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Profile

Ganaspis kimorum (Hymenoptera: Figitidae), a promising parasitoid for biological control of *Drosophila suzukii* (Diptera: Drosophilidae)

Judith M. Stahl[1,2,*], Xingeng Wang[3], Paul K. Abram[4], Antonio Biondi[5], Matthew L. Buffington[6], Kim A. Hoelmer[3], Marc Kenis[7], Fabrizio Lisi[1,5], Marco Valerio Rossi-Stacconi[8], M. Lukas Seehausen[7], Ariane Vossen[4,9], Warren H. L. Wong[4,10], Kent M. Daane[1]

[1]Department of Environmental Science, Policy, & Management, University of California Berkeley, Berkeley, CA, USA, [2]Health & Biosecurity, CSIRO, Canberra, Australian Capital Territory, Australia, [3]Beneficial Insects Introduction Research Unit, Agricultural Research Service, United States Department of Agriculture, Newark, DE, USA, [4]Department of Entomology, Agriculture and Agri-Food Canada, Agassiz Research & Development Centre, Agassiz, British Columbia, Canada, [5]Department of Agriculture, Food and Environment, University of Catania, Catania, Sicily, Italy, [6]Systemic Entomology Laboratory, Agricultural Research Service, United States Department of Agriculture, Washington, DC, USA, [7]Risk Analysis and Invasion Ecology, CABI, Delémont, Jura, Switzerland, [8]Plant Protection, Edmund Mach Foundation—Research & Innovation Center, San Michele All'adige, Trentino, Italy, [9]Department of Biological Sciences, University Montreal, Montreal, Quebec, Canada, [10]Faculty of Land and Food Systems, The University of British Columbia, Vancouver, British Columbia, Canada [*]Corresponding author, email: Judith.Stahl@csiro.au

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Ganaspis Foerster includes several cryptic species that are important larval parasitoids of the invasive pest *Drosophila suzukii* (Matsumura), spotted-wing drosophila (SWD). *Drosophila suzukii*, native to Asia, was first discovered in 2008 in North America and Europe, becoming a devastating pest of soft-skinned fruit crops. Biological control could be among the safest, most environmentally benign, and cost-effective methods for long-term and landscape-level management of this invasive pest. Foreign exploration in East Asia discovered several major larval *D. suzukii* parasitoids. One of them was initially described as *Ganaspis brasiliensis* (Ihering) and consisted of 2 major genetic groups (G1 and G3). The groups are now recognized as 2 different species, *Ganaspis kimorum* Buffington and *Ganaspis lupini* Buffington. The more host-specific species *G. kimorum* was selected and approved for field release in the United States in 2021 and has been widely released since 2022. Here, we provide a comprehensive overview of the parasitoid's taxonomy, current known distribution, biology, ecology, mass-rearing methods, and biological control potential.

Key words: classical biological control, spotted-wing drosophila, soft fruit, invasive insect pest

Eucoilinae (Hymenoptera: Figitidae) are a worldwide group of parasitoid wasps whose hosts appear to be restricted to muscomorph Diptera (Buffington et al. 2020). Among the roughly 80 genera are nearly 1,000 described species. The genus *Ganaspis* Foerster, described in 1869, has remained a "dumping ground" for many eucoiline species. As a result, of the 69 species currently assigned to the genus, only 24 are "probably" *Ganaspis* (Sosa-Calvo et al. 2024). Phylogenetically and morphologically, *Ganaspis kimorum* Buffington is one of the "actual" *Ganaspis*. However, that species went by the name "*Ganaspis brasiliensis* (Ihering) G1," with "G1" referring to its genetic group, since Nomano et al. (2017) demonstrated *G. brasiliensis* appeared to be composed of numerous genetic groups (also sometimes referred to as "lineages") or potentially cryptic species.

Several lines of evidence pointed toward *G. brasiliensis* G1 (now *G. kimorum*) and the related G3 (now *Ganaspis lupini* Buffington) being distinct species: behavioral experiments in the laboratory observed a difference in host range (Girod et al. 2018a, Seehausen et al. 2020) and mating incompatibilities (Seehausen et al. 2020, Hopper et al. 2024) while different populations of *G. brasiliensis* G1 were reproductively compatible (Stahl et al., submitted). Reeve and Seehausen (2019) initially provided evidence of protein differentiation between G1 and G3 of *G. brasiliensis*, providing some of the most compelling data that these 2 populations were in fact different species. Hopper et al. (2024) took this a major step forward, and sequenced entire genomes for G1 and G3 (now *G. kimorum* and *G. lupini*, respectively) populations from Asia and Canada. This project reported just over 1 billion base pairs per genome; G1 (*G. kimorum*) had around 60k genes, and G3 (*G. lupini*) had about 70k genes. Comparing these genomes, it is clear that although these 2 species are morphologically nearly indistinguishable, they had only 70–77% similarity in mapped assembly reads between lineages and 90–98% within lineages. These data are remarkable as some of these wasps were taken from sympatric localities in China. Furthermore, these data included representatives of the adventive population of *G. kimorum* in British Columbia, which was shown to be most closely related to *G. kimorum* from Japan (Tokyo) (Hopper et al. 2024).

Sosa-Calvo et al. (2024) provided more evidence of monophyly, as well as summarizing the biological and morphological evidence to date, concluding G1 in fact warranted species status, naming it *G. kimorum*, and named the related G3 *G. lupini*. This species recognition is important for scientific communication. In this specific case, *G. kimorum* has the high degree of host specificity required for use in classical biological control of *Drosophila suzukii* (Matsumura) (spotted-wing drosophila, SWD), and *G. lupini* has a broader host range and so may be less suitable for classical biological control of *D. suzukii*.

G. kimorum (Fig. 1) tends to be 1.5–1.75 mm in length, with no appreciable size difference in gender. Morphologically, *G. kimorum* is identical to *G. lupini*, save for the difference in the ovipositor clip (Sosa-Calvo et al. 2024), which is reduced in *G. kimorum*, and well-developed in *G. lupini*. Abram et al. (2022b) summarize the diagnostic differences among all the major parasitoids in the SWD system. The species most easily confused with *G. kimorum* would be *Leptopilina japonica* Novkovic & Kimura and *L. heterotoma* (Thomson) (Hymenoptera: Figitidae). These species can be separated by the morphology of the scutellum, as well as several other characteristics, and will be featured in an updated diagnostic study (P. K. A. and M. L. B., in prep). Species identification is best done, initially, by comparing barcode data with that of the Sosa-Calvo et al. (2024) study. Consulting the database of DNA sequence data for parasitoids of Drosophilidae developed by Lue et al. (2021), and the use of the diagnostic polymerase chain reaction primers developed by Gariepy et al. (2024), are also useful pathways to accurate identification.

Fig. 1. *Ganaspis kimorum* female grooming itself on a blueberry.

