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Wild host fruit–niche diversity of *Drosophila suzukii* in lowbush blueberry agroecosystems in Saguenay-Lac-Saint-Jean, Québec, Canada

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Abstract

Understanding movements of *Drosophila suzukii* (Diptera: Drosophilidae) into berry fruit crops from wild-fruit hosts in borders of semi-natural agroecosystems, such as lowbush blueberry, is important to determining harvesting time and managing wild-fruit diversity near crops. This study aimed to inventory the wild-fruit hosts associated with lowbush blueberry (Ericaceae) production in Québec, Canada, near the limits of lowbush blueberry's eastern North American range. We also tested the hypothesis that fruit traits of berry fruit species present in or near lowbush blueberry fields might explain field infestation levels. Flies of both sexes emerged from five wild-fruit species in 2016, to which six more species were added in 2017. The most productive wild-fruit hosts were *Cornus canadensis* (Cornaceae) and *Aralia hispida* (Araliaceae) (> 100 emerged flies/100 g of fruit) in 2016, to which *Prunus pensylvanica* (Rosaceae) and *Rubus idaeus* (Rosaceae) were added in 2017. Among nine variables considered in statistical modelling (fruit size, sugar content, and reflected colour bands) and taxonomic family (a nominal variable), none could explain field infestation levels over two years. In lab tests comparing fruits of *Cornus canadensis*, a common weed within fields, and lowbush blueberries, mated *D. suzukii* females laid twice as many eggs on blueberries, but both species were equally suitable for development.

Résumé

Comprendre les mouvements de *Drosophila suzukii* (Diptera : Drosophilidae) issus des bordures des cultures fruitières en agroécosystèmes tels le bleuets nain, est important pour planifier la récolte et gérer la végétation de bordure des champs. Cette étude visait à inventorier les fruits sauvages associés au bleuets nain (Ericaceae) au Québec, près de la limite septentrionale de sa distribution dans l'est de l'Amérique du Nord. Nous avons aussi testé l'hypothèse que des traits quantitatifs des fruits utilisés pourraient expliquer les niveaux d'infestations observés aux champs. Des mouches mâles et femelles en nombres quasi égaux ont émergé des fruits de 5 espèces sauvages en 2016, auxquelles s'en sont ajoutées 6 autres en 2017. Les espèces fruitières les plus productives étaient *Cornus canadensis* (Cornaceae) et *Aralia hispida* (Araliaceae) (>100 mouches/100 g de fruits) en 2016, auxquelles se sont ajoutées *Prunus pensylvanica* (Rosaceae) et *Rubus idaeus* (Rosaceae) en 2017. Entre neuf variables des fruits testées (grosesse, teneur en sucre, couleurs) en plus de la variable nominale Famille taxonomique, aucune n'a pu expliquer les taux d'infestations du bleuets cultivé durant deux saisons. Lors de tests en laboratoire comparant les fruits du *Cornus canadensis* à ceux du bleuets nain, les femelles accouplées ont préféré ces derniers au taux de 2:1, bien que les deux espèces convenaient également au développement.

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Introduction

Introduced in North America in 2008, the spotted-wing drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), has since spread throughout the continent (Asplen *et al.* 2015). The Saguenay-Lac-Saint-Jean region in boreal Québec, Canada, is near the northern limit of its distribution range, based on modelling (dos Santos *et al.* 2017; Fraimout *et al.* 2017; Langille *et al.* 2017; Ørsted and Ørsted 2019). The region is notable for widespread production of lowbush blueberry, *Vaccinium angustifolium* Aiton (Ericaceae), and is the dominant growing area of this small fruit in Québec (Agriculture and Agri-Food Canada 2019). Lowbush blueberry, a native berry fruit of northeastern America, prefers well-drained sandy and acidic soil, such as those found in forests where jack pine, *Pinus banksiana* Lambert (Pinaceae), is dominant (Thiffault *et al.* 2015). Blueberry fields consist of more or less landscaped forests where trees and shrubs are cut to promote native lowbush blueberry growth and propagation (Syndicat des producteurs de bleuets du Québec 2016). Cultivated areas are highly variable because farms can be family owned or structured as part of large cooperative groups with multiple fields. In both cases, fields are usually bordered by native forests and separated by windbreaks. Insecticide treatments are relatively infrequent because few insect pests cause sufficient damage to justify chemical control in the region; however, weeds pose a more serious problem. Treatments with herbicides are often required to control competing berry fruit species, such as Canadian bunchberry *Cornus canadensis* Linnaeus (Cornaceae) (Gagnon *et al.* 2016).

