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ARTICLE

Phenological and ecological differences between two tephritid flies (Diptera) in golden currant (Grossulariaceae) and implications for species coexistence

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Abstract
Communities comprising multiple temperate tephritid flies infesting the same host fruit may provide insights into how species partition resources to avoid competitive exclusion. Using *Euphranta canadensis* (Loew) and *Rhagoletis ribicola* Doane (Diptera: Tephritidae) that share golden currant, *Ribes aureum* Pursh (Grossulariaceae), as a model, we hypothesised that adults and larvae of these flies temporally divide host fruit to coexist. Fruit loads, fruiting phenology, fly catches, and larval infestation levels were determined in central Washington state, United States of America, in 2023, 2024, and 2025. Adult *E. canadensis* abundance peaked in May when most currants were immature and that of *R. ribicola* peaked in June when most currants were mature. Only *E. canadensis* larvae emerged from fruit collected in May; both species emerged from fruit collected in June; and only *R. ribicola* emerged from fruit collected in July. In June, larval niche overlap was 0.543–0.996, but no larvae emerged from 94–99% of fruit collected, suggesting currants can be an unlimited resource. Our results suggest that temporal partitioning of fruit resources and low infestation rates may help mitigate interspecific competition between *E. canadensis* and *R. ribicola*, with implications for monitoring or management of tephritid pests that co-occur in fruit trees.

Introduction

Ecological communities comprise multiple interacting species. When these species occupy the same trophic level and use the same limiting resource, theory indicates that they must in some way partition the shared resource to coexist and not competitively exclude one another (Schoener 1983; Holt 1987, 2001; Griffin and Silliman 2011). Flies in the family Tephritidae that live in subtropical or tropical regions generally use fruit from multiple hosts. This can reduce the risk of competitive exclusion when different flies infest different combinations of fruits to varying degrees. In temperate regions, tephritids are usually specialists on one or relatively few species of host plants, perhaps because of the shorter growing season and relatively few host species. In this case, specialising on different primary host plants can restrict interspecific competition between flies. However, there are examples in which more than one temperate

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tephritid fly species infest the fruit of the same host plant (Bush 1966). When more than one fly attacks the same host plant, this raises the question of how these species coexist without one species driving the other to extinction (Holt 2001).

The answer to this question is critical not just for illuminating our basic understanding of how biodiversity is maintained in nature but also has important applied economic implications. For example, invasions by exotic fruit fly pests into regions already occupied by other fly species may lead to niche partitioning or extinction, affecting control strategies (*e.g.*, Duyck *et al.* 2006; Ekesi *et al.* 2009; Lopes *et al.* 2015; Clarke and Measham 2022; Hassani *et al.* 2022). One example of this in temperate regions is the recent invasion of the European cherry fruit fly, *Rhagoletis cerasi* (Linnaeus) (Diptera: Tephritidae), into eastern North America (Prengaman 2017). There, *R. cerasi* could potentially interact with two native tephritid pests that attack commercially grown cherries as an alternate host: *Rhagoletis cingulata* (Loew), whose native host is *Prunus serotina* Ehrhart, black cherry (Rosaceae), and *Rhagoletis fausta* (Osten-Sacken), whose native host is *Prunus pensylvanica* Linnaeus filius, pin cherry (Rosaceae). The impact of the introduction of *R. cerasi* on the community of cherry-infesting *Rhagoletis* remains to be determined.

Available evidence from North America suggests that infestations of the same host fruit by *Rhagoletis* can result in several outcomes. In the Pacific Northwest of the United States of America, western cherry fruit fly, *Rhagoletis indifferens* Curran, and *R. fausta* both infest bitter cherry, *Prunus emarginata* (Douglas ex Hooker) Eaton (Rosaceae). *Rhagoletis fausta*, the rarer of the two species in the region, is active as adults 1–3 weeks earlier than *R. indifferens* is and generally occurs at higher elevations (Bush 1966). These differences may result in temporal and spatial niche partitioning of bitter cherry, allowing *R. fausta* to coexist with *R. indifferens* in sympatry. In contrast, there is also evidence of competitive exclusion occurring in *Rhagoletis*. In Massachusetts and Rhode Island, United States of America, both *Rhagoletis basiola* (Osten-Sacken) and *Rhagoletis pomonella* (Walsh) were reported to infest hips of *Rosa* spp. (Rosaceae) at the same time over two seasons (Prokopy and Berlocher 1980). *Rosa* is the primary host of *R. basiola* and is a secondary host of *R. pomonella* (whose primary native host is hawthorn, *Crataegus* spp. (Rosaceae)). However, *R. pomonella* appears to have subsequently gone extinct in roses, implying competitive exclusion in *Rosa* by *R. basiola*. These examples suggest that temporal or spatial partitioning, or both, may allow coexistence, whereas lack of partitioning may lead to exclusion.

Another case of two tephritids inhabiting a shared host fruit involves the flies *Euphranta canadensis* (Loew) and *Rhagoletis ribicola* Doane, native to the Pacific Northwest of the United States of America. There, *E. canadensis* and *R. ribicola* have been reported to attack native golden currant, *Ribes aureum* Pursh (Grossulariaceae), as their principal host, as well as introduced currants and gooseberries, since at least 1898 (Piper and Doane 1898). The flies' life histories appear similar, but many knowledge gaps about these flies remain. Both *E. canadensis* and *R. ribicola* are adapted to temperature zones that have cold winters, and both are univoltine. Both reportedly can lay as many as 200 eggs under the epidermis of currants (Jones 1937). Puparia of both live in soil for over 10 months and eclose as adults in the spring. Oviposition by *E. canadensis* begins about 2 weeks after flies emerge from soil, with eggs hatching after about 5–11 days (Paine 1912; Jones 1937). The larval stage lasts about 13 or 15 days (Mitchener 1927; Jones 1937). Oviposition by *R. ribicola* probably begins about 7–10 days after eclosion, if its timing is like that of other *Rhagoletis* (*e.g.*, Neilson *et al.* 1981). The larval stage of *R. ribicola* lasts 3–4 weeks (Piper and Doane 1898). How *E. canadensis* and *R. ribicola* ecologically partition golden currant fruit has been poorly studied, but several possible, nonmutually exclusive means can broadly be categorised as spatial, host fruit-related, demographic, and temporal partitioning, as follows.

With respect to spatial partitioning, the two flies may geographically overlap in only part of their respective ranges. As a result, migration from areas outside of their overlap zone, in this case the Pacific Northwest, may allow *E. canadensis* and *R. ribicola* to persist in sympatry despite strong interspecific competition between them in golden currant. In this regard, *E. canadensis* occupies a broader geographic range across North America than *R. ribicola* does, the latter being

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restricted to western North America (Foote *et al.* 1993). *Euphranta canadensis* may therefore be more successful than *R. ribicola* in more diverse habitats and in various other *Ribes* species besides *R. aureum* outside of where it co-occurs with *R. ribicola*, allowing it to persist in sympatry despite potentially being outcompeted on golden currant in the Pacific Northwest. Spatial mechanisms may largely depend on the ability of the two flies to survive in different climates, independent of host fruit-related, demographic, and temporal factors.

Host fruit-related differences refer to the possibility that *E. canadensis* and *R. ribicola* larvae feed in different parts of golden currant fruit that vary in their physical or chemical characteristics (*e.g.*, on the seeds or in the core of fruit *versus* in exterior regions).

Demographic considerations, such as generally low population sizes of *E. canadensis* and *R. ribicola*, may also result in larvae of the two flies rarely co-occurring in the same fruit. In this regard, limited collections in June and July of golden currants in central Washington state, United States of America (Yee 2008), suggest currants are not heavily infested by either species, thereby relaxing competition and allowing the two flies to share the same host plant.

Finally, *E. canadensis* and *R. ribicola* may temporally divide golden currant by attacking the plant at different times of the field season. This can result in larvae of the two species feeding in golden currant in different stages of fruit ripeness (*i.e.*, immature, ripe, decayed). If this is the case, then temporal partitioning of resources can have different consequences for larval success, depending on the stage of fruit ripeness. *Euphranta canadensis* and *R. ribicola* larvae may feed in golden currant at different stages of fruit maturation, when fruit may vary in their physical characteristics (*e.g.*, harder *versus* softer tissues), chemical properties (*e.g.*, greater *versus* lesser concentration of secondary compounds and toxins), or sugar content, or any combination thereof. Temporally dividing golden currant can also affect the flies' mating systems and oviposition choices. If *E. canadensis* and *R. ribicola* adults are active at different times of the season, they may prefer to mate on and oviposit into golden currant in different stages of fruit development, thereby reducing their chances of encountering one another and lessening reproductive interference between their offspring on shared host fruit.

Here, we focus on the role of seasonal differences in the distributions of *E. canadensis* and *R. ribicola* as a mechanism contributing to species coexistence. Little is known about the temporal overlap of the two flies, other than that *E. canadensis* adults occur earlier in the season than *R. ribicola* adults do (Piper and Doane 1898; Jones 1937), suggesting temporal partitioning of golden currant contributes to the coexistence of the two flies in the Pacific Northwest. We hypothesised that univoltine *E. canadensis* and *R. ribicola* adults and larvae partition golden currant fruit seasonally. While acknowledging the possible role of spatial and host fruit mechanisms, we also hypothesised that this, together with demography – specifically low infestation rates – help explain the two species' coexistence in golden currant. We asked the following questions: (1) How is fruiting phenology related to differences in seasonal catches of *E. canadensis* and *R. ribicola*, and do abundances of the two flies differ? (2) Do the two fly species differ in eclosion timings in the laboratory? (3) Do distributions of fly eggs and larvae depend on fruit maturity stages and, related to this, are eggs laid singly? (4) Do the two species tend to infest fruit of different stages and, from answering this question, what are the larval abundances and niche overlaps of larvae of the two species? and (5) Do emergence timings of larvae of the two fly species from fruit following fruit collection differ? For additional information to help interpret the results, we also determined currant bush sizes and fruit loads, seasonal air temperatures, and adult fly capture periods.

Materials and methods

General

The spatial and temporal sampling effort to answer each question and objectives posed in the last paragraph of the Introduction and the variables measured for each are presented in

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Table 1. Site information for collections/observations of golden currant (*Ribes aureum*), flies, and fly eggs and larvae (*Euphranta canadensis* and *Rhagoletis ribicola*) from central Washington state, United States of America, in the study. Given are years (2023, 2024, and/or 2025) for fly trapping, fruiting phenology observations, and fruit collections/counts.

Site	County	Coordinates; elevation (metres above sea level)	Fly trapping	Fruiting phenology	Fruit collections
Union Gap	Yakima	46.564722, −120.467778; 295	2024, 2025	2023, 2024, 2025	2023, 2024, 2025
Cowiche	Yakima	46.624989, −120.650629; 434	2024	2024	2024, 2025
Tampico	Yakima	46.887222, −120.897222; 711	2024	2024	2024
Selah	Yakima	46.638333, −120.526667; 329	—	—	2024, 2025
Tieton	Yakima	46.725972, −120.810944, 555	—	—	2024
Benton City	Benton	46.259867, −119.498300; 134	—	—	2025
Bickleton	Klickitat	45.832183, −120.526467; 304	—	—	2025
Ellensburg	Kittitas	46.936969, −120.505065; 438	—	—	2025
Fort Simcoe	Yakima	46.343991, −120.840546; 435	—	—	2025
Slavin Road	Yakima	46.542222, −120.842222; 650	—	—	2025
Nile	Yakima	46.841944, −120.951944; 623	—	—	2025
Zillah	Yakima	46.441667, −120.346667; 247	—	—	2025, fruit counts only

Supplementary material, Table S1. Here, we describe the study sites and the methodologies for each of the questions or objectives outlined in the supplementary table.

Study sites

The study was conducted at 12 sites within an approximately 120-km radius of Union Gap in Yakima County, Washington state, United States of America (Table 1). Nine of the sites (Union Gap, Cowiche, Selah, Tieton, Benton City, Ellensburg, Fort Simcoe, Slavin Road, and Zillah) are in or near riparian zones in the sagebrush–bunchgrass ecosystem. The Tampico and Nile sites are located near or in the ponderosa pine ecosystem. The Bickleton site is located in transitional sagebrush–ponderosa pine habitat.

Currant bush sizes and fruit loads (2025)

To document key currant plant traits, in 2025, we estimated heights, widths, and fruit loads of currant bushes. A bush refers to an individual currant plant, which is a multi-stemmed shrub, and fruit loads are numbers of fruit per branch portion. Height and width were estimated by standing next to bushes and relating the measures to the observer's known height and arm span. Fruit on three to five bushes at the Union Gap, Selah, Zillah, Nile, and Slavin Road sites were counted on 30 May and 2, 3, 4, and 5 June, respectively (Fig. 1A, B). For each bush, we took five main branches, looked at the top 30.5 cm of each branch, including all side branches, and counted the currants found on that portion.