Distribution

Surveys for *D. suzukii* parasitoids in Asia have been conducted in China, South Korea, and Japan. In China, surveys focused on the Southwest (Yunnan Province) (Girod et al. 2018a, Giorgini et al. 2019, X. G. W., unpublished data). Northeastern (Jilin and Liaoning Provinces), northern (Beijing), and central (Sichuan and Hubei Provinces) China (Girod et al. 2018b, Wang et al. 2022) have been covered with limited surveys to date. *G. kimorum* was found in Beijing, Sichuan, and many locations in Yunnan, but it has not yet been found in northeast China (Fig. 2A). The surveys in South Korea (Daane et al. 2016, X. G. W., unpublished data) have been conducted widely and *G. kimorum* was recovered in most surveyed areas from the Northeast (Gangwon Province) to the Southwest (South Jeolla Province) (Fig. 2A). In Japan, *G. kimorum* was found from Sendai to Nara (Girod et al. 2018a, Matsuura et al. 2018, Kimura and Mitsui 2020) (Fig. 2A).

G. kimorum is considered a temperate species based on these known distributions. A CLIMEX model predicts that *G. kimorum* can establish in the western, southeastern, and eastern coastal states in North America and most temperate European countries (Wang et al. 2020a). A *G. kimorum* population originating from Tokyo, Japan (Girod et al. 2018b) has been released since 2021 in Italy and 2022 in many states in the United States (Gariepy et al. 2024). Confirming the CLIMEX predictions, *G. kimorum* was released in several Italian locations (Lisi et al. 2022), but evidence of its establishment has been obtained so far only for Northern Italy (Fig. 2B) (Fellin et al. 2023). In addition, adventive populations of this parasitoid have been established in the Pacific Northwest (Fig. 2C) and its range seems to be contiguous between its known USA and Canadian range (Abram et al. 2020, 2022a, Beers et al. 2022). *G. kimorum* was also recovered following its release in Delaware, Georgia, Maryland, Oregon, Pennsylvania, and Washington, USA (Gariepy et al. 2024). The initial recovery in Washington is likely from the spread of the adventive population, which was already known to be present before releases. In East Asia, *G. kimorum* and *G. lupini* are largely sympatric: there are 53 recorded geographical coordinates of both species in East Asia, and both *G. kimorum* and *G. lupini* were recorded from 29 of the 53 sites (Fig. 2A). There are now at least 181 recorded site records of *G. kimorum* worldwide (Fig. 2).

Biology

Hosts

Historic host records of *G. kimorum* are somewhat obscured as these early surveys reported *Ganaspis* collected from *D. suzukii* as *G. brasiliensis* (Kasuya et al. 2013, Daane et al. 2016, Nomano et al. 2017, Giorgini et al. 2019) or *G.* cf. *brasiliensis* (Girod et al. 2018a), and the *G. brasiliensis* complex was only recently clarified, as described above. Most of the known host records for *G. kimorum* and *G. lupini* are based on collections in China, South Korea, and Japan for biological control programs conducted after *D. suzukii* emerged as a serious pest. These surveys reported that *Ganaspis* spp. was reared from *D. suzukii* as well as the closely related and morphologically similar *Drosophila pulchrella* Tan, Hsu, & Sheng and *D. subpulchrella* Takamori and Watabe, which are also characterized with a serrated ovipositor (Takamori et al. 2006). Therefore, emerged *G. kimorum* and *G. lupini* could have attacked *D. suzukii*, *D. pulchrella*, or *D. subpulchrella* in China (Girod et al. 2018a, Giorgini et al. 2019), or *D. subpulchrella* in Japan (Girod et al. 2018a) as the puparia of these species are morphologically similar.

A better description of host use by *G. kimorum* and *G. lupini* may be deduced from recent quarantine studies in Switzerland (Girod et al. 2018a, Seehausen et al. 2020) and California (Giorgini

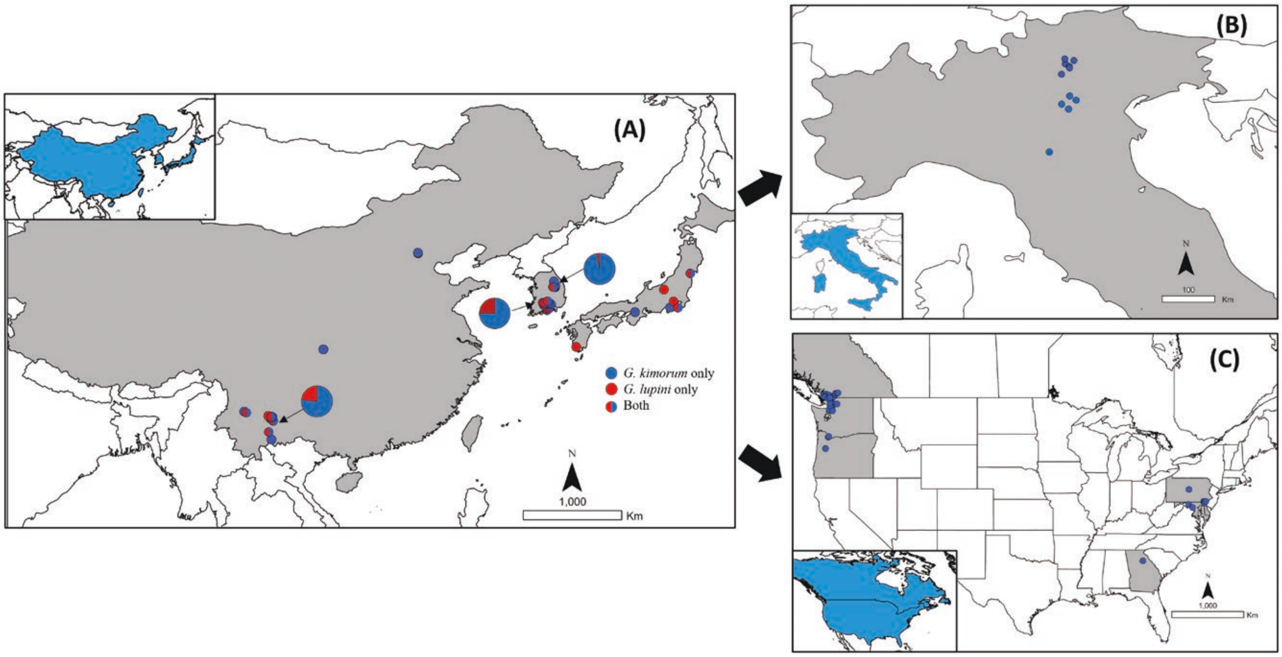

Fig. 2. A) Known distribution of *G. kimorum* and *G. lupini* in native East Asia; B) 3 inserted pie charts indicate the relative abundance of *G. kimorum* and *G. lupini* in Yunnan, China (Giorgini et al. 2019), Southern South Korea (K. M. D., unpublished data) and Central South Korea (X. G. W., unpublished data); as well as *G. kimorum* in introduced and established regions in Northern Italy; and C) adventive establishment of *G. kimorum* in Pacific Northwest and introduced and established regions in eastern North America. Data were combined based on Kasuya et al. 2013, Daane et al. 2016, Nomano et al. 2017, Girod et al. 2018b, Matsuura et al. 2018, Giorgini et al. 2019, Abram et al. 2020, Seehausen et al. 2020, Beers et al. 2022, Abram et al. 2022a, Fellin et al. 2023, Gariepy et al. 2024, K. M. D., unpublished data, and X. G. W., unpublished data.