Lowbush blueberry field borders can act as host plant reservoirs for insect pests such as *Drosophila suzukii* (Ballman and Drummond 2017; Drummond *et al.* 2019; Champagne-Cauchon *et al.* 2020), as in other small-fruit crops. Numerous studies have reported wild host species of *D. suzukii* in fruit crops, notably in North America (Lee *et al.* 2015; Klick *et al.* 2016; Diepenbrock *et al.* 2017; Thistlewood *et al.* 2019; Little *et al.* 2019; Urbaneja-Bernat *et al.* 2020) and Europe (Cini *et al.* 2012; Poyet *et al.* 2014; Arnó *et al.* 2016; Kenis *et al.* 2016; Tonina *et al.* 2016). At the same time, advances have elucidated fruit properties that might explain *D. suzukii*'s oviposition preferences and host fruit susceptibility (Lee *et al.* 2011; Poyet *et al.* 2014; Little *et al.* 2017), especially with respect to host fruit odours as attractants (reviewed in Cloonan *et al.* 2021). Visual cues, such as fruit colour, texture, shape, size, and structural complexity, have all been shown to affect host fruit use by *D. suzukii*, as reflected in its oviposition behaviour and offspring survival and development (Bellamy *et al.* 2013; Poyet *et al.* 2015; Rodriguez-Saona *et al.* 2019). Contrast between fruit colour and a fruit's immediate background (Kinjo *et al.* 2014) may also play a role in host fruit selection. Fruit firmness, acidity, and sugar content also contribute to host susceptibility (Lee *et al.* 2011; Burrack *et al.* 2013; Kinjo *et al.* 2014; Lasa *et al.* 2017). Based on various aspects of fruit preference and suitability, a host potential index has therefore been proposed to rank fruit crop species as potential hosts for *D. suzukii* (Bellamy *et al.* 2013).

Considerable efforts have been made to describe *D. suzukii*'s spread in Canada (briefly reviewed in Dixon and Moreau 2020), but little has been done yet to examine the impact of native boreal wild fruits at the limits of the fly's known range in reduced management crops such as lowbush blueberry. Our first goal in the present study was to inventory the wild-fruit hosts of *D. suzukii* in lowbush blueberry agroecosystems in the Saguenay-Lac-Saint-Jean region, Québec, Canada. We hypothesised that specific fruit characteristics of wild berry fruit species hosts associated with lowbush blueberry fields could explain the variation in field infestation levels by *D. suzukii*. We also investigated the host suitability of Canadian bunchberry, *C. canadensis*, fruit for *D. suzukii* because it is a common and widespread weed in the study region's lowbush blueberry fields. To do this, we compared blueberry and bunchberry fruit infestation levels in the field, and we determined *D. suzukii*'s oviposition preference for fruits of both species in choice and no-choice controlled laboratory

experiments. We hypothesised that *C. canadensis* could act as a gateway for *D. suzukii* infestation in lowbush blueberry crops because it is a highly attractive, potential early host. This study extends our understanding of the dynamics of *D. suzukii* in fruit crops in relation to alternative wild-fruit hosts that are present in lowbush blueberry semi-natural agroecosystems.