How is fruiting phenology related to differences in seasonal catches of *E. canadensis* and *R. ribicola*, and do abundances of the two flies differ? (2024, 2025)

To determine which currant fruit stages are associated with adult fly presence, we recorded fruit colours and fly catches on traps over the season in 2024 at Union Gap, Cowiche, and Tampico, representing low-, mid-, and high-elevation gradient sites, respectively. Each week from 23 April

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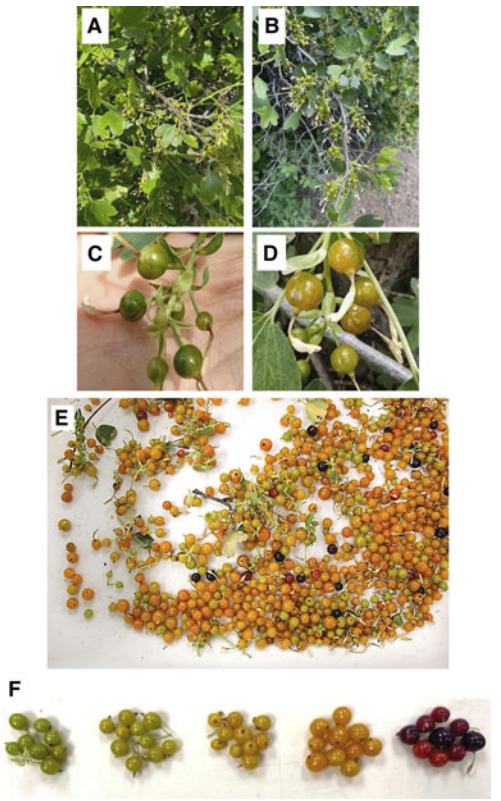


Figure 1. **A,** Lighter and **B,** heavier golden currant (*Ribes aureum*) fruit loads on bushes at Union Gap in central Washington state, United States of America, on 27 May 2025. Fruit colour maturation stages recorded in the study: **C,** green fruit (1 May); **D,** green–yellow fruit (14 May); and **E,** mix of yellow, yellow–orange, and orange–red fruit (11 June) when fruit reached peak size at Union Gap site in 2024. **F,** left to right: comparison of green, green–yellow, yellow, yellow–orange, and orange–red fruit collected from Slavin Road site, Washington state, United States of America, on 19 June 2025.

to 9 July at Union Gap and from 9 May to 9 July at Cowiche and Tampico, 10 fruit were sampled from each of 5–10 randomly chosen bushes spread over an approximately 0.07-km^2 area at each of the three sites. The sampled bushes were randomly chosen from week to week, so some bushes were sampled two or three times during the season.

Each fruit was visually categorised (Fig. 1C, D, E) into one of five different colour (fruit maturity) classes: (1) green; (2) yellow–green; (3) yellow; (4) yellow–orange, and (5) orange–red (Fig. 1F). We included dry fruit in the orange–red category. Multiple colour fruit stages occurred on bushes at the same time. Fruit on some bushes never turned red but remained orange, including when dried. Black fruit occurred on about three bushes and were included in the orange–red category.

To further determine seasonality of fruit maturity coinciding with fly catch timing, we measured diameter, weight, firmness, and sugar content of the fruit collected for fruit colour recordings. We measured fruit diameter with a calliper (Fowler High Precision, Canton, Massachusetts, United States of America), weight with a balance (Adventurer^{TM}, OHAUS, Pine Brook, New Jersey, United States of America), firmness *via* the grams reading in the dial of a fruit firmness penetrometer with a 1-mm diameter probe (QA Supplies, Norfolk, Virginia, United States of America), and percent sugar (total soluble solids) with a Brix refractometer (ATAGO N1, Tokyo, Japan).

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To associate fly catch equating to fly flight periods with fruiting phenology in 2024, one 14-cm × 23.5-cm sticky yellow rectangle trap (Multigard AM, Scentry Biologicals, Inc., Billings, Montana, United States of America) baited with an external sachet containing 27 g ammonium carbonate was deployed in each of 20 bushes 0.5–1.5 m above ground, including in the bushes used for fruit maturity recordings. Traps were positioned approximately 3–20 m apart, depending on where the bushes occurred and were spread over the approximately 0.07-km^2 sampling area. The traps were removed from bushes in July, after no fly was captured for two consecutive weeks. Flies were removed from traps weekly and transported to the laboratory, where they were counted and morphologically identified according to Foote *et al.* (1993). At Cowiche, we inadvertently combined data for male and female *E. canadensis* on 19 April 2024.

Currant bushes and flies were monitored at Union Gap in 2025, employing the same methods described above to determine whether the temporal distribution patterns observed in 2024 were consistent across years, using 10 new and 10 previously monitored bushes at the site. Traps were deployed in the bushes on 20 May, missing the earliest flight periods at the site. We monitored fruiting phenology and fly catches weekly by recording fruit colours and counting flies on traps in each of the 20 bushes until 9 July. We did not collect fruit for trait measurements in 2025.

Seasonal air temperatures and adult fly catch periods (2024 and 2025)

We documented air temperatures when adult *E. canadensis* and *R. ribicola* were active, as activity or survival (or both) at different temperatures may be a physiological trait correlated with fruiting development that keeps the species apart and contributes to coexistence. In 2024, we deployed two Hobo data loggers (Onset, Bourne, Massachusetts, United States of America) in currant bushes at the Union Gap and Cowiche sites. In 2025, we deployed one data logger at Union Gap. Hourly air temperatures and relative humidity were recorded during the entirety of the fruiting phenology and fly-catch monitoring periods in both years.

Do the two fly species differ in eclosion timings in the laboratory? (2024)

To evaluate the relationship of adult fly activity periods with eclosion timing, we reared *E. canadensis* and *R. ribicola* collected as larvae in infested fruit from Union Gap in 2024 to adulthood under controlled conditions (see the section, Do the two fly species tend to infest fruit of different stages? What are the abundances and niche overlaps of larvae of the two flies? (2023, 2024, and 2025), below, for 2024 fruit collection dates and numbers at Union Gap). Fruit were transported to the laboratory and placed in plastic tubs held at approximately 21 °C. Larvae emerging from fruit and pupating in the tubs were collected daily. Puparia were placed in moist white aquarium sand inside 59-mL plastic cups, each cup containing from one to 50 puparia. Puparia in cups were then chilled at a mean temperature of 3.7 °C (range, 2.6–5.3 °C) for 180–186 days. There were 22 and 72 replicate cups for *E. canadensis* and *R. ribicola*, respectively. Puparia in cups (100% relative humidity) were then transferred to a mean temperature of 23.8 °C (range, 20.3–26.7 °C) under a 16:8-hour light:dark photoperiod. Cups were monitored for newly eclosing flies on weekdays for 60 days following chilling, with adults collected on Monday assigned the preceding Sunday eclosion date.

Do distributions of fly eggs and larvae depend on fruit maturity stages and, related to this, are eggs laid singly? (2024)

In 2024, we determined (1) the distribution of eggs and larvae present in golden currant fruit at varying stages of maturation, and (2) the proportions of eggs laid singly into fruit. Fruit samples were randomly collected from five bushes in 2024 at Union Gap on 20 May and 10 and 17 June ($n = 334$–1089 fruit per date). In addition, one sample each was made on 17 June at Cowiche

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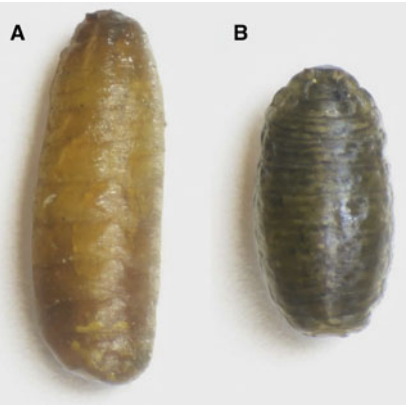


Figure 2. Puparia of **A,** *Euphranta canadensis* (4.35 mm length) and **B,** *Rhagoletis ribicola* (2.80 mm length; same scale) from golden currant (*Ribes aureum*) fruit at Union Gap, Washington state, United States of America, in June 2024.

($n = 1107$ fruit) and Selah ($n = 773$ fruit). Four samples were collected from 18 May to 7 June at Tampico ($n = 252$ total fruit). In the laboratory, currants were divided into the five colour stages (Fig. 1F). Fruit were classified into colour categories within approximately 4 hours of collection because we had found that fruit changed colour within one day of collection. Under a microscope, each fruit was examined and opened using forceps, and the numbers of eggs and larvae present counted. The species identity of fly eggs and larvae feeding within fruit were not determined.

Do the two fly species tend to infest fruit of different stages? What are the abundances and niche overlaps of larvae of the two flies? (2023, 2024, and 2025)

We determined whether larvae of *E. canadensis* and *R. ribicola* occur in different maturation stages of golden currant fruit and at different times of the season in 2023, 2024, and 2025 by rearing larvae from each fruit stage. Time and fruit stage maturity are naturally linked because fruit mature as the season progresses. Sampling strategies differed across the three years as we learned how to maximise information from collections. In 2023, collections were made at one site to determine when the two species infest fruit over the season; after we determined this, we incorporated more sites in 2024 to see if the result was repeatable across sites; after that, in 2025, we asked whether infestations by the two species could be divided into the three periods of May, June, and July, adjusting our fruit collections with this in mind. From data on infestation in different fruit stages in 2024 and 2025, we also obtained larval abundance and niche overlap metrics.

We randomly collected fruit from 5–20 bushes at six sites from 2023 to 2025 and transported the fruit to the laboratory for monitoring. In 2023, we sampled Union Gap; in 2024, we sampled Union Gap, Cowiche, and Tieton; and in 2025, we sampled Benton City, Bickleton, Ellensburg, Slavin Road, and Nile. In 2023, we collected fruit for 11 weeks, from 19 May to 14 July (21–2460 fruit per week; total of 4859). In 2024, collections were made 10 times, from 7 May to 2 July, at Union Gap (79–4482 fruit per date) and once each, on 7 June, at Cowiche (1095 fruit) and Tampico (896 fruit). In 2025, fruit were collected from 12 to 16 May, from 4 to 20 June, and from 9 to 17 July (589–8741 fruit per site per date), although not all sites were sampled during all three periods. We did not record the colours of fruit in 2023, but we did record them in 2024 and 2025. Fruit belonging to each of the five colour classes (Fig. 1F) in 2024 and 2025 were held in separate tubs for larvae to emerge and pupate. Puparia in the tubs were counted every 3–5 days until 30 days post-fruit collection, when all fruit had dried, after which no more larvae emerged. We stopped monitoring after 30 days and counted the dried fruit 1–2 months later, at which time no

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puparia were recovered. Puparia were identifiable to species: *E. canadensis* puparia (Fig. 2A) are elongate and tan, and *R. ribicola* puparia are stouter and dark grey or black (Fig. 2B).

Do emergence timings of larvae of the two fly species from fruit following fruit collection differ? (2024, 2025)

As an extension of the previous questions, in 2024, we investigated when larvae of the two species emerged from the same fruit collections. Differences in emergence timing could reflect different-aged immature insect stages being present in fruit, mitigating interspecific competition among larvae. Fruit from about 10–15 bushes at the Union Gap, Tieton, and Cowiche sites were collected. Colours of representative subsamples of fruit were recorded (89–4302 per collection date). We sampled bushes at Union Gap eight times, on 8 and 20 May, 10, 11, 17, 20, and 25 June, and 2 July (161–7280 fruit per collection date). We sampled bushes at Tieton three times, on 28 May, 19 June, and 3 July, and at Cowiche once, on 17 June (255–3578 fruit per collection date). Numbers of larvae that emerged every 1–3 days were counted until 30 days after fruit collection, and their species identities were recorded. In 2025, we also followed emergence timing from a Cowiche sample collected on 16 June (2988 fruit).

Statistics

Seasonal catches of *E. canadensis* and *R. ribicola*. We assigned a number to each week of the season to determine whether catch timing of *E. canadensis* and *R. ribicola* differed (week 1 was one week after traps were deployed, week 2 was two weeks after deployment, and so forth). We used the Mann–Whitney *U* test to analyse weeks of fly catches on traps at Union Gap, where data were not normal and (or) where variances were not equal (Shapiro–Wilk test and Brown–Forsythe test of homogeneity of variance were $P < 0.05$). An independent *t*-test was used for catch-time data from Cowiche, where data were normal with no differences in variances. We present means (± standard error of the mean) so that data are biologically meaningful, but we also present mean rank sums (adjusting for sample size) when the Mann–Whitney *U* test was used.

Overlap in trap catches of fly species. Overlap in catches between the two fly species was estimated in two ways. The first estimate was based on the method of Batkhan (2022), with the length of overlap in trap catches, equating to flight periods of the two species, calculated as the minimum (A2, B2) − maximum (A1, B1) + 1, where A2 and B2 represent the last weeks and A1 and B1 the first weeks of *E. canadensis* and *R. ribicola* catches, respectively. The second estimate was calculated as the percent overlap in which the two species co-occurred out of the total catches in the season.

Do abundances of the two flies differ?. We conducted four separate analyses of fly abundance. At the Union Gap site in 2024, we compared (1) female *E. canadensis versus* female *R. ribicola*, and (2) male *E. canadensis versus* male *R. ribicola*; at the Cowiche site in 2024, we also compared (3) females and (4) males of the two species separately. An insufficient number of flies were captured at Tampico for analyses. For each of the four analyses, we used the PROC GENMOD procedure in the Statistical Analysis System (SAS Institute Inc. 2023), which fits counts using the Poisson distribution in a generalised linear model. In the SAS output, the Pearson and deviance chi-square statistics divided by their degrees of freedom were substantially greater than 1, indicating overdispersion. We therefore modelled overdispersion using the negative binomial distribution, which resulted in significant maximum likelihood estimates of the dispersion parameter, suggesting the negative binomial was appropriate.