et al. 2019, Daane et al. 2021). Natural enemy selection for classical biological control programs now emphasizes increased host specificity to reduce risk to non-target species (Heimpel and Cock 2018, Hoddle et al. 2021). Host specificity testing under artificial conditions, common in quarantine studies, tends to represent the fundamental (or physiological) host range rather than the ecological host range (see Onstad and McManus 1996) and, therefore, can overestimate a parasitoid's host range (e.g., Haye et al. 2005). Girod et al. (2018a) used 5 non-target drosophilids and reported a Japanese population of *G.* cf. *brasiliensis* (now considered to be *G. kimorum*) was strictly specific to *D. suzukii*, whereas a population from China (now considered to be *G. lupini*) parasitized *D. melanogaster*, *D. suzukii* and, to a lesser extent, *D. subobscura* Collin. Giorgini et al. (2019) used 9 non-target species and Daane et al. (2021) used 24 non-target species and reported, respectively, that South Korean and Chinese population(s) of *Ganaspis* sp. parasitized *D. melanogaster*, *D. simulans* Sturtevant, and *D. suzukii* and, to a lesser extent, *D. persimilis* Dobzhansky and Epling; molecular examination of voucher specimens later indicated that the Chinese population used was *G. lupini* and the South Korean material was a mixed population of *G. kimorum* and *G. lupini*. With a better understanding of host preference within the *Ganaspis* spp. complex, Seehausen et al. (2020) showed that *G. lupini* readily attacked *D. suzukii*, *D. melanogaster*, and *D. simulans* whereas *G. kimorum* showed a strong preference for *D. suzukii* in fresh undamaged fruit but could, under laboratory conditions, attack *D. melanogaster* as well.

The quarantine host range studies naturally lead to a discussion of the actual ecological host range, with populations of *G. kimorum* clearly more specialized than those of *G. lupini*, and yet both were found sympatric and co-existing on the same host plants inhabited by *D. suzukii* (in South Korea) and by *D. suzukii* and/or *D. pulchrella* or *D. subpulchrella* (in China) (Fig. 2A). Other field evidence includes reports that *G. kimorum* populations in Japan only attacked *D. suzukii*-infested cherries (*Prunus* spp.) in ripening fruit (Nomano et al. 2017, Girod et al. 2018b, Matsuura et al. 2018). In contrast, *G. kimorum* populations from South Korea and (Kunming) China may prefer *D. suzukii* but have a slightly broader host range than the (Tokyo) Japanese material studied by Girod et al. (2018b) and Seehausen et al. (2020). To better understand the ecological host range, Seehausen et al. (2022) conducted a large-arena field cage study with *G. kimorum* (Tokyo) exposed to *D. suzukii* larvae in fresh fruits (blueberries *Vaccinium* sp. [Ericaceae] or elderberries *Sambucus nigra* L. [Adoxaceae]) and *D. melanogaster* in decomposing fruits. Their results show that *G. kimorum* overwhelmingly preferred *D. suzukii* in fresh fruits (15% parasitism) as compared with *D. melanogaster* in decomposing fruits (0.02% parasitism). Finally, field evidence from release efforts in Italy, and from the adventive establishment of *G. kimorum* in the Pacific Northwest, show that *G. kimorum* has thus far been collected exclusively from *D. suzukii* in fresh fruit (Abram et al. 2020, 2022b, Beers et al. 2022, Fellin et al. 2023). This strongly supports the hypothesis that the ecological host range of *G. kimorum* is somewhat exclusive to *D. suzukii* and, while it has the potential to attack other closely related drosophilid species, it will be rare in occurrence and pose little risk to non-target species.

Life Cycle and Reproductive Biology

After locating ripening fruit containing host larvae, adult female *Ganaspis* spp. use their ovipositor to pierce the fruit surface and the host larvae within. First-instar *D. suzukii* larvae are preferred over later instars for oviposition (Wang et al. 2018). *Ganaspis* spp. are solitary, larval koinobiont endoparasitoids: the host is not paralyzed during oviposition and the parasitoid larva feeds inside the host larvae. The host larva continues to grow until it is ultimately killed by the parasitoid larva after the fly larva forms its puparium. For *Ganaspis* sp., it takes 72 h for an egg to start hatching at 22 °C, and another 2–3 days to develop to the second larval instar (Wang et al. 2019). After the host larva forms a puparium, the parasitoid larva continues its development within the protection of the puparium and eventually consumes the entirety of its host. After pupating and completing its pre-imaginal development, the adult *Ganaspis* sp. chews a round opening from the puparium and emerges. *Ganaspis* spp. exhibit protandry with males developing faster than females; for example, development time from egg to adult for males is around 36 days while for females it is around 37 days for *G. kimorum* at 20 °C (L. M. S., unpublished data). Adult female *Ganaspis* sp. have an average of 40 mature eggs in their ovaries upon emergence and begin parasitizing hosts within the first 2 days after eclosion, with the greatest number of host larvae parasitized when the adult female wasps are between 5 and 10 days old (Wang et al. 2018). At 22 °C with honey water and *D. suzukii* larvae in an artificial diet, *Ganaspis* sp. adult females survive ~18 days and produce around 100 offspring per female. The proportion of female progeny decreases with increasing maternal age. The estimated *net reproduction rate* is 39.9, *intrinsic rate of increase* is 0.130, *mean generation time* is 28.5 days, and *doubling time* is 5.4 days (Wang et al. 2018). *Ganaspis* sp. shows a linear (type I) functional response to the tested host densities of *D. suzukii* in an artificial diet (Wang et al. 2020b).

Thermal Biology

The temperature sensitivity of *Ganaspis* sp. development was studied by Hougardy et al. (2019): below 17.2 °C a facultative diapause was triggered, but the response varied between populations of different geographical origin with all South Korean *Ganaspis* sp., but only a proportion of *Ganaspis* sp. from China, entering diapause at this temperature. At 15.9 °C, the fecundity of South Korean *Ganaspis* sp. was higher than that of Chinese *Ganaspis* sp., which could either be because host location and oviposition behavior of the South Korean *Ganaspis* sp. females were less affected or because their eggs provide better cold hardiness.

To study the temperature-dependent development of insects close to threshold temperatures, insects can be transferred between extreme (low or high) and optimum temperatures (Régnière et al. 2012). Using this method with *G. kimorum*, the lower developmental threshold for pre-imaginal parasitoids of both male and female was determined to be around 11 °C, and the fastest development occurred at around 30 °C (M. L. S. and M. K., unpublished data). While the parasitoid and its host cannot survive when reared continuously at these extreme temperatures, these results are useful to consider when calculating development times under fluctuating temperatures (e.g., natural conditions) at the beginning of the season or during heat waves. *G. kimorum* males generally have shorter lifespans than females. When provided with honey water ad libitum, the optimal temperature for male longevity is about 15 °C (40 days on average), while non-ovipositing females live the longest at 20 °C (80 days on average) (M. L. S. and M. K., unpublished data). Preliminary results of cold hardiness studies (M. L. S. and M. K., unpublished data) suggest that while adult wasps are sensitive to cold temperatures, pre-imaginal stages can survive longer periods of a week to a month at temperatures close to freezing.