Materials and methods

Study sites

Wild-fruit sampling was performed over a two-year period in the Saguenay-Lac-Saint-Jean region, Québec, Canada. Eight blueberry fields were sampled in 2016, and 10 were sampled in 2017 (Supplementary material, Table S1), covering a 50-km radius area where most of the region's lowbush blueberry production is located. Commercial lowbush blueberry farms of average size, with multiple fields, were preferred over smaller, family-owned farms. Selected fields (at least 100 m wide \times 600 m long) were bordered by forests dominated by native jack pine and separated from each other by windbreaks. Typically, lowbush blueberry culture in the region follows a two-year cycle: one harvesting year followed by a regenerative, mowing, and vegetative growth year. A three-year cycle (two harvesting years) is also practised (Syndicat des producteurs de bleuets du Québec 2016). To ensure availability of wild berry fruits for sampling during a harvest year, different fields located within the same farm or immediate locality were sampled in 2016 and 2017 unless selected fields were harvested for a second year. No insecticide treatments were performed on any sampled fields.

Wild-fruit diversity and use for egg laying by *Drosophila suzukii*

Wild berry fruit and blueberries were regularly sampled from 17 May to 25 October 2016 and from 11 May to 28 October 2017. Fruits were sampled at each site where and when they were available and starting at the late-ripening stage of each species, as indicated by observable changes in fruit colour with maturity. Next to each blueberry field, fruits were sampled in a preselected forested border area forming a rectangle (50 \times 50 m) on one side of the field. On each sampling occasion, we collected 150 g of cultivated lowbush blueberries near the edge of the field and up to 50 g of ripe or ripening fruits of each wild-fruit species available in the border. Sampling was performed at weekly intervals, except in July and August, which is when fruit availability peaks. In July and August, we sampled twice a week for greater time resolution of fruit use in the high season.

Fresh fruit samples were weighed without delay using a portable Scout Pro SP2001 balance (Ohaus Corporation, Pine Brook, New Jersey, United States of America) and were assembled in 50-g lots in 160-mL plastic bottles (Richards Packaging, Montréal, Québec, Canada) covered with muslin fabric at one end for ventilation. Fruit samples were brought to the laboratory within 24 hours of sampling to be incubated in Conviron E15 growth chambers (Controlled Environments Ltd., Winnipeg, Manitoba, Canada) under standard conditions (20 °C, 65 % relative humidity, 16:8-hour light:dark photoperiod) and for up to 21 days. Emerged adult *D. suzukii* flies were counted and sexed, and any aborted larvae and pupae were also recorded, if present.

Complementary measures on wild fruit

In 2017, the physical and optical properties of wild berry fruits and lowbush blueberries were measured in July and August from weekly samples from each available wild-fruit species. For each sample, individual fruit diameter and weight ($n = 10$) were obtained with a CD-6" digital caliper (Mitutoyo Corporation, Kawasaki, Japan) and a portable balance. Sugar content in °Brix was

measured from juice extracts ($n = 2$) of five common fruit species with a Master-53T handheld refractometer (Atago, Tokyo, Japan).

Complete reflected visible light spectra were measured once on ripe fruits of each species at the peak of wild-fruit availability in August using a Pika II hyperspectral imaging camera and Spectronon 5.1 software (Resonon, Bozeman, Montana, United States of America) under 35-W halogen lights coupled with diffusers. The average normalised measures of complete reflected spectra were obtained for five fruits of each species. The reflected visible spectrum was subdivided into six wavelength fractions: violet (400–450 nm), blue (450–495 nm), green (495–570 nm), yellow (570–590 nm), orange (590–620 nm), and red (620–750 nm). The integral under the spectral curve was used to compare the relative contribution of each colour band to the colour differences between the fruits of each species.

Canadian bunchberry versus lowbush blueberry fruit preference experiments

In 2018, experiments under laboratory conditions were designed to compare *D. suzukii* oviposition preferences between Canadian bunchberries and lowbush blueberries. Laboratory-established colonies of *D. suzukii* were reared on a raw banana diet under standard conditions, as described above. Individuals were isolated at the pupal stage in 1.5-mL microtubes (Sarstedt, Newton, North Carolina, United States of America) with a punctured hole in the cap and a drop of water. Young emerging flies (0–48 hours old) were placed together to form pairs (male and female) and allowed to freely mate during an additional 48-hour period before the start of the preference test. Flies also had access to fresh water and a sugar solution at emergence and throughout the experiment.