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Do the two fly species differ in eclosion timings in the laboratory?. Laboratory eclosion times generated for adult *E. canadensis versus R. ribicola* from larvae from 2024 collections were compared using an independent *t*-test for females (normal, equal variances) and a Mann–Whitney *U* test for males.

Do distributions of fly eggs and larvae depend on fruit maturity stages, and related to this, are eggs laid singly?. We conducted R × C contingency analyses to determine if numbers of eggs and larvae in golden currants depended on fruit colour stage. To determine if proportions of different colour fruit with eggs and larvae within fly species differed, tests of multiple proportions, followed by Tukey-type multiple comparisons (Zar 1999), were performed.

Do the two fly species tend to infest fruit of different stages, and what are the larval abundances? (2023, 2024, and 2025). To determine if week of larval infestation (and therefore fruit stage) by *E. canadensis* differs from that by *R. ribicola* at Union Gap in 2023, we used a Mann–Whitney *U* test by designating week 1 as 19 May, up to week 9 as 14 July. Each larva was considered an observation and was assigned a week (1–9) according to the date it was detected infesting a golden currant fruit. For 2024 and 2025 infestation data, the infestation index for both species was the percentage of total fruit producing larvae within each of the five different fruit colour stages. Data for both species within sites in May, June, and July were analysed using a test of multiple proportions, followed by Tukey-type multiple comparisons. The analyses did not include cases in which no fruit of a specific colour stage was found infested on a collection date within a site.

Abundances of larval *E. canadensis* and *R. ribicola* in golden currant fruit (combining all fruit maturation stages) were calculated as numbers of larvae per fruit and analysed using a Wilcoxon signed-ranks test. Abundances in May, June, July, and all months combined were calculated using each site–date combination for 2024 and for 2025 as a replicate. One site within a month could be two replicates if sampled on different dates or years.

What are the niche overlaps of larvae of the two flies?. Resource niche overlap between *E. canadensis* and *R. ribicola* was calculated for the June 2024 and June 2025 fruit collections from which both species emerged from fruit, and for all months (May, June, and July) and sites combined for each year, using data collected on infestation of fruit of different stages as indicated by larval emergence. The total number of *E. canadensis* or *R. ribicola* larvae emerged from all fruit colour stages was determined. Then the proportions of larvae out of the total from each stage were determined, and the overlap was calculated based on the formula of Pianka (1974), following Krebs (2014), using the five fruit colour stages as food types, where P_{ij} and P_{ik} are the proportions of *E. canadensis* (*j*) and *R. ribicola* (*k*) larvae that emerged from a specific fruit colour stage (*i*) out of total proportion of larvae across all stages, respectively:

$$O_{jk} = \frac{\Sigma_i^n p_{ij} p_{ik}}{\sqrt{\Sigma_i^n p_{ij}^2 \Sigma_i^n p_{ik}^2}} \quad (1)$$

Do emergence timings of larvae of the two fly species from fruit following fruit collection differ?. For the 2024 post-collection larval emergence data, we conducted Mann–Whitney *U* tests to determine emergence days of *E. canadensis versus R. ribicola*. Sufficient larvae of the two species were collected to enable the analyses only for the Union Gap 10–17 June, Tieton 19 June, and

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Cowiche 17 June collections. Insufficient larvae were collected for the other six site–date combinations for analyses.

Results

Currant bush sizes and fruit loads (2025)

The average size of representative currant bushes at the five sites (Union Gap, Selah, Zillah, Nile, and Slavin Road) in 2025 was 1.8 ± 0.1 m tall (mean ± standard error of the mean) and 2.0 ± 0.2 m wide. The mean of number of fruit was 68 ± 16 per 30.5 cm of branch (range: 26–115). We estimated that more than 50% of bushes across sites had more than 5000 fruit, although fruit numbers were highly variable.

How is fruiting phenology related to differences in seasonal catches of *E. canadensis* and *R. ribicola*? (2024, 2025)

At Union Gap in 2024, only flowers were present on 1 April, but green fruitlets appeared by mid-April, followed by a succession of green to orange–red (and dry) fruit from April to July (Fig. 3A). All fruit dried and deteriorated by mid-July. Fruit of maximum size and orange–red colour indicative of full maturity were seen on 11 June (Fig. 3B), after which fruit declined in firmness while increasing in sugar levels (Fig. 3C). The first adult *E. canadensis* flies (Fig. 3D) were recorded on 16 April, when 80% of golden currant bushes at sites still had only blossoms and the remaining 20% had green fruit. The first *R. ribicola* catches (Fig. 3E) occurred on 21 May, when all bushes had green fruit, 90% had green–yellow fruit, 60% had yellow fruit, and 10% had yellow–orange fruit. Currant fruit stage, *E. canadensis* and *R. ribicola* catch, and fly overlap metrics are shown in Table 2.

At Union Gap in 2025, *E. canadensis* adults were caught earlier and were largely gone by the time numbers of *R. ribicola* began increasing. Sixty per cent of bushes had green fruit on 27 May (Fig. 4A), when most *E. canadensis* were caught on traps (Fig. 4B). Sixty per cent of bushes had green–yellow fruit and 85% had yellow fruit on 3 June (Fig. 4A), when the peak number of female *R. ribicola* was caught (Fig. 4C). Peak male *R. ribicola* catch occurred on 10 June, when 20% of bushes had green–yellow fruit and 60% had yellow fruit.

At Cowiche in 2024, fruit were increasing in size (Fig. 5A), were relatively firm, and had no detectable sugar levels (Fig. 5B) on 9 May, when *E. canadensis* abundance peaked (Fig. 5C). In contrast, *R. ribicola* (Fig. 5D) was first caught on 24 May, when fruit had stabilised in size. Currant fruit stage, *E. canadensis* and *R. ribicola* catch, and fly overlap metrics are shown in Table 2.

At Tampico in 2024, maximum fruit size (Fig. 6A), decreased firmness, and increased sugar levels (Fig. 6B) occurred in early July. Although only seven total flies were caught over the season at this site, *E. canadensis* (Fig. 6C) adults were trapped before fruit were at maximum size, when they were firm with no detectable sugar. In contrast, *R. ribicola* adults (Fig. 6D) were caught when fruit had reached maximum size, with declining firmness and 16.6% sugar content. Therefore, fruit maturity–fly detection relationships were similar at Tampico in 2024 to those at the two other sites. Due to the low fly catch numbers, we do not include Tampico data in Table 2.

Do abundances of the two flies differ? (2024)

Assuming traps were equally attractive to both species (no data tested this assumption), at Union Gap in 2024, female *E. canadensis* was approximately 15 times more abundant than *R. ribicola* (47.6 ± 10.8 *versus* 3.1 ± 1.1 flies per trap; $z = 3.68$; $P = 0.0002$), with male *E. canadensis* approximately nine times more abundant than male *R. ribicola* (33.5 ± 8.1 *versus* 3.9 ± 1.5 flies per trap; $z = 3.24$; $P = 0.0012$). However, at Cowiche (starting on 7 May), abundance of female *E. canadensis* and female *R. ribicola* did not differ (6.7 ± 1.7 and 5.9 ± 3.3 flies per trap,

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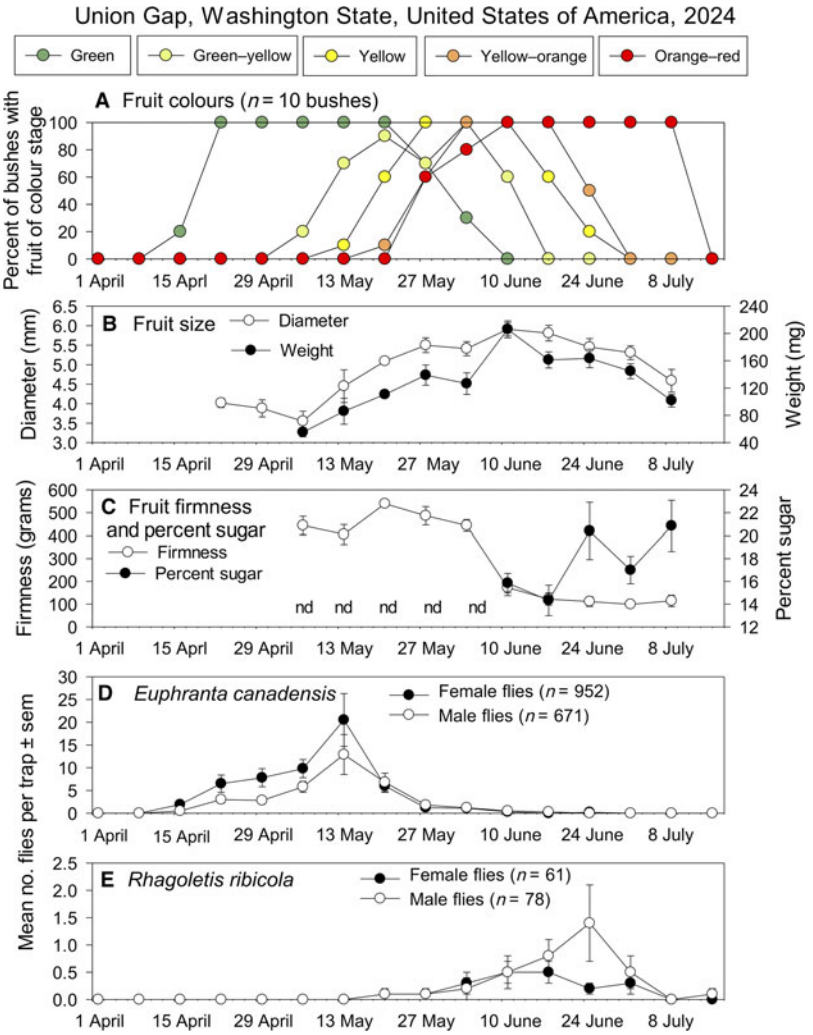


Figure 3. Seasonal distributions of golden currant (*Ribes aureum*) fruit and flies at Union Gap in Washington state, United States of America, in 2024: **A,** golden currant fruit colours; **B,** fruit size ± standard error of the mean; **C,** fruit firmness and percent sugar content ± standard error of the mean; **D,** numbers of flies per trap ± standard error of the mean for *Euphranta canadensis*; and **E,** *Rhagoletis ribicola*. There were no fruit on 1 April; only flowers. nd = sugar not detectable. Note: From 1 April to 21 May, the red colour was superimposed on other colours (green–yellow, yellow, and yellow–orange) along the x-axis. Dry fruit are included in orange–red category.

respectively; $z = 0.24$; $P = 0.8131$), nor did abundance of male *E. canadensis* and male *R. ribicola* (9.8 ± 2.4 and 5.7 ± 2.8 flies per trap, respectively; $z = 1.15$; $P = 0.2482$). As shown in Figures 6C and 6D, only seven total flies (four *E. canadensis* and three *R. ribicola*) were trapped at Tampico, so data from that site were not analysed statistically.

Seasonal air temperatures and adult fly catch periods (2024, 2025)

In 2024 at Union Gap (Fig. 7A) and Cowiche (Fig. 7B), more *E. canadensis* than *R. ribicola* were caught during the earlier, cooler part of the season (means per day are averaged from 24 hourly points). The mean temperature when *E. canadensis* was caught from 16 April to 25 June was 15.5 °C (range: 7.6–24.1 °C) *versus* 19.9 °C for *R. ribicola* (10.9–29.2 °C) from 21 May to 16 July.

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Table 2. Golden currant (*Ribes aureum*) fruit stage (± standard error of the mean), *Euphranta canadensis* and *Rhagoletis ribicola* capture (± standard error of the mean), and fly overlap metrics at Union Gap and Cowiche in Washington state, United States of America, in 2024. Fruit colours: G = green; Y–G = yellow–green; y = yellow; Y–O = yellow–orange; O–R = orange–red. Numbers before colours are numbers of bushes out of a maximum of 10 with fruit of that colour. Fruit colours were not recorded in Cowiche. "Female and male" means both sexes were on traps on the same date. [a]Male *R. ribicola* in Union Gap peaked on 25 June: fruit colour: 2 Y, 5 Y–O, 10 O–R; fruit diameter: 5.45 mm; fruit firmness: 111.3 grams; percent sugar: 20.4. [b]Week 1 was 1 week after traps were deployed, week 2 was 2 weeks after deployment, and so forth.