Ecology

Seasonal Ecology and Host Plant Associations

The seasonal ecology of *G. kimorum* in its native range has not been studied in detail. However, during foreign exploration for *D. suzukii* parasitoids in Japan, China, and South Korea, *Ganaspis* spp. were found emerging from *D. suzukii*-infested fruit on several different host plant species collected from May to September (Daane et al. 2016, Girod et al. 2018b, Giorgini et al. 2019). The adventive establishment of *G. kimorum* in the Pacific Northwest of North America (British Columbia, Canada, and Washington, USA) (Abram et al. 2020, Beers et al. 2022) and large-scale field releases in Italy have presented more opportunities to study its seasonal ecology and host plant associations in the field in greater detail. Figure 3 shows the current state of knowledge of *G. kimorum* seasonal life cycle in British Columbia, Canada.

Knowledge of the seasonal ecology of *G. kimorum* in North America is still limited, with the only available study conducted during a single year in the southern coastal region of British Columbia, Canada (Abram et al. 2022a). In this region, *G. kimorum* adults were first found parasitizing *D. suzukii* in an early-fruiting host plant species (salmonberry, *Rubus spectabilis* Pursh [Rosaceae]), and were subsequently found throughout the growing season parasitizing *D. suzukii* in a variety of fruiting host plants until October (Fig. 3), with the predominant late-season plant host being Himalayan blackberry, *Rubus armeniacus* Focke (Rosaceae). This pattern of seasonal presence, in combination with heat unit accumulation in relation to published estimates of degree day development requirements (Hougardy et al. 2019) suggests that *G. kimorum* completes 2 generations per growing season in British Columbia. Abram et al. (2022a) reported no obvious seasonal trends in *G. kimorum* parasitism levels on *D. suzukii*, but there were strong trends associated with host plant species: *G. kimorum* tended to parasitize *D. suzukii* at the highest levels in small fruits (e.g., *Sambucus* spp.) whereas the co-occurring larval parasitoid *L. japonica* tended to predominate in larger fruits (e.g., *Rubus* spp.). This confirms results from Asia (Giorgini et al. 2019) and is in partial agreement with data obtained in Italy, where wild blackberry (*Rubus ulmifolius* Schott) and elderberry appeared to be preferred plant hosts for *G. kimorum*, with 76.9% and 61.1% of the total sampled *G. kimorum* emerging from collections of these fruits in 2021 and 2022, respectively (Fellin et al. 2023). This association with smaller fruit could be due to *G. kimorum*'s shorter ovipositor (Earley et al. 2023, Fellin et al. 2023). It was also noted that *G. kimorum* parasitism in British Columbia was first observed an average of 10–22 days after *D. suzukii* infestation was first detected in a host plant, suggesting that *G. kimorum* may lag behind its host in colonization of host plants as they ripen over the course of the season, creating spatio-temporal "refuges" for *D. suzukii*. However, this hypothesis needs to be tested in more study years and locations. Globally, the parasitoid has now been recorded from *D. suzukii* in 38 different host plant species in 9 families (Table 1).

Overwintering

Overwintering is a crucial part of the establishment of classical biological control agents. The overwintering biology of *G. kimorum* has not been studied in the field in its native range, but it is currently being investigated with the adventive population in British Columbia, Canada (A. V. and P. K. A., unpublished data) and in field cages in Switzerland. It is known that *G. kimorum* overwinters inside host puparia near the soil surface in British Columbia, as evidenced by *D. suzukii* puparia collected from the soil during the overwintering period yielding emerging *G. kimorum* adults (Capko et al. 2024). The sieving and flotation method developed by Capko et al. (2024) to extract parasitized *D. suzukii* puparia from soil could be used in future studies to investigate the overwintering biology and survival of *G. kimorum* in more detail.

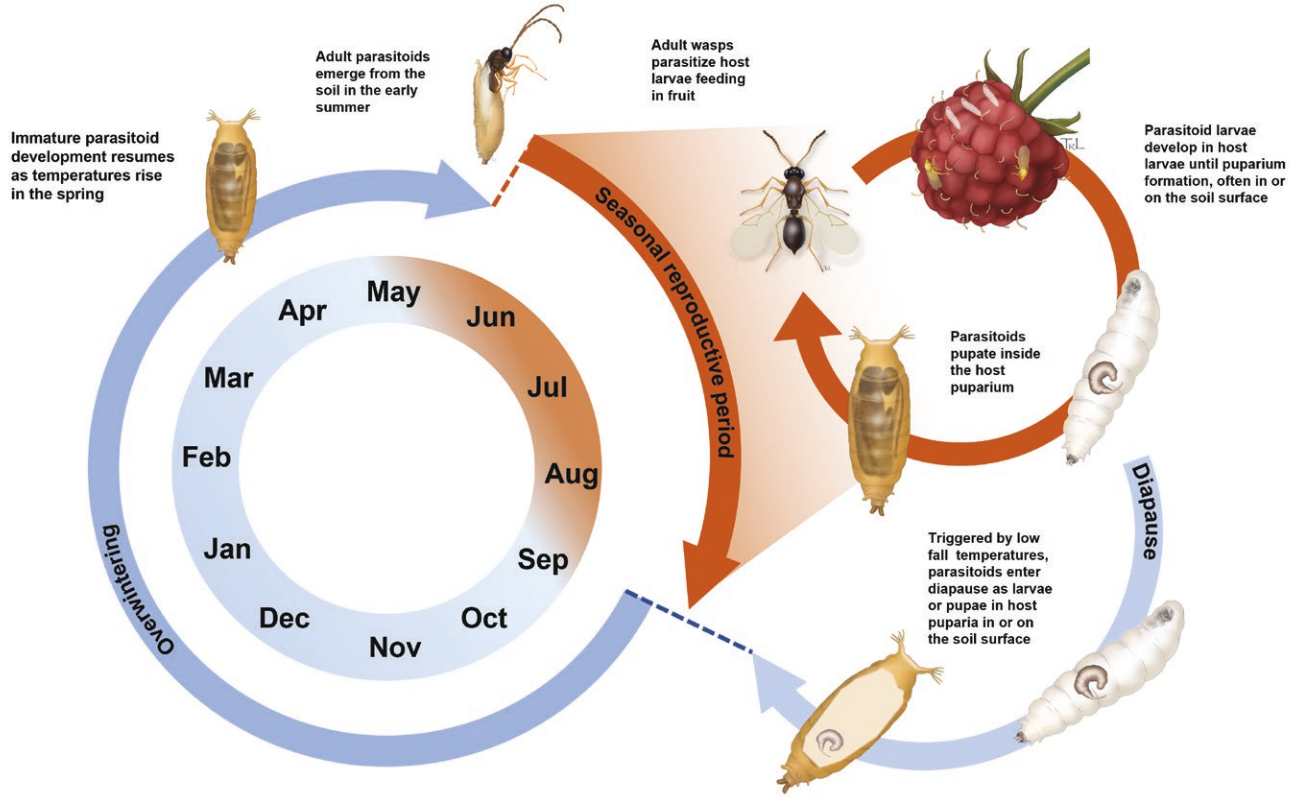

Fig. 3. Seasonal ecology of *G. kimorum* in British Columbia, Canada. The overwintering life stage is yet to be confirmed. Individual artwork by Taina Litwak, USDA ARS Systemic Entomology Laboratory.