Mature fruits of Canadian bunchberry and lowbush blueberry were collected in late July 2018 in a blueberry field in Saint-Thomas-Didyme, Québec, Canada (Supplementary material, Table S1). Sampling at that time ensured that fruits were not infested by *D. suzukii*, and this was confirmed with the incubation of control fruit lots from which no flies emerged and with the absence of *D. suzukii* adults in cider-vinegar traps from complementary sampling (Guay *et al.*, unpublished data).

No-choice experiment. Presumably mated fly pairs ($n = 26$) from the colony were equitably assigned to one of two fruit-species treatments (Canadian bunchberry or lowbush blueberry) in an arena consisting of a 160-mL, meshed, clear plastic container, with access to one fruit of either species. A single fruit was exposed to each fly pair for 2–3 days, after which the fruit was replaced with a new fruit of the same species, which was exposed for a similar duration. *Drosophila suzukii* eggs can have a very short development time; after three days, some eggs may hatch, especially on optimal fruits. Fruits were thus renewed three times over a 10–12-day period of the early adult life periods of *D. suzukii* pairs, for a total of four exposed fruits per fly pair. After being retrieved, each fruit was observed under a stereomicroscope to count laid eggs, as revealed by presence of egg respiratory filaments emerging from the fruit surface near oviposition marks (Atallah *et al.* 2014).

Choice experiment. The design of the choice experiment was similar to that of the no-choice experiment described above, except that fly pairs ($n = 13$) had access to single fruits of both species. Fruits were similarly replaced three times to cover a 10–12-day period of reproduction, for a total of four exposed fruits of each species per fly pair. Each fruit was observed to count laid eggs.

Statistical analyses

All statistical analyses were performed using SAS, version 9.4 (SAS Institute, Cary, North Carolina, United States of America).

Infestation levels of field-collected wild fruit. For both years (2016 and 2017), *D. suzukii* fruit infestation levels (number of flies emerged per 100 g of fruit) between wild-fruit species were compared using PROC MIXED, with species as a fixed effect. Because of variable occurrence of maturing fruits among species between sites and sampling dates, we pooled data from all locations, and we limited sampling dates to August and September because this period typically matched lowbush blueberry harvest. Infestation levels were log-transformed to attain normality, and weeks were grouped to allow model convergence.

Infestation levels in relation to wild-fruit visual and physical stimuli. Wild-fruit properties pertain to measured visual stimuli (means of diameter; amount of reflected visible light in violet, blue, green, yellow, orange, and red colour bands; and sugar content (°Brix)). Nominal taxonomic variables for each species (family, genus) were added as explanatory variables to account for other, undetermined fruit-specific stimuli that influence selection by *D. suzukii* gravid females (e.g., fruit firmness and fragrance). The hypothesis that fruit properties (including taxonomy) could explain fruit field-infestation levels during the period of blueberry harvest (August and September) in the study region was tested using PROC GLM.

Canadian bunchberry versus lowbush blueberry fruit preference experiments

For the no-choice experiment, female daily egg-laying rate was analysed using PROC GLIMMIX, with fruit species, time into experiment, and the fruit species × time interaction as fixed effects and fruit species within each fly pair as a random effect. For the choice experiment, PROC GLIMMIX was used, with fruit species, time, and fruit species × time interaction as fixed effects and fly pair as a random effect.

Results

Wild-fruit diversity and use by *Drosophila suzukii*

In total, 11 wild berry fruit species were collected in 2016 (Fig. 1A), and 16 species were collected in 2017 (Fig. 1B). The availability of these species' fruits for sampling varied with year and field site, as expected. Among sampled fruit species in 2016 and 2017, 5 and 11, respectively, were recorded as suitable hosts for full development up to fly emergence of *D. suzukii* (Table 1; Supplementary material, Table S2). Wild-fruit species *Aralia hispida* (Araliaceae), *Prunus pensylvanica* (Rosaceae), and *Sorbus americana* (Rosaceae) are reported here for the first time as suitable hosts for *D. suzukii* (Table 1). Additional wild hosts, *Viburnum nudum* var. *cassinoides* (Adoxaceae), *Ilex mucronata* (Aquifoliaceae), *Cornus canadensis*, *C. sericea* (Cornaceae), *Vaccinium angustifolium*, *Aronia melanocarpa* (Rosaceae), *Prunus virginiana* (Rosaceae), and *Rubus idaeus* (Rosaceae), are also recorded in the region of this study. The five wild-fruit species from which no *D. suzukii* flies emerged (Table 1) were *Maianthemum canadense* (Asparagaceae), *Arctostaphylos uva-ursi* (Ericaceae), *Gaultheria procumbens* (Ericaceae), *Amelanchier bartramiana* (Rosaceae), and wild strawberry, *Fragaria virginiana* (Rosaceae).

