMa

Huang YR, Dong YY, Huang WJ et al (2020) Overwintering distribution of the leafminer fly *Liriomyza trifolii* in subarctic birch forest: evidence of a recent outbreak. J Appl Entomol 133:491–499. https://doi.org/10.1111/j.1439-0418.2008.01380.x

Kang L, Chen B, Wei JN, Liu TX (2009) Roles of thermal adaptation and chemical ecology in *Liriomyza* distribution and control. Annu Rev Entomol 54:127–145. https://doi.org/10.1146/annurev.ento.54.110807.090507

Kirichenko N, Augustin S, Kenis M (2019) Invasive leafminers on woody plants: a global review of pathways, impact, and management. J Pest Sci 92:93–106. https://doi.org/10.1007/s10071-018-1009-6

Larew HG, Knodel-Montz JJ, Poe SL (1986) *Liriomyza trifolii* (Burges) (Diptera: Agromyzidae) overwinters outdoors in Maryland. Proc Entomol Soc Wash 88:189

Lei ZR, Zhu CJ, Zhang CQ (2007) Risk analysis of invasive *Liriomyza trifolii* (Burges) in China. Plant Prot 33:37–41. https://doi.org/10.3969/j.issn.0529-1542.2007.01.010

Li XW, Li D, Zhang ZJ et al (2021) Supercooling capacity and cold tolerance of the South American tomato pinworm, *Tuta absoluta*, a newly invaded pest in China. J Pest Sci 94:845–858. https://doi.org/10.1007/s10340-020-01301-y

Linden A (1993) Overwintering of *Liriomyza bryoniae* and *Liriomyza huidobrensis* (Diptera: Agromyzidae) in the Netherlands. Proc Exp Appl Entomol 4:145–150

Milosavljević I, El-shafie HAF, Faleiro JR, Hoddle CD, Lewis M, Hoddle MS (2019) Palingmeddon: the wasting of ornamental palms by invasive palm weevils, *Rhynchophorus sp.*, J Pest Sci 92:143–156. https://doi.org/10.1007/s10340-018-1044-3

Parrella MP (1987) Biology of *Liriomyza*. Annu Rev Entomol 32:201–224. https://doi.org/10.1146/annurev.en.32.010187.001221

Reitz SR, Trumble JT (2002) Competitive displacement among insects and arachnids. Annu Rev Entomol 47:435–465. https://doi.org/10.1146/annurev.en.47.091201.145227

Rota-Stabelli O, Ometto L, Tait G et al (2020) Distinct genotypes and phenotypes in European and American strains of *Drosophila suzukii*: implications for biology and management of an invasive organism. J Pest Sci 93:77–89. https://doi.org/10.1007/s10340-019-01172-y

Sakamaki M, Miura K, Chi YC (2005) Interspecific hybridization between *Liriomyza trifolii* and *Liriomyza sativae*. Ann Entomol Soc Am 98:470–474. https://doi.org/10.1603/0013-8746(2005)098[0470:IHBLTA]2.0.CO;2

Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian niche through a century of climate change. Proc Natl Acad Sci 106:19637–19643. https://doi.org/10.1073/pnas.0901562106

Tokumaru S, Abe Y (2005) Interspecific hybridization between *Liriomyza sativae* Blanchard and *L. trifolii* (Burges) (Diptera: Agromyzidae). Appl Entomol Zool 40:551–555. https://doi.org/10.1097/WNR.0b013e32832ea601

Wang HH, Reitz SR, Xiang JC, Smagge G, Lei ZR (2014) Does temperature-mediated reproductive success drive the direction of species displacement in two invasive species of leafminer fly? PLoS ONE 9:e98761. https://doi.org/10.1371/journal.pone.0098761

Zeng J, Liu YQ, Zhang HW, Liu J, Jiang YY, Wyckhuys KA, Wu KM (2009) The management of the leafminer *Tuta absoluta* (Diptera: Agromyzidae) in China. Entomotaxonomia 18:311–312

Xing ZL, Zhang LY, Wu SY, Yi H, Gao YL, Lei ZR (2017) Niche comparison among two invasive leafminer species and their parasitoid *Opius biroi*: implications for competitive displacement. Sci Rep 7:1–6. https://doi.org/10.1038/s41598-017-04562-3

Zeng J, Liu YQ, Zhang HW, Liu J, Jiang YY, Wyckhuys K, Wu KM (2020) Global warming modifies long-distance migration of an agricultural insect pest. J Pest Sci 93:569–581. https://doi.org/10.1007/s10340-019-01187-5

Zhou X, Kang L (2000) Cold tolerance of the leafminer *Liriomyza sativae* (Dipter, Agromyzidae). J Appl Entomol 124:185–189. https://doi.org/10.1046/j.1365-2656.2000.00463.x

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