Studies under laboratory conditions suggested that *G. lupini* enters a temperature (rather than photoperiod)-driven facultative diapause in the prepupal stage inside the host's puparium (Hougardy et al. 2019). The identity of the overwintering developmental stage is supported for *G. kimorum* by data demonstrating that the prepupal or pupal stage is somewhat cold-hardy and can endure 28 d at 0 °C (M. L. S. and M. K., unpublished data). In contrast, overwintering field cage studies in Switzerland (M. L. S., unpublished data) with *G. kimorum* suggested that small parasitoid larvae within fly pupae had survived temperatures as low as −6 °C. Thus, either *G. kimorum* is able to overwinter at various developmental stages or there are differences in overwintering biology between biotypes, genetic groups, or different *Ganaspis* sp. Studies are still underway to verify in which life stage *G. kimorum* overwinters, to characterize the timing of *G. kimorum* diapause induction under field conditions in British Columbia, and to better understand the abiotic factors (temperature, photoperiod) influencing diapause induction (A. V. and P. K. A., unpublished data).

After field releases in Italy, successful overwintering of *G. kimorum* was observed across multiple years at several valley bottom locations between 90 and 620 meters above sea level (m a.s.l.). Individuals of the exotic parasitoid were recovered from fruit samples collected in spring 2022 and 2023, following releases in summer 2021 and 2022, respectively. The landscape may have played a major role in these findings, particularly in an Alpine region, such as the province of Trento, where release sites spanned 4 altitudinal zones: thermo-mediterranean (0–200 m a.s.l.), meso-mediterranean (200–600 m a.s.l.), supra-mediterranean (600–1200 m a.s.l.), and montane zone (above 1.200 m a.s.l.). Above a certain altitude, winter temperatures could have been too low to allow survival of *G. kimorum*. It is also possible that *G. kimorum* individuals released at higher altitudes moved toward lower sites following the fall altitudinal migration of *D. suzukii* to exploit gradual changes in temperature, food, and ovipositional resources (Rossi-Stacconi et al. 2016, Tait et al. 2018).

Interactions with Other Parasitoids

Understanding competitive interactions between parasitoids is key to defining major aspects of biology and ecology of exotic natural enemies (Godfray 1994, Harvey et al. 2013), as well as for predicting potential implications for pest suppression as the main outcome of classical biological control programs (Mills 2006, Heimpel and Mills 2017). A diverse group of parasitoids attacks *Drosophila* species, including larval parasitoids of the genera *Asobara* (Hymenoptera: Braconidae), *Leptopilina*, and *Ganaspis*, and pupal parasitoids belonging to *Trichopria* (Diapriidae), *Pachycrepoideus*, and *Spalangia* (Pteromalidae) genera (Wang et al. 2020c). Surveys in South Korea (Daane et al. 2016), China (Girod et al. 2018b, Giorgini et al. 2019), and Japan (Girod et al. 2018b, Kimura and Mitsui 2020) discovered at least 19 larval parasitoid species associated with *D. suzukii*. Among them, *G. kimorum*, *G. lupini*, and *L. japonica* were often collected from *D. suzukii* and its 2 close relatives *D. pulchrella* and *D. subpulchrella* infesting the same fruit, and they may face strong competition.

A recent laboratory study showed that *Ganaspis* sp. and *L. japonica* differ crucially in developmental rates of their early immature stages; *L. japonica* eggs hatched much faster than *Ganaspis* sp. and consequently prevailed during intrinsic competition against the latter (Wang et al. 2019). However, *Ganaspis* sp. adults discriminated strongly against hosts previously parasitized by *L. japonica*,

Table 1. Host plants associated with *Ganaspis kimorum* in the parasitoid's native and introduced regions

Family	Host plants	Country	Reference
Adoxaceae	*Sambucus adnata* Wall.	China	Girod et al. 2018b
Adoxaceae	*Sambucus nigra* (L.)	Italy	Fellin et at. 2023
Adoxaceae	*Sambucus racemosa* L.	Canada	Abram et al. 2020, 2022a
Adoxaceae	*Sambucus williamsii* Hance	China	Girod et al. 2018b
Caprifoliaceae	*Lonicera maacki* Maxim.	China	Girod et al. 2018b
Elaeagnace	*Elaeagnus umbellata*	USA	Gariepy et al. 2024
Ericaceae	*Gaultheria shallon* Pursh	Canada	Abram et al. 2020, 2022a
Ericaceae	*Vaccinium corymbosum* (L.)	Canada	Abram et al. 2020, 2022a
Ericaceae	*Vaccinium parvifolium* Sm.	Canada	Abram et al. 2020, 2022a
Moraceae	*Morus alba* L.	Italy	Fellin et at. 2023
Moraceae	*Morus* sp.	China	Girod et al. 2018b
Myricaceae	*Myrica rubra* Siebold & Zucc.	China	Girod et al. 2018b
Rhamnaceae	*Frangula alnus* Mill.	Italy	Fellin et at. 2023
Rosaceae	*Cerasus speciosa* (Koidzumi)	Japan	Matsuura et al. 2018
Rosaceae	*Fragaria moupinensis* Cardot.	China	Giorgini et al. 2019
Rosaceae	*Fragaria × ananassa*	Canada	Abram et al. 2020, 2022a
Rosaceae	*Prunus cerasoides* D. Don.	China	Girod et al. 2018b
Rosaceae	*Prunus* (*Cerasus*) sp.	China	Girod et al. 2018b
Rosaceae	*Prunus avium* L.	Canada	Abram et al. 2020, 2022a
Rosaceae	*Prunus donarium* Sieb.	Japan	Kasuya et al. 2013
Rosaceae	*Prunus emarginata* (Dougl. ex Hook.) Eaton	Canada	Abram et al. 2020, 2022a
Rosaceae	*Prunus mahaleb* L.	Italy	Fellin et at. 2023
Rosaceae	*Prunus serotina* Ehrh.	USA	Gariepy et al. 2024
Rosaceae	*Prunus serrulata* Lindl.	China	Girod et al. 2018b, Matsuura et al. 2018
Rosaceae	*Rubus allegheniensis*	USA	Gariepy et al. 2024
Rosaceae	*Rubus armeniacus* (Focke)	Canada, USA	Abram et al. 2020, 2022a, Beers et al. 2022, Gariepy et al. 2024
Rosaceae	*Rubus coreanus* Miq.	South Korea	Daane et al. 2016, Wang et al. unpul. data
Rosaceae	*Rubus foliosus* Weihe	China	Giorgini et al. 2019
Rosaceae	*Rubus fruticosus* (L.)	Canada, Italy	Abram et al. 2020, 2022a, Beers et al. 2022
Rosaceae	*Rubus idaeus* (L.)	Canada, Italy	Abram et al. 2020, 2022a, Beers et al. 2022
Rosaceae	*Rubus niveus* Thunb.	China	Giorgini et al. 2019
Rosaceae	*Rubus phoenicolasius* Maxim	South Korea, USA	Daane et al. 2016, Gariepy et al. 2024, Wang et al. unpul. data
Rosaceae	*Rubus sp., subgenus Rubus (Eubatus) cv Chester*	USA	Gariepy et al. 2024
Rosaceae	*Rubus spectabilis* Pursh	Canada	Abram et al. 2020, 2022a
Rosaceae	*Rubus* spp.	South Korea, USA	Daane et al. 2016, Gariepy et al. 2024, Wang et al. unpul. data
Rosaceae	*Rubus ulmifolius* Schott	Italy	Fellin et at. 2023
Solanaceae	*Solanum nigrum* L.	China	Girod et al. 2018b