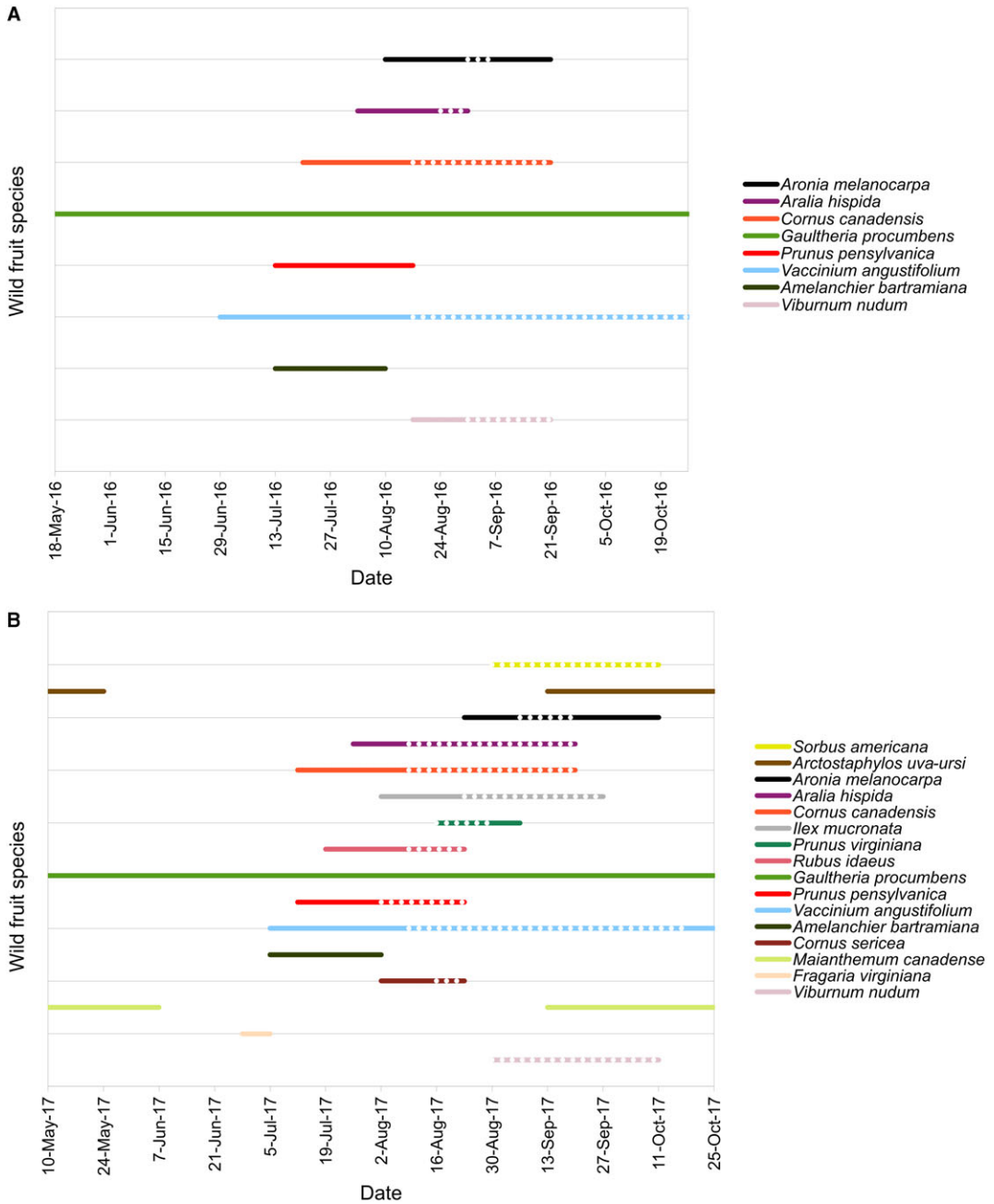


Fig. 1. Fruit-maturation phenology of wild-fruit species sampled in lowbush blueberry, *Vaccinium angustifolium*, agroecosystems in Saguenay-Lac-Saint-Jean, Québec, Canada in **A**, 2016 ($n = 8$) and **B**, 2017 ($n = 16$). Dotted lines represent sampling periods during which *Drosophila suzukii* adult flies emerged under controlled conditions from collected fruits.

Table 1. Wild-fruited plant species¹ recorded as potential *Drosophila suzukii* hosts capable of supporting full development in the present study and in other North American studies.

	New host	Emergence (number of samples)		Previous records	References
		2016	2017		
Adoxaceae					
<i>Viburnum nudum</i> var. <i>cassinoides</i> (Linnaeus) Torrey and A. Gray		+ (1)	+ (4)	Nova Scotia, Maine	Little <i>et al.</i> 2019 ² ; Ballman and Drummond 2017 ³
Aquifoliaceae					
<i>Ilex mucronata</i> (Linnaeus) Powell <i>et al.</i>		- (1)	+ (4)	Maine	Ballman and Drummond 2017 ⁴ ; Little <i>et al.</i> 2019 ⁵
Araliaceae					
<i>Aralia hispida</i> Ventenat	+	+ (1)	+ (2)	no previous record	
Cornaceae					
<i>Cornus canadensis</i> Linnaeus ⁶		+ (5)	+ (10)	Maine	Ballman and Drummond 2017 ⁷
<i>Cornus sericeae</i> Linnaeus ⁸			+ (1)	Oregon	Lee <i>et al.</i> 2015 ⁹ Little <i>et al.</i> 2019 ¹⁰
Ericaceae					