Union Gap (2024) – fruit and fly metrics				
	First flies		Peak flies	
Fruit variable	Female and male *E. canadensis* 16 April	Female and male *R. ribicola* 21 May	Female and male *E. canadensis* 14 May	Female *R. ribicola* 11 June; 18 June[a]
Fruit colour (10 bushes)	2 G	10 G, 9 Y–G, 6 Y, 1 Y–O	10 G, 7 Y–G, 1 Y	6 Y–G, 10 Y, 10 Y–O, 10 O–R; 6 Y, 10 Y–O, 10 O–R
Fruit diameter (mm)	< 4	5.09 ± 0.05	4.45 ± 0.42	5.91 ± 0.17; 5.81 ± 0.20
Fruit firmness (grams)	Not measured	539.2 ± 11.1	404.8 ± 43.6	173.0 ± 35.9; 122.2 ± 27.0
Percent sugar	Not detectable	Not detectable	Not detectable	15.9 ± 0.9; 14.33 ± 1.3

Union Gap (2024) – Fly capture metrics			
	E. canadensis	*R. ribicola*	Mann–Whitney *U* statistics on mean rank sums
Females, mean capture week[b]	6.2 ± 0.1 weeks	11.1 ± 0.4 weeks	10.5 *versus* 27.5; $Z = -4.90$; $P < 0.001$
Males, mean capture week[b]	6.6 ± 0.2 weeks	12.6 ± 0.4 weeks	10.0 *versus* 27.0; $Z = -4.94$; $P < 0.001$
Overlap of female *E. canadensis* with female *R. ribicola*			6 weeks
Overlap of male *E. canadensis* with male *R. ribicola*			5 weeks
Percent seasonal overlap of *E. canadensis* with *R. ribicola*			21.1%
Percent seasonal overlap of *R. ribicola* with *E. canadensis*			87.8%

Cowiche (2024) – fruit and fly metrics				
	First flies		Peak flies	
Fruit variable	Female and male *E. canadensis* 29 April	Female and male *R. ribicola* 24 May	Female and male *E. canadensis* 9 May	Female and male *R. ribicola* 2 July
Fruit diameter (mm)	~3	4.38 ± 0.12	3.42 ± 0.10	6.32 ± 0.19
Fruit firmness (grams)	Not measured	529.0 ± 16.9	682.3 ± 21.5	124.8 ± 9.4
Percent sugar	Not detectable	Not detectable	Not detectable	15.8 ± 0.4

Cowiche (2024) – Fly capture metrics			
	E. canadensis	*R. ribicola*	Independent *t*-test statistics
Females, mean capture week[b]	2.1 ± 0.2 weeks	6.3 ± 0.4 weeks	$t = -10.00$; $P < 0.0001$
Males, mean capture week[b]	3.2 ± 0.2 weeks	6.2 ± 0.4 weeks	$t = -7.03$; $P < 0.0001$
Overlap of female *E. canadensis* with female *R. ribicola*			5 weeks
Overlap of male *E. canadensis* with male *R. ribicola*			4 weeks
Percent seasonal overlap of *E. canadensis* with *R. ribicola*			40.8%
Percent seasonal overlap of *R. ribicola* with *E. canadensis*			58.9%

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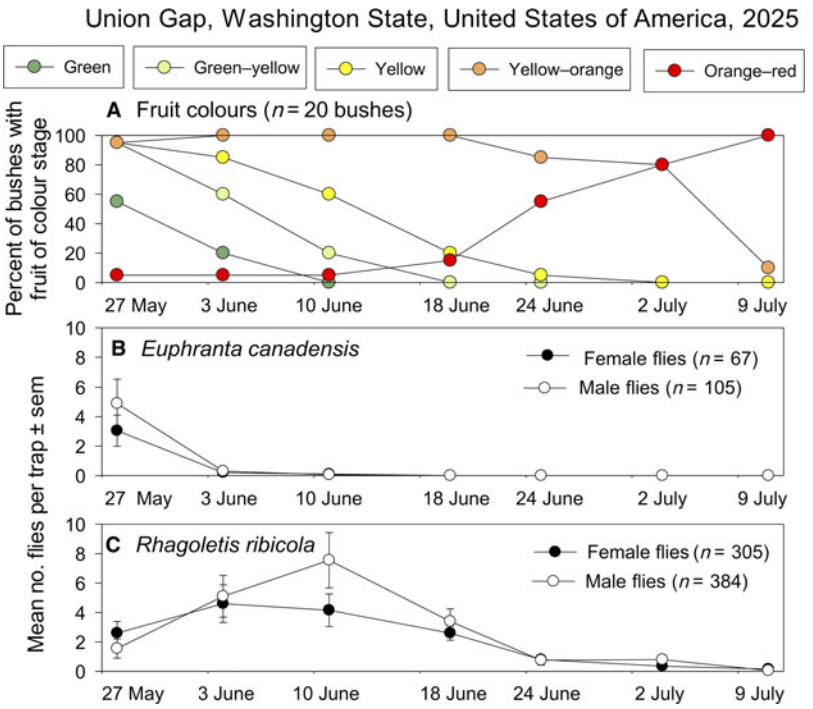


Figure 4. Seasonal distributions of golden currant (*Ribes aureum*) fruit and flies at the Union Gap site in Washington state, United States of America, in 2025: **A,** golden currant fruit colours; **B,** numbers of flies per trap ± standard error of the mean for *Euphranta canadensis*; and **C,** *Rhagoletis ribicola*. Dry fruit are included in orange–red category.

Mean relative humidity during each of the two respective periods was 50.5% and 49.5%. At Cowiche, the mean temperature when *E. canadensis* was caught from 29 April to 25 June was 14.8 °C (–2.1–35.0 °C) *versus* 18.1 °C (0.2–41.0 °C) when *R. ribicola* was caught from 24 May to 9 July. Mean relative humidity during each of the two respective periods was 53.3% and 49.5%. In 2025 at Union Gap (not shown in a figure), the mean temperature between 20 May and 9 July when *R. ribicola* was caught was 20.0 °C (5.1–36.7 °C), close to that of 2024, with a mean relative humidity of 58.6%.

Do the two fly species differ in eclosion timings in the laboratory? (2024)

Under laboratory conditions, *E. canadensis* eclosed earlier than *R. ribicola* (Fig. 8A, B), which is consistent with the earlier catches of *E. canadensis* in the field. In addition, females of both species (Fig. 8A) eclosed before males of their own species did (Fig. 8B), matching the sex-related difference observed in the field trapping studies. For *E. canadensis* females, the mean day of eclosion (15.6 ± 1.1 days) was significantly earlier than that of *R. ribicola* females (22.5 ± 0.3 days; $t = -8.93$; $P < 0.0001$). Similarly, for *E. canadensis* males, the mean eclosion day (17.0 ± 1.0 days) was significantly earlier than that of *R. ribicola* males (23.3 ± 0.2 days; mean rank sums of 24.0 *versus* 57.7; $z = -5.16$; $P < 0.001$).

Do distributions of fly eggs and larvae depend on fruit maturity stages, and related to this, are eggs laid singly? (2024)

Table 3 shows that yellow–orange fruit in June at the Union Gap and Selah sites (the two locations with sufficient data) was the class of fruit most heavily infested with eggs and larvae

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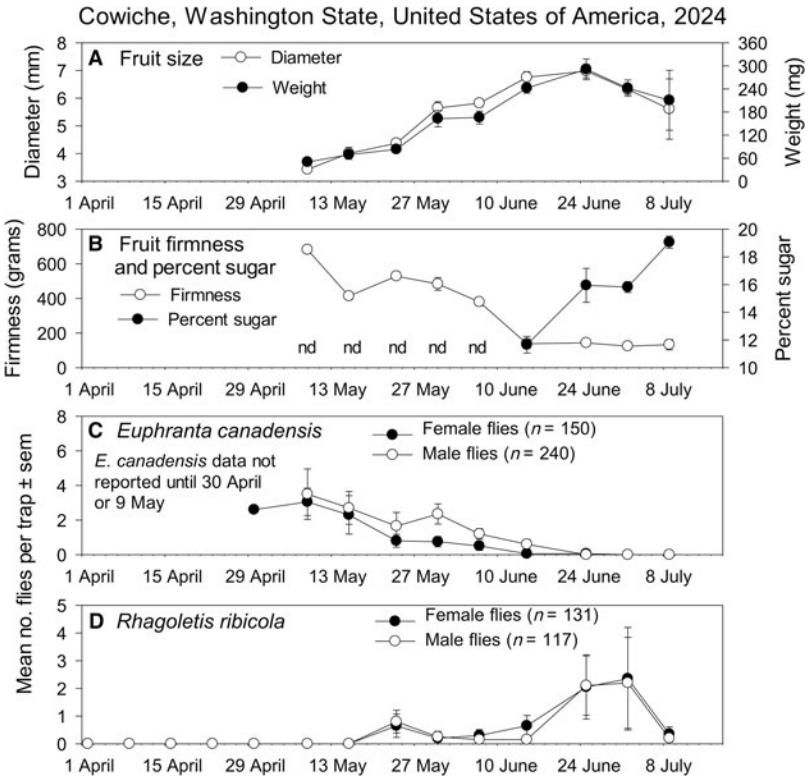


Figure 5. Seasonal distributions of golden currant (*Ribes aureum*) fruit and flies at the Cowiche site in Washington state, United States of America, in 2024: **A,** fruit size ± standard error of the mean; **B,** fruit firmness and percent sugar content ± standard error of the mean; **C,** numbers of flies per trap ± standard error of the mean for *Euphranta canadensis*; and **D,** *Rhagoletis ribicola*. nd, sugar not detectable.

(21.6% and 60.4% of the total detected, respectively), followed by yellow and orange–red fruit, and then green–yellow fruit. Considering the yellow–orange fruit stage from Union Gap, Cowiche, Selah, and Tampico combined ($n = 1239$ fruit total from 31 May and June collection dates), the percentage of fruit with eggs and larvae was 15.9%. Out of 422 total eggs and larvae (not distinguished to fly species) detected in 4009 currants assayed, 96.7% occurred singly (97.2% of 290 eggs at Union Gap, 100% of 15 eggs at Cowiche, and 94.9% of 117 eggs at Selah; no eggs in Tampico fruit samples).

Do the two fly species tend to infest fruit of different stages, and what are the larval abundances? (2023, 2024, and 2025)

Only larvae of *E. canadensis* and *R. ribicola* emerged from golden currant fruit in all three years of the study. Significant differences were detected in the time when *E. canadensis* and *R. ribicola* larvae infested golden currant fruit, with the pattern remaining consistent across years. We did not classify fruit into different stages in 2023 at Union Gap, but we can infer that earlier-season fruit are less mature than later-season fruit. In 2023 at Union Gap (Fig. 9), 31 of the 32 *E. canadensis* larvae (96.9%) emerged in May from less mature fruit stages than from fruit in June, when 29 of 32 *R. ribicola* larvae (90.6%) emerged. Correspondingly, the larval infestation week of golden currant fruit by *E. canadensis* larvae was significantly earlier than that by *R. ribicola* (2.4 ± 0.2 *versus* 6.1 ± 0.1 weeks, respectively; mean rank sums of 17.0 and 48.0, respectively; $z = -6.67$; $P < 0.001$).

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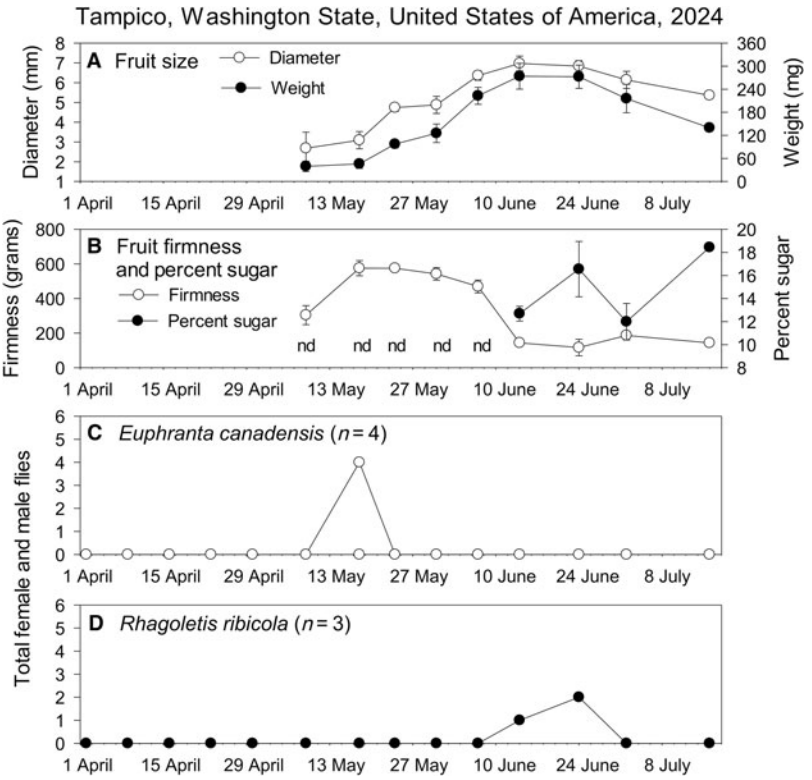


Figure 6. Seasonal distributions of golden currant (*Ribes aureum*) fruit and flies at the Tampico site in Washington state, United States of America, in 2024: **A,** fruit size ± standard error of the mean; **B,** fruit firmness and percent sugar content ± standard error of the mean; **C,** numbers of flies per trap ± standard error of the mean for *Euphranta canadensis*; and **D,** *Rhagoletis ribicola*. nd, sugar not detectable.

Table 4 shows percentages of golden currant fruit in different maturation stages producing fly larvae in May, June, and July 2024. Only *E. canadensis* larvae emerged from fruit collected in May at Union Gap, mostly from the green–yellow stage of fruit. However, both *E. canadensis* and *R. ribicola* emerged from fruit collected in June. Most *E. canadensis* emerged from yellow fruit (45.2% of all stages present at the time), whereas most *R. ribicola* emerged from orange–red fruit (also 45.2% of all stages present). The intermediate yellow–orange stage (28.7% of all fruit in June) was most likely to have larvae of both species. Only *R. ribicola* larvae emerged from fruit collected in July, when all fruit were orange–red or dried (Table 4).