whereas *L. japonica* did not discriminate against hosts containing pre-imaginal *Ganaspis* sp. Strong interspecific discrimination by *Ganaspis* sp. is likely one of the ecological mechanisms that contributes to co-existence with *L. japonica* in its native range and leads to the complementary impact of both parasitoids on host mortality. This might be crucial in view of the widespread distribution of adventive *L. japonica* populations in the *G. kimorum* release areas (Gariepy et al. 2024).

Some generalist pupal *Drosophila* parasitoid species, such as *Trichopria drosophilae* (Perkins) and *Pachycrepoideus vindemiae* Rondani, readily attack and develop from *D. suzukii* (Wang et al. 2020c). With *G. kimorum*, like many larval parasitoids of *Drosophila*, being a koinobiont solitary endoparasitoid, a host parasitized by *G. kimorum* could be subsequently attacked by pupal parasitoids. Indeed, *P. vindemiae* was able to successfully develop on *D. suzukii* puparia containing all pre-imaginal stages of *Ganaspis* sp., although parasitism success was significantly higher in later, rather than early stages of *Ganaspis* sp. (Hougardy et al. 2022). *T. drosophilae* was only able to successfully develop on *D. suzukii* puparia containing early instars of *Ganaspis* sp. (Hougardy et al. 2022).

Although *G. kimorum* has been exclusively recorded from *D. suzukii* in the field (Matsuura et al. 2018), laboratory tests also showed that *G. kimorum* can attack and develop from a few other closely related species, such as *D. melanogaster* (Seehausen et al. 2020). *D. melanogaster* is a cosmopolitan, and perhaps the most common *Drosophila* species, and many common parasitoids such as *Asobara tabida* Nees (Hymenoptera: Braconidae), *L. heterotoma* and *L. boulardi* (Barbotin et al.) can readily attack it (e.g., Fleury et al. 2009). Although *D. suzukii* is a pest of fresh fruit and *D. melanogaster* typically breeds in damaged or rotting fruit, both species may co-occur since *D. suzukii* can also develop on decaying fruit, especially during periods when there is limited availability of more preferred ripening fruits (e.g., Bal et al. 2017). *G. kimorum* may potentially interact directly with those more generalist and common larval *Drosophila* parasitoids (*A. tabida*, *L. heterotoma*, and *L. boulardi*) that rarely successfully emerge from *D. suzukii* but can readily parasitize *D. suzukii* and induce high host mortality (Wang et al. 2020b). It is possible that some of these parasitoids may be able to develop occasionally in *D. suzukii* after it is parasitized by suitable parasitoids such as *G. kimorum* or *L. japonica* that have suppressed the host's immune response, i.e., kleptoparasitism (Kraaijeveld 1999). Thus, various direct and indirect interactions between *G. kimorum* and resident parasitoids could occur in the aftermath of invasions of exotic *D. suzukii* and the introduction of several of its parasitoids. *G. kimorum* may benefit by avoiding competition with more generalist larval parasitoid species attacking *Drosophila* species in rotting fruit by attacking *D. suzukii* in fresh fruit on the plants (Giorgini et al. 2019, Fellin et al. 2023).

Mass Rearing

For both augmentative, as well as classical, biological control programs that target an area-wide establishment and spread of an exotic agent like *G. kimorum*, producing large numbers of the natural enemy to release is of paramount importance. The methods for rearing *G. kimorum* and *G. lupini* have recently been described by Rossi-Stacconi et al. (2022). Although the study presents 2 separate rearing programs, a small scale for research purposes and a large scale for mass production and field releases, the steps of the 2 protocols mostly overlap and are suitable for each of the 2 species. A key aspect of these rearing methods lies in the substrate used to offer the parasitoid host, since neither of the 2 species performs well in a pure artificial diet. *Ganaspis lupini* accepts hosts within modified substrates (i.e., a mix of *Drosophila* medium and mashed fruit), whereas *G. kimorum* production drops dramatically when hosts are not within fresh fruit. These requirements are most likely related to the parasitoid's foraging behavior, and the low parasitization rates observed on a pure artificial diet could be due to a lack of fundamental stimuli exploited by the parasitoid during the host-searching process. Whether such stimuli are chemical, mechanical, or of a different kind remains to be assessed. The current rearing method using fresh fruit is economically limiting for a mass rearing scaled for potential augmentative releases.

Experiments to develop an artificial diet for *G. kimorum* are currently underway, but if the development of a suitable artificial parasitization substrate for *G. kimorum* proves to be unattainable, improvement of the mass-rearing efficiency can still be achieved through the optimization of host and parasitoid densities. Another key aspect that is currently being investigated is whether the parasitoid can be stored at low temperatures without significant deterioration of fitness-related traits. Slowing down the metabolism to extend parasitoids' lifespan is a valuable method to reduce the cost of colony maintenance during periods when production is not required or to increase the shelf-life of fresh individuals (Colinet and Boivin 2011). In this context, temperature manipulation is emerging as a promising technique for pest management programs and a cold storage protocol has been developed to optimize parasitoid production and synchronize *G. kimorum* releases with pest outbreaks (Lisi et al. 2024c). This recent study revealed differences in cold tolerance among different pre-imaginal life stages of *G. kimorum*, with parasitoid larvae and pupae suitable to be successfully stored at 10 °C for 6 and 2 weeks, respectively.

Potential Biological Control Impact

Given that *D. suzukii* is a direct pest of fruit with a low threshold of damage tolerance, it is not realistic to expect *G. kimorum* to act as a stand-alone tool like some classical biological control introductions have been—rather, it will likely be one control method among several that contributes to the management of *D. suzukii* infestations by reducing fly populations on a landscape level by acting mainly in non-crop habitats. This will help restrain the pest's population buildup in the early season and may reduce or delay the need to protect crops with insecticide applications. In the absence of models to estimate or forecast the potential biological control impact of *G. kimorum*, this section discusses which factors might be influencing the biological control program using the current state of knowledge.