<i>Arctostaphylos uva-ursi</i> (Linnaeus) Sprengel		- (1)	- (2)	no previous record	Little <i>et al.</i> 2019 ¹¹ Thistlewood <i>et al.</i> 2019 ¹²
<i>Gaultheria procumbens</i> Linnaeus		- (2)	- (5)		Poyet <i>et al.</i> 2015 ¹³
<i>Vaccinium angustifolium</i> Aiton		+ (8)	+ (10)	New Jersey	Urbaneja-Bernat <i>et al.</i> 2020 ¹⁴
Liliaceae					
<i>Maianthemum canadense</i> Desfontaines		- (1)	- (7)	no previous record	
Rosaceae					
<i>Amelanchier bartramiana</i> (Tausch) Max Roemer		- (7)	- (3)	no previous record	Little <i>et al.</i> 2019 ¹⁵
<i>Aronia melanocarpa</i> (Michaux) Elliott		+ (1)	+ (2)	Wisconsin	Hietala-Henschell <i>et al.</i> 2017 ¹⁶ ; Little <i>et al.</i> 2019 ¹⁷
<i>Fragaria virginiana</i> Duchesne			- (1)	no previous record ¹⁸	
<i>Prunus pensylvanica</i> Linnaeus <i>filius</i>	+	- (5)	+ (10)	no previous record	Little <i>et al.</i> 2019 ¹⁹
<i>Prunus virginiana</i> Linnaeus			+ (1)	British Columbia, New York state, Maine	Thistlewood <i>et al.</i> 2019 ²⁰ ; Elsensohn and Loeb 2018 ²¹ ; Ballman and Drummond 2017 ²²

(Continued)

Table 1. (Continued)

	New host	Emergence (number of samples)		Previous records	References
		2016	2017		
<i>Rubus idaeus</i> Linnaeus			+ (2)	Maine	Ballman and Drummond 2017 ²³
<i>Sorbus americana</i> Marshall	+		+ (4)	no previous record	Lee <i>et al.</i> 2015 ²⁴

¹All native in eastern North America.