Table 5 shows that May 2025 fruit produced only *E. canadensis*, with more *E. canadensis* emerging from yellow to orange–red fruit (33.0 and 47.2%) than from green or green–yellow fruit. In addition to data in Table 5, a 16 May 2025 collection from Union Gap of 4795 currants that were not divided into colour classes produced 31 *E. canadensis* and no *R. ribicola* puparia. Similarly, 17 039 currants collected on the same day from Cowiche and not divided by colour produced 28 *E. canadensis* and no *R. ribicola* puparia.

Table 6 shows that June 2025 fruit produced both *E. canadensis* and *R. ribicola*. Variability occurred in the percentages of both fly species infesting fruit of different colour stages across the 10 site–date combinations as expected, with generally low infestations (0–55.7% per fruit colour stage for *E. canadensis* and 0–29% for *R. ribicola*) accounting for some nonsignificant differences within site–date combinations. However, overall percentages (combining all site–dates; in the "Totals" row, bottom of Table 6) that produced *E. canadensis* did not differ in the most immature *versus* most mature fruit. Specifically, percentage infestations of fruit by *E. canadensis* were

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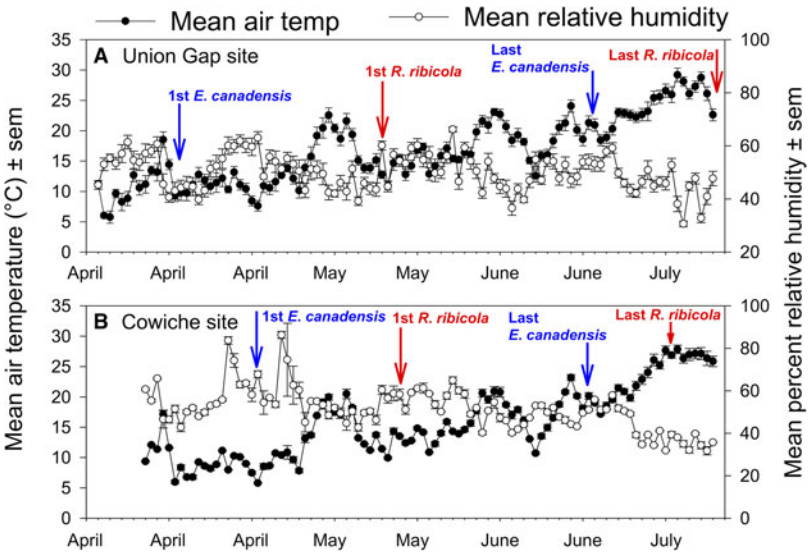


Figure 7. Mean daily seasonal air and relative humidity ± standard error of the mean (from two data loggers) and first and last trap catches of *Euphranta canadensis* and *Rhagoletis ribicola* in golden currant (*Ribes aureum*) bushes at: **A,** Union Gap and **B,** Cowiche sites in Washington state, United States of America, in 2024.

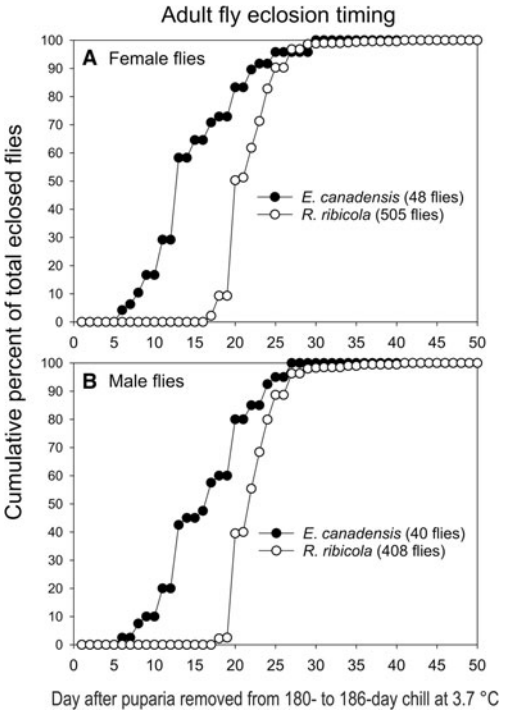


Figure 8. Cumulative eclosion curves of adult **(A)** female and **(B)** male *Euphranta canadensis* and *Rhagoletis ribicola* reared from golden currant (*Ribes aureum*) fruit collected at Union Gap, Washington state, United States of America, at 23.8 °C in the laboratory after puparia were chilled for 180–186 days at 3.7 °C.

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green = green–yellow = yellow, and green = orange–red. In contrast, higher overall infestation percentages by *R. ribicola* (totals, last row in Table 6) occurred in more mature fruit than in less mature fruit. Specifically, percentage infestations by *R. ribicola* of fruit were orange–red = yellow–orange > yellow > green–yellow, with no infestation in the green, the most immature stage. A 9 June 2025 collection of 5523 currants from Fort Simcoe that were not separated by colour produced 36 *E. canadensis* and 88 *R. ribicola* puparia, again showing co-occurrence of the two species in June fruit collections.

In July 2025 (no table shown), only orange–red fruit were present. Only *R. ribicola* emerged from 7.1% of 11 363 orange–red fruit across four sites. The sites and fruit numbers are as follows: Union Gap, 9 July: 3398 fruit and 68 puparia; Nile, 9 July: 2437 fruit and 704 puparia; Slavin, 10 July: 4394 fruit and 17 puparia; Ellensburg, 19 July: 1134 fruit and 16 puparia.

From the infestation data, we calculated the percentages of fruit that did not produce larvae, assuming one larva per fruit. In 2023, no larva emerged from 98.7% of 4859 fruit that produced 64 larvae collected from Union Gap. In 2024, no larva emerged from 94.4% of a total of 15 887 fruit that produced 890 larvae; in addition, none emerged from 91.4% of 2573 yellow–orange fruit (Table 4; May, June, and July: the 15 887 total fruit is the sum of all numbers inside the parentheses in the table; total larvae can be calculated based on summing up all percentages). In 2025, no larvae emerged from 95.5% of 88 137 total fruit, which produced 3966 larvae, and no larvae emerged from 91.3% of 11 344 yellow–orange fruit sampled from May to June from eight sites (total 2025 fruit are from Table 5, May; Table 6, June; also from May and June fruit that were not colour classified, and July (no table) fruit; all numbers stated in the three previous paragraphs).

In the May 2024 and 2025 fruit collections, the mean larval abundances across all fruit stages and sites were 0.0274 ± 0.0156 larvae/fruit for *E. canadensis* and no (0) larvae/fruit for *R. ribicola* (n = 39 755 total fruit). In June collections, mean larval abundances were 0.0306 ± 0.0159 larvae/fruit for *E. canadensis* and 0.0625 ± 0.0240 larvae/fruit for *R. ribicola* (n = 48 424 total fruit; z = –0.8475, P = 0.3953). In July collections, no *E. canadensis* was present, but the mean larval abundance of *R. ribicola* was 0.0771 ± 0.0537 (15 845 total fruit). For the entire season combined, the mean larval abundances were 0.0238 ± 0.0096 for *E. canadensis* and 0.0485 ± 0.0169 for *R. ribicola* (z = –0.7714, P = 0.4413).

What are the niche overlaps of larvae of the two flies? (2024, 2025)

Niche overlap was based on percentages of *E. canadensis* and *R. ribicola* larvae infesting golden currant fruit of the same colour (maturation) stage within sites at the same time of the season. No niche overlap was detected in May 2024 (Table 4) and May 2025 (Table 5; only *E. canadensis* emerged from May samples in both years) or in July 2024 (Table 4) and July 2025 (no table; only *R. ribicola* emerged from July samples in both years).

For June fruit collections (June 2024, Table 4; June 2025, Table 6) from which both *E. canadensis* and *R. ribicola* larvae emerged, sufficient data were obtained for only five of 13 date–site combinations to allow niche-overlap estimates. These sites were Union Gap and Tampico in 2024 and Benton City, Cowiche, and Ellensburg in 2025. Tables 4 and 6 show these sites and the infestations in them across the fruit colour stages used to determine proportions for the niche overlap formula provided in Materials and methods. In June 2024, niche overlap between species was 0.649 at Union Gap and 0.543 at Tampico. In June 2025, it was 0.996 at Benton City, 0.986 at Cowiche, and 0.982 at Ellensburg. Based on these estimates, a relatively high degree of niche overlap was limited to only one portion of the season. When considering the entire season comprising May, June, and July for all sites, overall niche overlap was reduced to 0.425 in 2024 and to 0.582 in 2025.

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Table 3. Numbers of eggs and larvae of *Euphranta canadensis* and *Rhagoletis ribicola* infesting different maturation stages of golden currant (*Ribes aureum*) fruit at four sites in Washington state, United States of America, in May and June 2024. Fruit colour stages: G = green; G–Y = green–yellow; Y = yellow; Y–O = yellow–orange; O–R = orange–red. Numbers in parentheses are the number of fruit in a given maturation stage collected at random and analysed for infestation on the indicated date at a site. For No. eggs and No. larvae, R × C contingency tests were conducted to test dependence of eggs or larvae on fruit maturation (colour) stage. For percentages of fruit stages with eggs or larvae, tests of multiple proportions followed by Tukey-type multiple comparisons were conducted. Green fruit were not included in either of these two analyses. Percentages of fruit infested with eggs or larvae on given collecting dates at sites followed by the same letter are not significantly different ($P > 0.05$). [a]Two eggs in one fruit. [b]Two eggs in each of three fruit. [c]One egg in one fruit with one larva. [d]Two larvae in one fruit; — = no or too few puparia for analysis.

Site	Date	Variable	G	G–Y	Y	Y–O	O–R	Statistics
Union Gap	20 May	No. eggs	8 (334)	0	0	0	0	—
		No. larvae	0	0	0	0	0	—
		% fruit with eggs or larvae	2.4	0	0	0	0	—
Union Gap	10, 17 June	No. eggs	0 (3)	20[a] (328)	47 (364)	156[b] (754)	34 (346)	$\chi^2 = 48.14$; $P < 0.0001$
		No. larvae	0	0	3	10	12	$\chi^2 = 13.96$; $P < 0.0001$
		% fruit with eggs or larvae	0	5.8[c]	13.7[b]	21.6[a]	13.3[b]	$\chi^2 = 47.26$; $P < 0.0001$
Tampico	18–31 May	No. eggs, larvae	0 (168)	0 (12)	0	0	0	—
	7 June	No. eggs, larvae	0	0	(23)	0 (49)	0	—
Selah	14 June	No. eggs	0 (9)	16[a] (389)	32 (201)	9[c] (48)	16[a] (126)	$\chi^2 = 30.54$; $P < 0.0001$
		No. larvae	0	0	17	22[c, d]	5	$\chi^2 = 152.78$; $P < 0.0001$
		% fruit with eggs or larvae	0	3.9[c]	24.4[b]	60.4[a]	15.9[b]	$\chi^2 = 137.36$; $P < 0.0001$
Cowiche	17 June	No. eggs	0	2 (401)	1 (226)	2 (394)	0 (86)	$\chi^2 = 1.36$; $P = 0.7149$
		No. larvae	0	5	2	3	0	$\chi^2 = 0.53$; $P = 0.9124$
		% fruit with eggs or larvae	0	1.8	1.3	1.3	0	$\chi^2 = 1.28$; $P = 0.7337$

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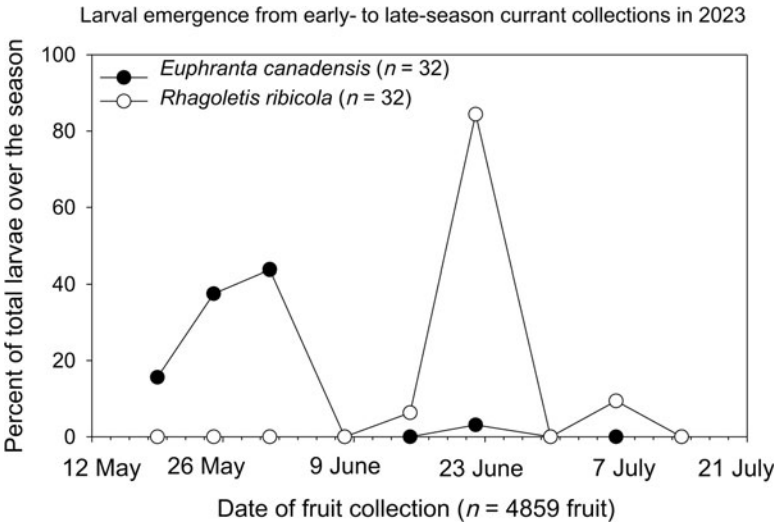


Figure 9. Seasonal distributions of *Euphranta canadensis* and *Rhagoletis ribicola* larvae emerging from golden currant (*Ribes aureum*) fruit collected at Union Gap in Washington state, United States of America, in 2023.