The use of appropriate monitoring techniques is crucial for assessing the success of *G. kimorum* releases in terms of the presence and abundance of parasitoids, parasitism of *D. suzukii*, and potential non-target effects (Abram et al. 2022b). In addition to the standard monitoring methods such as trapping of adult *D. suzukii*, repeated fruit collections in crop and non-crop habitats from the plant and ground are necessary to avoid underestimating parasitoid performance and accurately assess release success (Abram et al. 2022b, Fellin et al. 2023).

So far, field releases of *G. kimorum* have been conducted in Italy, Switzerland, France, Israel, and the United States, and release permits are currently being obtained in other countries in Europe. In Italy, field releases of *G. kimorum* started in 2021 following the release permit granted by the federal government (Lisi et al. 2022). Specific data are only available for the province of Trento in Northeast Italy, where *G. kimorum* was released at 12 locations in 2021 and at 20 locations in both 2022 and 2023. Following its releases, *G. kimorum* was monitored through extensive seasonal fruit sampling. The parasitoid was recovered at 50% of the release locations in 2021, 20% in 2022, and 35% in 2023. In addition, the recovery rate from fruit samples increased each year, rising from 2.6% in 2021 to 3.7% in 2022 and reaching 5.8% in 2023 (Fellin et al. 2023, M. V. R. S., unpublished data). As for the *G. kimorum* populations in their native range in Asia, the impact of *G. kimorum* releases on *D. suzukii* populations is as of yet unknown. However, parasitoid emergence data from sampled areas in Asia reporting that *Ganaspis* spp. had an average parasitism rate of between 18% and 40% depending on the host plant (Giorgini et al. 2019) provide an idea of what releases will be hoping to achieve.

The ecological success of classical biological control programs depends on the ability of the exotic species to establish itself in new areas following multiple field releases (Heimpel and Mills 2017). Environmental, ecological, and human influences can affect the success of releases. Environmental and climatic suitability of the relevant geographical regions directly affect the adaptation potential of the biological control agent (Hokkanen and Sailer 2008). In this context, Wang et al. (2020c) predicted that the areas where releases of *G. kimorum* have already been approved, specifically southern Europe and both coasts of North America (Beers et al. 2022, Lisi et al. 2022), provide a climate suitable for *G. kimorum* establishment. However, the microclimatic variability and habitat structure prevailing in these regions could directly influence the country-wide outcomes of field releases (Hokkanen and Sailer 2008). To date, released *G. kimorum* proved to be able to reproduce and overwinter in temperate climatic areas of Northern Italy (Fellin et al., 2023). The lower recovery of *G. kimorum* in 2022 than the previous year (see previous paragraph) could be related to the specific climatic conditions of the season: the weather during the second year of releases had been particularly mild during winter (January–February), with frost events in March–April followed by an abnormally warm and dry period May–October. Those unusual weather conditions heavily impacted the fruiting of most *D. suzukii* host plants, shifting the ripening time forward and generally reducing the availability of wild fruit to the flies. Wasp recoveries in other release sites are still under investigation. Meanwhile, the establishment of adventive populations of *L. japonica* in Northern Italy (Puppato et al. 2020), as well as *L. japonica* and *G. kimorum* in northwestern North America (Canada and the United States) (Abram et al. 2020, Beers et al. 2022) suggest a better adaptation in temperate climate regions than in hotter and drier ones, such as southern Italy and California. Further field surveys are needed to verify if microclimate will limit the establishment of *G. kimorum* (Wang et al. 2020a). Given the parasitoid's wide distribution, there is potential to explore and compare geographically diverse populations of *G. kimorum* to identify strains that can adapt to various climate zones within the invaded regions of *D. suzukii* in North America and Europe. Geographic variations in key ecological traits, especially climatic adaptability, among *G. kimorum* populations in East Asia, may necessitate introducing different strains to regions where the already released strains failed to establish.

Besides climate, ecological features of release sites could be crucial in determining release success. Laboratory data showed that other parasitoids of *D. suzukii* present at release sites can outcompete *G. lupini* in multiparasitized hosts (Wang et al. 2019, Hougardy et al. 2022), so *L. japonica* being present at many *G. kimorum* release sites could have an impact on both *G. kimorum* establishment and *D. suzukii* control that needs to be assessed (Gariepy et al. 2024). Moreover, landscape heterogeneity could affect wasp ecology as *D. suzukii* populations move between crop and non-crop hosts during the year (Kenis et al. 2016). Because the damaging pre-imaginal stages (i.e., larvae) of *D. suzukii* are abundant close to harvest, *G. kimorum* need to match with their hosts both spatially and temporally for successful pest suppression (Tait et al. 2021). Agricultural landscapes with fewer non-crop habitats are associated with lower parasitism by classical biological control agents and higher pest abundance (Grab et al. 2018). Therefore, the level of *G. kimorum* establishment and spread necessary to reduce *D. suzukii* populations on an area-wide scale might be easier to achieve in heterogenous landscapes containing semi-natural habitats with *D. suzukii* non-crop host plants serving as refuges. Indeed, after *G. kimorum* field releases in Italy, more *G. kimorum* recaptures were observed in sites with high landscape complexity (i.e., presence of forests, hedgerows, fallows, and other semi-natural habitats) than in sites with a high density of croplands (M. V. R. S., unpublished data). Crop systems are also likely to receive pesticides that would be harmful to *Ganaspis* spp. Multiple releases both in crop and non-crop habitats as done in Italy could promote *G. kimorum* dispersal, overwintering, and seasonal synchronization with the pest and enhance the overall success of an area-wide biological control program (Fellin et al. 2023).

Current *D. suzukii* management approaches can affect the success of the biological control program (Messing and Brodeur 2018). The high profitability of berry crops and the market demand for undamaged fruit leads growers in many countries to rely on calendar-based treatments with broad-spectrum insecticides mainly targeting adult flies (Tait et al. 2021). Those broad-spectrum insecticides include organophosphates, carbamates, pyrethroids, spinosyns, and diamides (e.g., Van Timmeren and Isaacs 2013, Shawer 2020, Demchak 2024), while insecticide applications in organic production mainly rely on spinosad and pyrethrum (Van Timmeren and Isaacs 2013, Gress and Zalom 2019, Sial et al. 2019). Widespread reliance on insecticides can be expected to negatively impact *G. kimorum* populations in crop fields. Recent laboratory and field studies confirmed the high toxicity of several insecticides, commonly used against *D. suzukii*, for *G. kimorum* following residual and topical exposures (Fellin et al. 2024, Lisi et al. 2024a). In particular, spinosad use is not recommended concurrent with parasitoid releases because of its high toxicity on *G. kimorum*, although it is a mainstay of especially organic management of *D. suzukii* (Gress and Zalom 2019). Hence, in areas where the landscape is dominated by unmanaged habitats near crops, the main role of *G. kimorum* will be to suppress fly populations in these natural environments. However, other biopesticides commonly used in agroecosystems affected by *D. suzukii*, such as the entomopathogens *Bacillus thuringensis* subsp. *kurstaki* and *Beauveria bassiana*, or those under investigation, such as garlic essential oil nanoemulsion, proved to be safe and compatible with *G. kimorum*. This provides new insights into the potential of combining *G. kimorum* releases and bioinsecticide applications for optimized integrated pest management (IPM) strategies (Lisi et al. 2024b). While insecticides are the prevalent management tactic for *D. suzukii* in many countries, other IPM tactics potentially more compatible with parasitoid releases are also in use. Those include cultural management (reviewed in Schöneberg et al. 2021), attract-and-kill mechanisms (e.g., Rossi-Stacconi et al. 2020, Urbaneja-Bernat et al. 2022), and the development of release of sterile *D. suzukii* males (Sassù et al. 2021). The latter would be expected to be compatible with *G. kimorum* releases since it has no direct interactions with parasitoids. Attract-and-kill strategies should not negatively impact biological control if the components attracting *D. suzukii* are species-specific. While most cultural control mechanisms, such as short harvest intervals or pruning, are unlikely to impact parasitoids significantly, destroying culled fruit could remove parasitoids as well as flies from the system. However, with the main goal of *G. kimorum* releases being to impact *D. suzukii* in unmanaged landscapes rather than crop fields or orchards, crop management will likely be less impactful than the other factors discussed in this section.

While *D. suzukii* is primarily known as an agricultural pest, it is increasingly shown to have negative effects on natural ecosystems as well. The invasive insect can compete with other drosophilids, feeding on non-crop plants in forests potentially leading to the disruption of seed dispersal of native plants and impacting native bird and insect populations (Roche et al. 2021, 2023, Bühlmann and Gossner 2022). Apart from contributing to agricultural pest management, classical biological control can have the goal of protecting natural ecosystems (Van Driesche et al. 2010). Consequently, reducing *D. suzukii* populations with *G. kimorum* in unmanaged habitats could have positive environmental effects by decreasing the amount of insecticides applied against flies migrating from natural habitats to crop fields, and by reducing the impact of *D. suzukii* in non-crop habitats such as forests.

Open Questions

Despite years of intensive research on *G. kimorum* (as *G. brasiliensis*), several important questions remain unanswered. Some of these questions are being addressed with current research activities, and others will be a focus of future projects. Here, we highlight a few of those so far unanswered questions and potential issues that have not yet been mentioned.

First, while recent studies highlighted the presence of distinct cryptic species grouped under the taxonomic status of *Ganaspis* sp. (Seehausen et al. 2020, Sosa-Calvo et al. 2024), most research on life history parameters (Wang et al. 2018, Hougardy et al. 2019), foraging behavior (Biondi et al. 2021), and competition with other parasitoids (Wang et al. 2019, Hougardy et al. 2022) were only conducted on *G. lupini* or on populations that later were found to be a mixture of the 2 species. Since *G. lupini* and *G. kimorum* show differences not just at the molecular and reproductive levels but also at the ecological level (Girod et al. 2018a, Seehausen et al. 2020), follow-up investigations in the above-mentioned areas should aim to compare *G. kimorum* with *G. lupini* and other sibling species. It will also be helpful to obtain a better resolution of the different *Ganaspis* species distributions in Asia, specifically in temperate regions where the climate matches current and future release areas. Comparing the overwintering biology of different *Ganaspis* species as well as between *G. kimorum* populations sourced from locations with different climates will be of particular interest.

For the long-term success of a biological control program against *D. suzukii* with *G. kimorum*, parasitoid releases at first, and natural population build-ups at a later stage, should be compatible with current and future management techniques. While first screenings on the acute toxicity and sublethal effects of pesticides recommended to control *D. suzukii* has been conducted for *G. kimorum* (Fellin et al. 2024, Lisi et al. 2024a, b), more research is necessary to support planning and decision-making for future release programs and ease the integration of biocontrol within IPM packages.

A common issue in biological control concerns the limitations of the original genetic material. The implementation of a classical biocontrol program involves multiple steps and several years can pass from the first foreign exploration to the final release of an exotic biological control agent. During this time, the original colony of the agent is maintained in quarantine facilities for efficacy and risk assessments, often without any addition of genetic variability from further collections of wild individuals. In such situations, repeated rearing can affect the life history traits of the population and cause potential inbreeding depression (Henter 2003, Kuriwada et al. 2010, Szűcs et al. 2019), potentially leading to the gradual loss of key ecological and biological traits (Gariepy et al. 2015). The *G. kimorum* population that is being used for biological control programs in Europe and the United States derives from about 50 wild individuals collected in Naganuma Park (Tokyo, Japan) in 2016 (Girod et al. 2018b) and has been inbred since then. In case future new collections of genetic material from the same area will be carried out, research should aim to compare the genetics and life history traits of this released population with those of the newly collected population. Similarly, it would be of great interest to make a comparison between *G. kimorum* individuals that were recovered after the overwintering in the release areas and those from the original rearing. In addition, the consequences of genetic admixture of different *G. kimorum* populations should be investigated; for example, if laboratory-maintained populations are being introduced within or near regions that already have adventively established *G. kimorum* populations. Genetic admixture of different populations of the same species of biological control agents can theoretically have both positive (e.g., heterosis) and negative (e.g., outbreeding depression, symbiont-induced cytoplasmic incompatibility) consequences, and so the decision of whether to encourage population admixture should be carefully considered (reviewed in Heimpel and Mills 2017).

So far, the biological control program against SWD with *G. kimorum* has been a massive success in collaborative research at the national and international levels. It has leveraged extensive collaborations among dozens of ecologists, biological control specialists, systematics experts, and molecular biologists. It has taken *G. kimorum* from a virtually unknown cryptic organism hidden within a taxonomic "dumping bin" to a species that has been clearly defined from other members of its species complex that might be less suitable for biological control using the highest modern standards of integrative taxonomy. It is now reared in laboratories around the world for classical biological control releases, and will hopefully help to reduce the environmental and economic burdens of one of the world's most serious invasive pests.

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Author contributions

Judith Stahl (Conceptualization, Investigation, Methodology, Project administration, Writing—original draft, Writing—review & editing [equal]), Xingeng Wang (Conceptualization, Data curation, Investigation, Project administration, Visualization, Writing—original draft, Writing—review & editing [equal]), Paul Abram (Investigation, Visualization, Writing—original draft, Writing—review & editing [equal]), Antonio Biondi (Investigation, Writing—original draft, Writing—review & editing [equal]), Matthew Buffington (Investigation, Writing—original draft, Writing—review & editing [equal]), Kim A. Hoelmer (Investigation, Writing—original draft, Writing—review & editing [equal]), Marc Kenis (Investigation, Writing—original draft, Writing—review & editing [equal]), Fabrizio Lisi (Investigation, Writing—original draft, Writing—review & editing [equal]), Marco Valerio Rossi Stacconi (Investigation, Visualization, Writing—original draft, Writing—review & editing [equal]), Martin Seehausen (Investigation, Writing—original draft, Writing—review & editing [equal]), Ariane Vossen (Investigation, Visualization, Writing—original draft, Writing—review & editing [equal]), Warren Wong (Visualization, Writing—original draft, Writing—review & editing [equal]), and Kent Daane (Funding acquisition, Investigation, Supervision, Writing—original draft, Writing—review & editing [equal])

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