Do emergence timings of larvae of the two fly species from fruit following fruit collection differ? (2024, 2025)

Figures 10 and 11 show the emergence timings of larvae of *E. canadensis* and *R. ribicola* following fruit collections. Green fruit collected in May 2024 produced only *E. canadensis*, with less ripe fruit from 8 May (Union Gap, Fig. 10A) producing larvae on average more than 3 weeks after collection and riper fruit from 20 and 28 May producing larvae 2–13 days after collection (Union Gap, Fig. 10B; Tieton, Fig. 11A). Fruit collected in June 2024 produced both species, with the emergence of *E. canadensis* occurring statistically earlier than that of *R. ribicola* (Union Gap, Fig. 10C, D; Tieton, Fig. 11B; Cowiche, Fig. 11C). For fruit collections on the four June sample periods that were infested by both species, *E. canadensis* larvae emerged 5.5–10.7 days (mean, 8.3 days) earlier on average than *R. ribicola* did (range and mean from: Union Gap, 10–17 June: 12.2 days − 6.7 days = 5.5 days, Fig. 10C; Union Gap, 20, 25 June: 10.7 days − 3.5 days = 7.2 days, Fig. 10D; Tieton, 19 June: 14.9 days − 4.2 days = 10.7 days, Fig. 11B; Cowiche, 17 June: 16.0 days − 6.4 days = 9.6 days, Fig. 11C). Only *R. ribicola* larvae emerged from July 2024 fruit (Union Gap, Fig. 10E; Selah, Fig. 11D), within 14 days following collection, earlier than from less mature fruit. Patterns seen in 2024 were also detected in 2025. From 2988 yellow–orange fruit collected at Cowiche on 16 June (not shown in a figure), 21 *E. canadensis* emerged from 17 to 25 June, and 50 *R. ribicola* emerged from 24 June to 4 July. Thus, only a 1-day overlap was observed in interspecific larval emergence in 2025.

Discussion

Temporal partitioning

In the *E. canadensis*–*R. ribicola*–golden currant system in central Washington state, we found evidence for temporal resource partitioning of shared fruit resources, an axis of niche differentiation facilitating species coexistence (Chesson 2000). The differences in phenology of the two fly species appear to largely result from the earlier adult eclosion time of *E. canadensis*. Previous studies have shown that eclosion time is genetically controlled in *Rhagoletis* (Ragland *et al.* 2017; Doellman *et al.* 2018; Dowle *et al.* 2020; Meyers *et al.* 2020; Calvert *et al.* 2021).

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Table 4. Percentages of golden currant (*Ribes aureum*) fruit in different maturation stages producing *Euphranta canadensis* (EC) and *Rhagoletis ribicola* (RR) puparia at three sites in Washington state, United States of America, from May to July 2024. Numbers in parentheses are numbers of fruit in the specific maturation stage collected at random and analysed for infestation on the indicated date at a site. Fruit colour stages: G = green; G–Y = green–yellow; Y = yellow; Y–O = yellow–orange; O–R = orange–red. Percentages followed by the same letter are not significantly different (Tukey-type multiple comparisons, $P > 0.05$). [a]Dried fruit, only in July; — = no or too few puparia for analysis.

Site	Date	Fly	No. puparia	G	G–Y	Y	Y–O	O–R	Within fly: χ^2; P
Union Gap	7–28 May	EC	117	1.4d (2000)	13.6c (418)	32.8ab (64)	17.9bc (28)	31.6a (19)	207.03; < 0.0001
		RR	0	0	0	0	0	0	—
Union Gap	4–24 June	EC	446	1.3ab (149)	2.4a (994)	4.5a (1168)	0.9a (2329)	0.7b (2245)	79.31; < 0.0001
		RR	619	0.7d	5.1c	8.0bc	8.3b	12.5a	66.71; < 0.0001
Cowiche	7 June	EC	24	0 (93)	0.4 (516)	0.7 (268)	0 (162)	5.4 (56)	—
		RR	4	1.1	0.4	0	1.1	0	—
Tampico	7 June	EC	22	0 (108)	1.3 (550)	6.6 (151)	7.4 (54)	3.0 (33)	—
		RR	7	0	1.3	0	0	0	—
Union Gap	2 July	EC	0	—	—	—	—	0 (4482)	—
		RR	264	—	—	—	—	5.9[a]	—

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Table 5. Percentages of golden currant (*Ribes aureum*) fruit in different maturation stages producing *Euphranta canadensis* (EC) and *Rhagoletis ribicola* (RR) puparia at four sites in Washington state, United States of America, in May 2025. Numbers in parentheses are numbers of fruit in the specific maturation stage collected at random and analysed for infestation on the indicated date at a site. Fruit colour stages: G = green; G–Y = green–yellow; Y = yellow; Y–O = yellow–orange; O–R = orange–red. Percentages followed by the same letter are not significantly different (Tukey-type multiple comparisons; $P > 0.05$). — = no or too few puparia for analysis.

Site	Date	Fly	No. puparia	G	G–Y	Y	Y–O	O–R	Within fly: χ^2; P
Benton City	12 May	EC	579	4.0c (3679)	24.2b (999)	34.4a (292)	33.0ab (97)	47.2a (89)	532.76; < 0.0001
		RR	0	0	0	0	0	0	—
Bickleton	14 May	EC	0	0 (3394)	0 (38)	0 (0)	0 (0)	0 (0)	—
		RR	0	0	0	0	0	0	—
Selah	16 May	EC	26	2.2b (912)	3.6b (111)	66.7a (3)	0 (0)	0 (0)	30.11; < 0.0001
		RR	0	0	0	0	0	0	—
Ellensburg	16 May	EC	0	0 (5560)	0 (218)	0	0	0	—
		RR	0	0	0	0	0	0	—
Totals		**EC**	**605**	**1.2c (13 545)**	**18.0b (1366)**	**39.7a (295)**	**33.0ab (97)**	**47.2a (89)**	**1960.68; < 0.0001**
		RR	**0**	**0**	**0**	**0**	**0**	**0**	—

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Table 6. Percentages of golden currant (*Ribes aureum*) fruit in different maturation stages producing *Euphranta canadensis* (EC) and *Rhagoletis ribicola* (RR) puparia at eight sites in Washington state, United States of America, in June 2025. Numbers in parentheses are numbers of fruit in the specific maturation stage collected at random and analysed for infestation on the indicated date at a site. Fruit colour stages: G = green; G–Y = green–yellow; Y = yellow; Y–O = yellow–orange; O–R = orange–red. Percentages followed by the same letter are not significantly different (Tukey-type multiple comparisons; $P > 0.05$). — = no or too few puparia for analysis.

Site	Date	Fly	No. puparia	G	G–Y	Y	Y–O	O–R	Within fly: χ^2; P
Nile	4 June	EC	45	3.7b (272)	2.3b (1,326)	33.3a (15)	0 (0)	0 (0)	39.65; < 0.0001
		RR	3	0	0.2	0	0	0	—
Slavin	5 June	EC	353	2.8b (71)	2.5b (8,424)	56.6a (182)	55.7a (61)	0 (3)	1099.69; < 0.0001
		RR	0	0	0	0	0	0	—
Benton City	12 June	EC	367	0 (0)	0 (0)	0 (0)	0 (15)	22.8 (1607)	—
		RR	345	0	0	0	13.3	21.3	0.39; 0.5321
Cowiche	16 June	EC	26	0 (56)	0 (397)	0.2 (604)	0.5 (804)	0.7 (3018)	2.54; 0.2813
		RR	75	0	0.8	0.7	2.2	1.7	7.26; 0.0642
Bickleton	18 June	EC	0	0 (0)	0 (62)	0 (147)	0 (226)	0 (515)	—
		RR	1	0	0	0.7	0	0	—
Union Gap	18 June	EC	1	0 (0)	0 (0)	0 (52)	0.02 (4448)	0 (164)	—
		RR	690	0	0	0	15.3a	6.7b	7.24; 0.0071
Slavin	18 June	EC	4	0 (0)	0 (0)	0.1 (932)	0.09 (3393)	0 (842)	—
		RR	28	0	0	0.4	0.7	0.1	4.15; 0.1258
Selah	20 June	EC	1	0 (0)	0 (12)	0 (31)	0.3 (324)	0 (222)	—
		RR	165	0	0	16.1	29.3	29.3	1.53; 0.4665
Nile	20 June	EC	6	0 (0)	0 (243)	0.1 (1592)	0.3 (1386)	0 (393)	—
		RR	86	0	0.4b	2.4ab	3.1a	0.8b	11.20; 0.0107
Ellensburg	20 June	EC	13	0 (0)	0 (333)	0.5 (370)	0.7 (590)	0.8 (893)	0.23; 0.8930
		RR	155	0	3.9c	3.0bc	7.6ab	9.6a	20.82; 0.0001
Totals		**EC**	**816**	**3.0ab (399)**	**2.3b (10 797)**	**2.9b (3925)**	**0.5c (11 247)**	**5.1a (7657)**	**413.44; < 0.0001**
		RR	**1547**	**0**	**0.2c**	**1.6b**	**8.0a**	**7.3a**	**911.95; < 0.0001**

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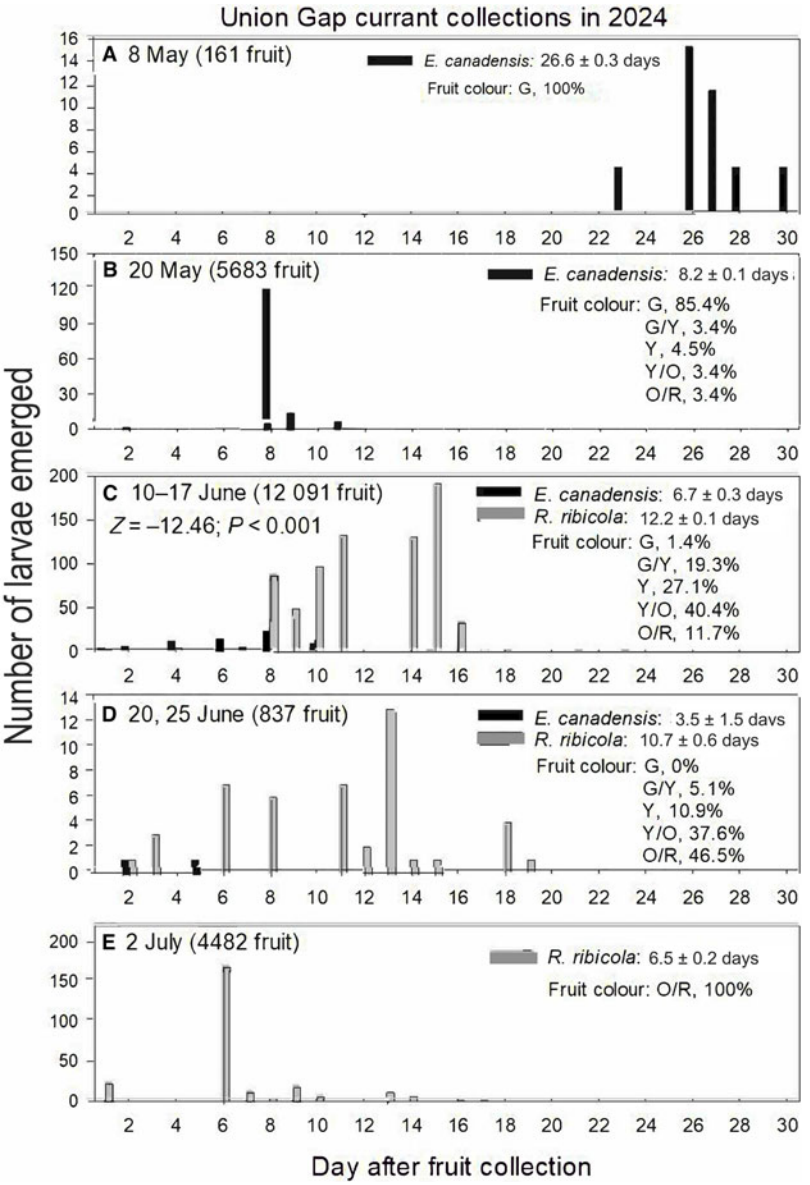


Figure 10. Larval emergence times for *Euphranta canadensis* and *Rhagoletis ribicola* in the laboratory from golden currant (*Ribes aureum*) fruit following their collection on different dates at Union Gap in Washington state, United States of America, in 2024: **A,** 8 May; **B,** 20 May; **C,** 10–17 June; **D,** 20, 25 June; and **E,** 2 July. Mean ± standard error of the mean for larval emergence of the two flies are given along with distributions of fruit colours for each collection date. *Z* statistic is from Mann–Whitney *U* test for mean rank sums.

Whether the same is true in *Euphranta* remains to be determined. Regardless, *E. canadensis*' earlier eclosion time likely results in the fly being reproductively active earlier, females ovipositing sooner in the season into more green fruit, and larvae feeding and emerging earlier in the year from golden currant than is observed for *R. ribicola*, reducing interspecific competition. At least in the laboratory, larval infestation of the same resource at the same time by two tephritid fly species can reduce measures of fly fitness (Liendo *et al.* 2018).

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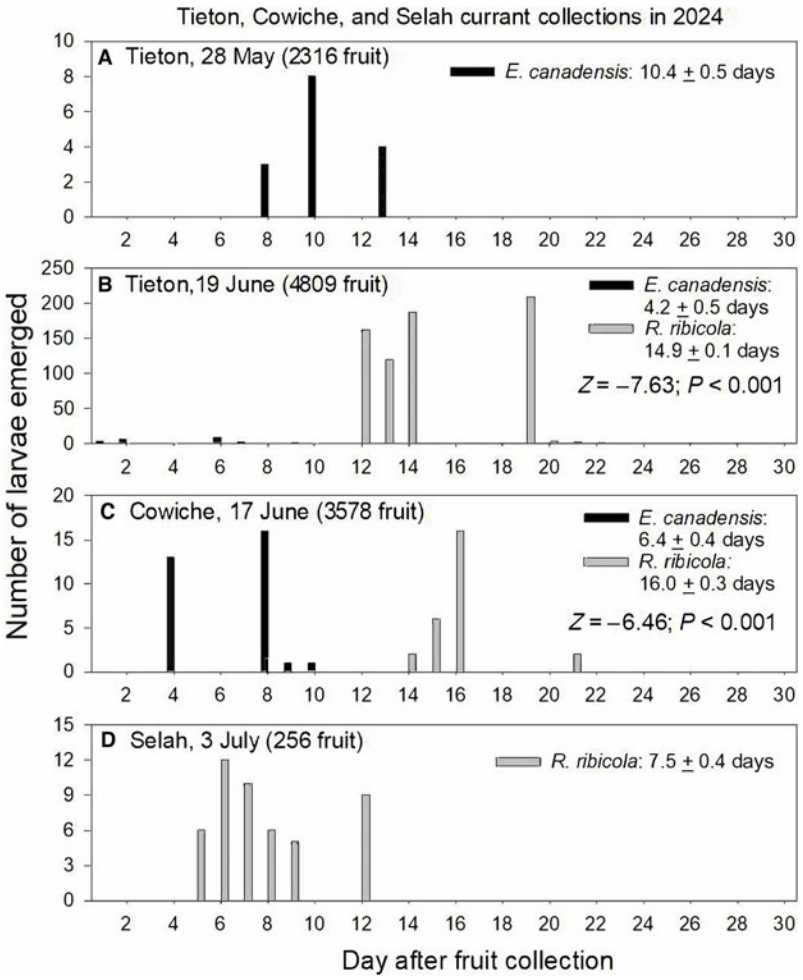


Figure 11. Larval emergence times for *Euphranta canadensis* and *Rhagoletis ribicola* in the laboratory from golden currant (*Ribes aureum*) fruit following their collection on different dates at three sites in Washington state, United States of America, in 2024: **A,** Tieton, collected 28 May; **B,** Tieton, collected 19 June; **C,** Cowiche, collected 17 June; and **D,** Selah, collected 3 July. Mean ± standard error of the mean for larval emergence of the two flies are given for each collection date. Fruit colours were not recorded for these collections. *Z* statistic is from Mann–Whitney *U* test for mean rank sums.

Presumably fruit and temperature factors associated with April to May or June in the past selected for when *E. canadensis* and *R. ribicola* adults are active. Specifically, less mature fruit, as indicated by smaller size, greater firmness, and less or no detectable sugar content, are associated with adult *E. canadensis* presence. Conversely, more mature fruit, greater fruit size, and less firm fruit with higher sugar levels are associated with *R. ribicola* presence. There also appears to be a cooler temperature niche for *E. canadensis* and a warmer temperate niche for *R. ribicola* that are associated with the maturation of fruit stages and leading to oviposition by flies. One can hypothesise that fruit and temperature factors play a role in coexistence if *E. canadensis* fares poorly when it ecloses in late season, and *vice versa* for *R. ribicola*.

Analysis of populations of the more widespread *E. canadensis* in other regions and other currant–gooseberry hosts would shed light on the source of selection for the fly species' earlier phenology compared to that of *R. ribicola*. If *E. canadensis* ecloses earlier than *R. ribicola* does only where the two species co-occur, this would support ecological character displacement.

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Alternatively, if *E. canadensis* differs similarly throughout its range, this would imply that selection for earlier eclosion enabled subsequent range or host expansion (or both) for the fly, allowing for *E. canadensis* and *R. ribicola* to co-occur. In support of the latter hypothesis, in Winnipeg, Canada, where *R. ribicola* has not been reported (Bush 1966; Foote *et al.* 1993), Mitchener (1927) observed that *E. canadensis* oviposited into currants that were three-quarters green. This suggests that earlier adult eclosion and a preference for attacking early fruit evolved in *E. canadensis* independently of the presence of *R. ribicola*.

The temporal division of limiting food resources has been observed for a wide range of insects and, therefore, given the ubiquity of insects and phytophagous insects in particular, would appear common in nature (*e.g.*, Headrick and Goeden 1990; Inbar and Wool 1995; Debouzie *et al.* 1996; Albrecht and Gotelli 2001; Yadav and Singh 2005; Agarwal and Rastogi 2009; Venner *et al.* 2011; Hood *et al.* 2021; Reut *et al.* 2021). However, temporal partitioning of host fruit resources has rarely been reported for temperate tephritids. Also, in the case of two temperate tephritids attacking knapweed, temporal partitioning did not appear to be a factor in coexistence (Mays and Kok 2003). Although temporal resource division helps ameliorate competition, the results of the present study also point to the likely involvement of other factors, such as fly behaviour, resource availability, and fly abundance, in allowing *E. canadensis* and *R. ribicola* to coexist.

Behavioural mechanisms

Females of both species appear to oviposit singly into fruit, thereby largely avoiding instances of multiple infestation. Such behaviour could reduce both intra- and interspecific competition. It can be hypothesised that if *R. ribicola* is like 10 other *Rhagoletis* species (Prokopy 1981), it deposits an oviposition-deterring pheromone that reduces the chances of conspecifics ovipositing into an egg-occupied fruit. Intraspecific larvae thus do not compete or risk cannibalisation (Balduf 1959). Interspecific competition could be avoided even further if there is interspecific recognition of oviposition-deterring pheromones. It is not known whether *E. canadensis* has an oviposition-deterring pheromone. Evidence for or against such pheromones playing a role in coexistence could be provided through experiments that expose clean fruit to *E. canadensis* or *R. ribicola*. Observations can then be made to determine whether flies of either or both species that sting fruit drag their aculei and deposit liquid on fruit. The fruit could then be exposed to flies and their behavioural responses to fruit recorded.

Resource availability and fly abundances

It can be hypothesised that low infestation levels of golden currants relative to high fruit abundance on bushes may also mitigate competition and contribute to species coexistence. Niche overlap was high for *E. canadensis* and *R. ribicola* in June. However, this may not result in interspecific competition if golden currant fruit are not a limiting resource for either tephritid species at this time. Under this scenario, coexistence can be maintained even when niche overlap measures are high (Pianka 1974; Sale 1974; Rusterholz 1981). The possibility of high resource levels that allow coexistence has been suggested for two moths attacking the same fruit stage of *Schoepfia schreberi* (Schoepfiaceae), which can occur and persist in high numbers during some parts of the season (López-Ortega *et al.* 2013). The same may be true for *E. canadensis* and *R. ribicola*. Additional studies on the availability of usable host resources throughout the field season and additional years of surveys at more sites would be necessary to confirm this hypothesis. Based on observations at our field sites in central Washington, it appears that golden currant fruit loads are high on plants in May and June, when flies are present. Specifically, visual estimates suggested more than 5000 fruit per plant for three consecutive years at the Union Gap site. However, this does not mean that of all these fruit or bushes are suitable for oviposition or

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infestation: Piper and Doane (1898), for example, reported that *R. ribicola* infestations in Washington are heavy in a few bushes but not in others within a patch.

Infestation rates of *R. ribicola* in currants and gooseberries outside of Washington state have not been reported, and it is therefore not possible to determine whether the low larval abundances – less than 10% of fruit with larvae – seen across sites in the present study are typical in other regions of western North America. However, *E. canadensis* infestations in California and Oregon, United States of America, were "heavy" in currant and gooseberry (Paine 1912; Jones 1937), although it is possible that fly population sizes or genetics due to climate or other unknown factors have changed over the last 100 years. In contrast to our results, other fruit in central Washington might be a limiting resource for *Rhagoletis*, forcing flies to lay eggs into already infested fruit. For example, 35–100% of sweet and tart cherries and 22–95% of bitter cherries can be infested by *R. indifferens*, 2–32% of snowberry fruit can be infested by *Rhagoletis zephyria* Snow, 4–27% of rose hips can be infested by *R. basiola*, and 100% of walnuts can be infested by *Rhagoletis completa* Cresson (Yee 2005, 2008).

We currently lack sufficient long-term data to know whether fruit loads in golden currants tend to be heavy in most years, as during the 2023–2025 period of the present study. If years occur when currant fruit loads are low, fly populations may decline as a result in succeeding years and may take many years to recover, which would explain the low infestation rates here. Low fruit loads may also increase rates of multiple infestation, increasing levels of competition. Surveys of fruit loads over larger geographic areas and more years are needed to support the hypothesis that low infestations play a role in coexistence.

In general, more widespread species tend to be more successful than rarer species (Brown 1984). This would imply that *E. canadensis*, being more widespread, should be more successful or more abundant than *R. ribicola*. However, although *E. canadensis* adults were significantly more abundant than *R. ribicola* at the Union Gap and Cowiche sites in 2024, we did not detect a significant difference in larval abundance between the two species in golden currant fruit. One possible explanation for this is that *E. canadensis* is less fecund than *R. ribicola*, because higher adult populations should be associated with greater larval abundance. For example, at Union Gap, *R. ribicola* was more abundant in 2025 (Fig. 4) than in 2024 (Fig. 3), and larval abundances in June 2025 and 2024 were correspondingly 0.148 and 0.09 larvae/fruit, respectively. Alternatively, differences in natural mortality, dispersal, or oviposition site (*i.e.*, bush location) may exist between the species. More work is needed to resolve the differences in abundances of adult and larval life stages of *E. canadensis* and *R. ribicola* infesting golden currant.

Comparative systems

We are aware of several other potential examples of seasonal partitioning of shared host fruit resources in temperate tephritids in addition to the *E. canadensis* and *R. ribicola* system described here and those involving cherry-infesting flies discussed in the Introduction. Specifically, walnut-infesting flies in the *Rhagoletis suavis* (Loew) species group form three different secondary contact zones in the United States of America (Bush 1966; Glover *et al.* 2018). In all three zones, different pairs of walnut flies co-occur and attack the same species of *Juglans* (Juglandaceae) host and even infest the same trees. In each contact zone, one of the two flies ecloses 2–4 weeks earlier in the season than the other, implying temporal subdivision of shared walnut resources similar to the temporal subdivision of currants by *E. canadensis* and *R. ribicola* observed in the present study. Another tephritid example centres on juniper-infesting species in the genera *Paraterellia* and *Rhagoletis*: this system is even more like the *E. canadensis* and *R. ribicola* system in that different tephritid genera are involved. In the *Paraterellia–Rhagoletis* system, several cases have been observed in which the two taxa attack the same *Juniperus* (Cupressaceae) host in sympatry but differ significantly by more than a month when they eclose as adults and infest juniper cones as

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larvae (Jeffrey L. Feder, unpublished data). Other examples of temporal resource partitioning among temperate tephritid fruit flies may await discovery and verification.

Applied implications

The results of the present study have applied implications for invasive fruit fly pests. Understanding temporal partitioning can help inform monitoring and management decisions for tephritid pests that co-occur in fruit trees. For example, if *R. cerasi*, which is invasive in eastern North America (Barringer 2018), transitions from honeysuckles to cherries, it might infest cherries earlier than the native pest *R. cingulata* does (Vogt *et al.* 2010). If the two species coexist due to temporal partitioning of cherries, traps for detecting flies need to be deployed earlier and the fly management period will be prolonged. Fly pressure may increase due to the presence of the two pests. Also, *R. cerasi* has yet to be found in the Pacific Northwest, where a major commercial cherry industry is located, but it could alter timing of and increase sprays for fly control if it invades the region, depending on how it interacts with *R. indifferens*, the native fly attacking cherries in the region (Prengaman 2017). Therefore, understanding insect life history timing is not only important for understanding the creation and maintenance of species biodiversity but also has applied significance for pest management.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.4039/tce.2026.10074.

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References

Agarwal, V.M. and Rastogi, N. 2009. Food resource and temporal partitioning amongst a guild of predatory agroecosystem-inhabiting ant species. Current Zoology, **55**: 366–375. https://doi.org/10.1093/czoolo/55.5.366.

Albrecht, M. and Gotelli, N.J. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia, **126**: 134–141. https://doi.org/10.1007/s004420000494.

Balduf, W.V. 1959. Obligatory and facultative insects in rose hips: their recognition and bionomics. Illinois Biological Monographs. Volume 26. University of Illinois Press, Urbana, Illinois, United States of America. Available from https://www.biodiversitylibrary.org/bibliography/50286 [accessed 16 July 2026].

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Barringer, L. 2018. First record of the European cherry fruit fly, *Rhagoletis cerasi* (Linnaeus) (Diptera: Tephritidae), in North America. Insecta Mundi, **0622**: e1126. Available from https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=2132&context=insectamundi [accessed 16 July 2026].

Batkhan, L. 2022. Calculating the overlap of date/time intervals. SAS Blogs: SAS Users. SAS Institute Inc., Cary, North Carolina, United States of America. Available from https://blogs.sas.com/content/sgf/2022/01/13/calculating-the-overlap-of-date-time-intervals/#:~:text=Overlap%20%3D%20min(A2%2C%20B2,two%20lower%20boundaries%2C%20plus%201 [accessed 16 July 2026].

Brown, J.H. 1984. On the relationship between abundance and distribution of species. American Naturalist, **124**: 255–279. Available from https://www.jstor.org/stable/2461494 [accessed 16 July 2026].

Bush, G.L. 1966. The taxonomy, cytology, and evolution of the genus *Rhagoletis* in North America (Diptera, Tephritidae). Bulletin of the Museum of Comparative Zoology, **134**: 431–562, Available from https://www.biodiversitylibrary.org/part/20075 [accessed 16 July 2026].

Calvert, M.B., Doellman, M.M., Feder, J.L., Hood, G.R., Meyers, P., Egan, S.P., *et al.* 2021. Genomically correlated trait combinations and antagonistic selection contributing to counterintuitive genetic patterns of adaptive diapause divergence in *Rhagoletis* flies. Journal of Evolutionary Biology, **35**: 146–163. https://doi.org/10.1111/jeb.13952.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics, **31**: 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343.

Clarke, A.R. and Measham, P.F. 2022. Competition: a missing component of fruit fly (Diptera: Tephritidae) risk assessment and planning. Insects, **13**: 1065. https://doi.org/10.3390/insects13111065.

Debouzie, D., Heizmann, A., Desouhant, E., and Menu, F. 1996. Interference at several temporal and spatial scales between two chestnut insects. Oecologia, **108**: 151–158. https://doi.org/10.1007/BF00333226.

Doellman, M.M., Egan, S.P., Ragland, G.J., Meyers, P.J., Hood, G.R., Powell, T.H.Q., *et al.* 2018. Standing genetic variation in eclosion time and the genomics of host race formation in *Rhagoletis pomonella* fruit flies. Ecology and Evolution, **9**: 393–409. https://doi.org/10.1002/ece3.4758.

Dowle, E.J., Powell, T.H.Q., Doellman, M.M., Meyers, P.J., Calvert, M.B., Walden, K.K.O., *et al.* 2020. Genome-wide variation and transcriptional changes in diverse developmental processes underlie the rapid evolution of seasonal adaptation. Proceedings of the National Academy of Sciences United States of America, **117**: 23960–23969. https://doi.org/10.1073/pnas.2002357117.

Duyck, P.-F., David, P., Junod, G., Brunel, C., Dupont, R., and Quilici, S. 2006. Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Réunion. Ecology, **87**: 1770–1780. https://doi.org/10.1890/0012-9658(2006)87[1770:IOCMIS]2.0.CO;2.

Ekesi, S., Billah, M.K., Nderitu, P.W., Lux, S.A., and Rwomushana, I. 2009. Evidence for competitive displacement of *Ceratitis cosyra* by the invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) on mango and mechanisms contributing to the displacement. Journal of Economic Entomology, **102**: 981–991. https://doi.org/10.1603/029.102.0317.

Foote, R.H., Blanc, P.L., and Norrbom, A.L. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press (Comstock Publishing), Ithaca, New York, United States of America.

Glover, M.M., Egan, S.P., Hood, G.R., Rull, J., Aluja, M., and Feder, J.L. 2018. Phylogeography of walnut-infesting *Rhagoletis suavis* (Diptera: Tephritidae) flies. Insect Systematics and Diversity, **2**: 1–9. https://doi.org/10.1093/isd/ixy002.

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Griffin, J.N. and Silliman, B.R. 2011. Resource partitioning and why it matters. Nature Education Knowledge, **3**: 49. Available from https://www.nature.com/scitable/knowledge/library/resource-partitioning-and-why-it-matters-17362658/ [accessed 16 July 2026].

Hassani, I.M., Delatte, H., Ravaomanarivo, L.H.R., Nouhou, S., and Duyck, P.-F. 2022. Niche partitioning *via* host plants and altitude among fruit flies following the invasion of *Bactrocera dorsalis*. Agricultural and Forest Entomology, **24**: 575–585. https://doi.org/10.1111/afe.12522.

Headrick, D.H. and Goeden, R.D. 1990. Resource utilization by larvae of *Paracantha gentilis* (Diptera: Tephritidae) in capitula of *Cirsium californicum* and *C. proteanum* (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington, **92**: 512–520. Available from https://biostor.org/reference/55912 [accessed 16 July 2026].

Holt, R.D. 1987. On the relationship between niche overlap and competition: the effect of incommensurable niche dimensions. Oikos, **48**: 110–114. https://doi.org/10.2307/3565696.

Holt, R.D. 2001. Species coexistence. *In* Encyclopedia of Biodiversity. Volume 5. Academic Press, Elsevier, Amsterdam, The Netherlands. Pp. 413–426. Available from https://people.clas.ufl.edu/rdholt/files/105.pdf [accessed 16 July 2026].

Hood, G.R., Blankinship, D., Doellman, M.M., and Feder, J.L. 2021. Temporal resource partitioning mitigates interspecific competition and promotes coexistence among insect parasites. Biological Reviews, **96**: 1969–1988. https://doi.org/10.1111/brv.12735.

Inbar, M. and Wool, D. 1995. Phloem-feeding specialists sharing a host tree: resource partitioning minimizes interference competition among galling aphid species. Oikos, **73**: 109–119. https://doi.org/10.2307/3545732.

Jones, S.C. 1937. The currant and goose-berry maggot or yellow currant fly (*Epochra canadensis*) Loew. Station Circular 121. Oregon State System of Higher Education. Oregon State College, Agricultural Experiment Station, Corvallis, Oregon, United States of America. 11 pp. Available from https://digitalcollections.library.oregon.gov/nodes/view/312296 [accessed 16 July 2026].

Krebs, C.J. 2014. Niche measures and resource preferences. Chapter 14 [online]. *In* Ecological Methodology. Third edition. University of British Columbia, Department of Zoology, Vancouver, British Columbia, Canada. Pp. 598–655. Available from https://www.zoology.ubc.ca/~krebs/downloads/krebs_chapter_14_2021.pdf [accessed 16 July 2026].

Liendo, M.C., Parreño, M.A., Cladera, J.L., Vera, M.T., and Segura, D.F. 2018. Coexistence between two fruit fly species is supported by the different strength of intra- and interspecific competition. Ecological Entomology, **43**: 294–303. https://doi.org/10.1111/een.12501.

Lopes, G.N., Souza-Filho, M.F., Gotelli, N.J., Lemos, L.J.U., Godoy, W.A.C., and Zucchi, R.A. 2015. Temporal overlap and co-occurrence in a guild of sub-tropical tephritid fruit flies. PLOS One, **10**: e0132124. https://doi.org/10.1371/journal.pone.0132124.

López-Ortega, M., Pérez-Rodríguez, P., Rojas, J.C., Soto Hernández, R.M., López-Mata, L., and Rico-Gray, V. 2013. Host use and resource sharing by fruit-/seed-infesting insects on *Schoepfia schreberi* (Olacaceae). Environmental Entomology, **42**: 231–239. https://doi.org/10.1603/EN12284.

Mays, W.T. and Kok, L.T. 2003. Population dynamics and dispersal of two exotic biological control agents of spotted knapweed, *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae), in southwestern Virginia from 1986 to 2000. Biological Control, **27**: 43–52. https://doi.org/10.1016/S1049-9644(02)00182-2.

Meyers, P.J., Doellman, M.M., Ragland, G.J., Hood, G.R., Egan, S.P., Powell, T.H.Q., *et al.* 2020. Can the genomics of ecological speciation be predicted across the divergence continuum from host races to species? A case study in *Rhagoletis*. Philosophical Transactions of the Royal Society B, **375**: 20190534. https://doi.org/10.1098/rstb.2019.0534.

Mitchener, A.V. 1927. The currant fruit-fly, *Epochra canadensis* Loew, in Manitoba; and, optimum feeding temperatures for the dark-sided cut-worm, *Euxia messoria* Harris. M.Sc. thesis. University of Manitoba, Winnipeg, Canada. Available from https://hdl.handle.net/1993/4615 [accessed 16 July 2026].

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Neilson, W.T.A., Knowlton, A.D., and McRae, K.B. 1981. Preoviposition and oviposition periods of the apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae). The Canadian Entomologist, **113**: 1061–1067. https://doi.org/10.4039/Ent1131061-12.

Paine, J.H. 1912. The yellow currant fly or gooseberry fruit fly (*Epochra canadensis* Loew.). Psyche, **19**: 139–244. https://doi.org/10.1155/1912/81618.

Pianka, E.R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Science United States of America, **71**: 2141–2145. https://doi.org/10.1073/pnas.71.5.2141.

Piper, C.V. and Doane, R.W. 1898. Insects injurious to currants and gooseberries. Washington State Agricultural College and School of Science Experiment Station Extension Bulletin 36. Washington State Agricultural College, Pullman, Washington, United States of America. 16 pp. https://doi.org/10.7273/000003412.

Prengaman, K. 2017. European cherry fruit fly found in NY [online]. *In* Good Fruit Grower. Yakima, Washington, United States of America. Available from https://www.goodfruit.com/european-cherry-fruit-fly-found-in-NY/ [accessed 16 July 2026].

Prokopy, R.J. 1981. Oviposition-deterring pheromone system of apple maggot flies. *In* Management of Insects Pests Using Semiochemicals: Concepts and Practice. *Edited* by E.R. Mitchell. Springer, Boston, Massachusetts, United States of America. Pp. 477–494. https://doi.org/10.1007/978-1-4613-3216-9_40.

Prokopy, R.J. and Berlocher, S.H. 1980. Establishment of *Rhagoletis pomonella* (Diptera: Tephritidae) on rose hips in southern New England. The Canadian Entomologist, **112**: 1319–1320. https://doi.org/10.4039/Ent1121319-12.

Ragland, G.J., Doellman, M.M., Meyers, P.J., Hood, G.R., Egan, S.P., Powell, T.H.Q., *et al.* 2017. A test of genomic modularity among life-history adaptations promoting speciation with gene flow. Molecular Ecology, **26**: 3926–3942. https://doi.org/10.1111/mec.14178.

Reut, M., Chrabąszcz, M., and Moniuszko, H. 2021. Timing is everything: temporal and spatial niche segregation in *Curculio* spp. (Coleoptera: Curculionidae) associated with oak trees. Insects, **12**: 687. https://doi.org/10.3390/insects12080687.

Rusterholz, K.A. 1981. Niche overlap among foliage-gleaning birds: support for Pianka's niche overlap hypothesis. The American Naturalist, **117**: 395–399. https://www.jstor.org/stable/2460542 [accessed 16 July 2026].

Sale, P.F. 1974. Overlap in resource use, and interspecific competition. Oecologia, **17**: 245–256. https://doi.org/10.1007/BF00344924.

SAS Institute Inc. 2023. SAS/STAT® 15.3 User's Guide. SAS Institute Inc., Cary, North Carolina, United States of America. Available from https://documentation.sas.com/doc/en/stathpug/15.3/titlepage.htm [accessed 16 July 2026].

Schoener, T.W. 1983. Field experiments on interspecific competition. The American Naturalist, **122**: 240–285. Available from https://www.jstor.org/stable/2461233 [accessed 16 July 2026].

Venner, S., Pélisson, P.F., Bel-Venner, M.C., Débias, F., Rajon, E., and Menu, F. 2011. Coexistence of insect species competing for a pulsed resource: toward a unified theory of biodiversity in fluctuating environments. PLOS One, **6**: e18039. https://doi.org/10.1371/journal.pone.0018039.

Vogt, H., Köppler, K., Dahlbeck, W., and Hensel, H. 2010. Observations of *Rhagoletis cingulata*, an invasive species from North America, on cherry in Germany. *In* Integrated Fruit Protection in Fruit Crops: Proceedings of the 7th International Conference on Integrated Fruit Production at Avignon, France. *Edited* by J.V. Cross, M. Brown, and J. Fitzgerald. INRA, Unité de pathologie végétale, Avignon, France. Pp. 273–277. Available from https://www.openagrar.de/receive/openagrar_mods_00010975 [accessed 16 July 2026].

Yadav, J.P. and Singh, B.N. 2005. Coexistence of three different *Drosophila* species by rescheduling their life history traits in a natural population. Journal of Genetics, **84**: 283–293. https://doi.org/10.1007/BF02715798.

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Yee, W.L. 2005. Seasonal distributions of eggs and larvae of *Rhagoletis indifferens* (Diptera: Tephritidae) in cherries. Journal of Entomological Science, **40**: 158–166. Available from https://jes.kglmeridian.com/meridian/jes/published/rest/pdf-watermark/v1/journals/ents/40/2/article-p158.pdf/watermark-pdf/ [accessed 16 July 2026].

Yee, W.L. 2008. Host plant use by apple maggot, western cherry fruit fly, and other *Rhagoletis* species (Diptera: Tephritidae) in central Washington state. The Pan-Pacific Entomologist, **84**: 163–178. https://doi.org/10.3956/2007-48.1.

Zar, J.H. 1999. Biostatistical Analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, United States of America.

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