²Emerged from fruits in Nova Scotia, Canada 2017.

³Not infested in Maine, United States of America in 2015–2016 (four sites).

⁴Infested in Maine, 2015 (one site).

⁵Not infested in Newfoundland, Canada, 2017.

⁶Also known as *Chamaepericlymenum canadense* (Linnaeus) Ascherson and Graebner.

⁷Infested in Maine, 2015–2016 (12 sites).

⁸Also known as *Swida sericea* (Linnaeus) Holub.

⁹Infested in Oregon, United States of America, 2010–2013 (five counties).

¹⁰Not infested in 2017 (cultivated endemic).

¹¹Sampled in Atlantic provinces, Canada in 2017, no infestation reported.

¹²Not infested in Okanagan Valley, British Columbia, Canada (many sites, 2010–2016).

¹³Tested as (European) exotic host (Poyet *et al.* 2015); eggs fail to hatch (Poyet 2014).

¹⁴Blueberry infested in forests bordering cultivated blueberry, 2015–2016 (5–6 sites).

¹⁵Not infested in Atlantic Canada, 2017, citizen science project; other *Amelanchier* spp. not infested in Michigan, United States of America (2011) and Oregon (2012); suitable congeneric hosts known in Europe (Thistlewood *et al.* 2019).

¹⁶Infested in Wisconsin, United States of America, 2015, suboptimality revealed in bioassays.

¹⁷Not infested in Atlantic Canada, 2017, citizen science project.

¹⁸Fruits support full development (Gong *et al.* 2016).

¹⁹Not infested in Atlantic provinces, 2015.

²⁰Infested in Okanagan, British Columbia, four years in early 2010s.

²¹Fruits infested in New York State, United States of America in 2013 (16 sites).

²²Negative in Maine, 2015–2016 (9–15 sites).

²³*Rubus* spp. sampled in 2015–2016 (15 and 9 sites).

²⁴Not infested in Oregon, 2012 (one site).

Seasonal variation

Of the five berry fruit species sampled that were not used as hosts by *D. suzukii* in the present study, bearberry, *A. uva-ursi*, and Canada mayflower, *M. canadense*, were sampled only in 2017, and eastern wintergreen, *G. procumbens* (2016 and 2017), was sampled at both the start and end of the growing season. In 2016, the species infested the earliest, in the third week of August, were *C. canadensis* and *V. angustifolium*, followed in the next two weeks by *A. hispida*, *A. melanocarpa*, and *V. nudum* var. *cassinoides* (Fig. 1A). In 2017, with sampling extended to 16 species, the earliest infestation occurred on *P. pensylvanica* during the first week of August (Fig. 1B), about one week earlier than on *A. hispida*, *C. canadensis*, and *R. idaeus* and at the same time as infestation of lowbush blueberry. Infestation of *C. sericea* and *P. virginiana* fruits, and then of *S. americana* and *A. melanocarpa*, followed in late August to early September. In 2016, wild-fruit species with the longest period of infestation were *C. canadensis* (six weeks, up to the third week of September) and wild *V. angustifolium* (10 weeks, up to the third week of October; Fig. 1A). In 2017, fruit species that were infested the longest were *S. americana* and *V. nudum* var. *cassinoides*, infested at the same time for seven weeks up to the second week of October, and lowbush blueberry *V. angustifolium*, infested for 11 consecutive weeks up to the third week of October (Fig. 1B). Seasonal fruit suitability of *A. hispida* also lasted seven weeks but occurred three weeks earlier (Fig. 1B).

Infestation-level variation with fruit species

Infestation level (flies emerged per 100 g) strongly varied between fruit species for both 2016 ($F_{4, 16} = 86.36$, $P < 0.0001$; Fig. 2A) and 2017 ($F_{9, 39} = 5.47$, $P < 0.0001$; Fig. 2B). Poor statistical discrimination between species is attributable at least in part to unequal fruit species

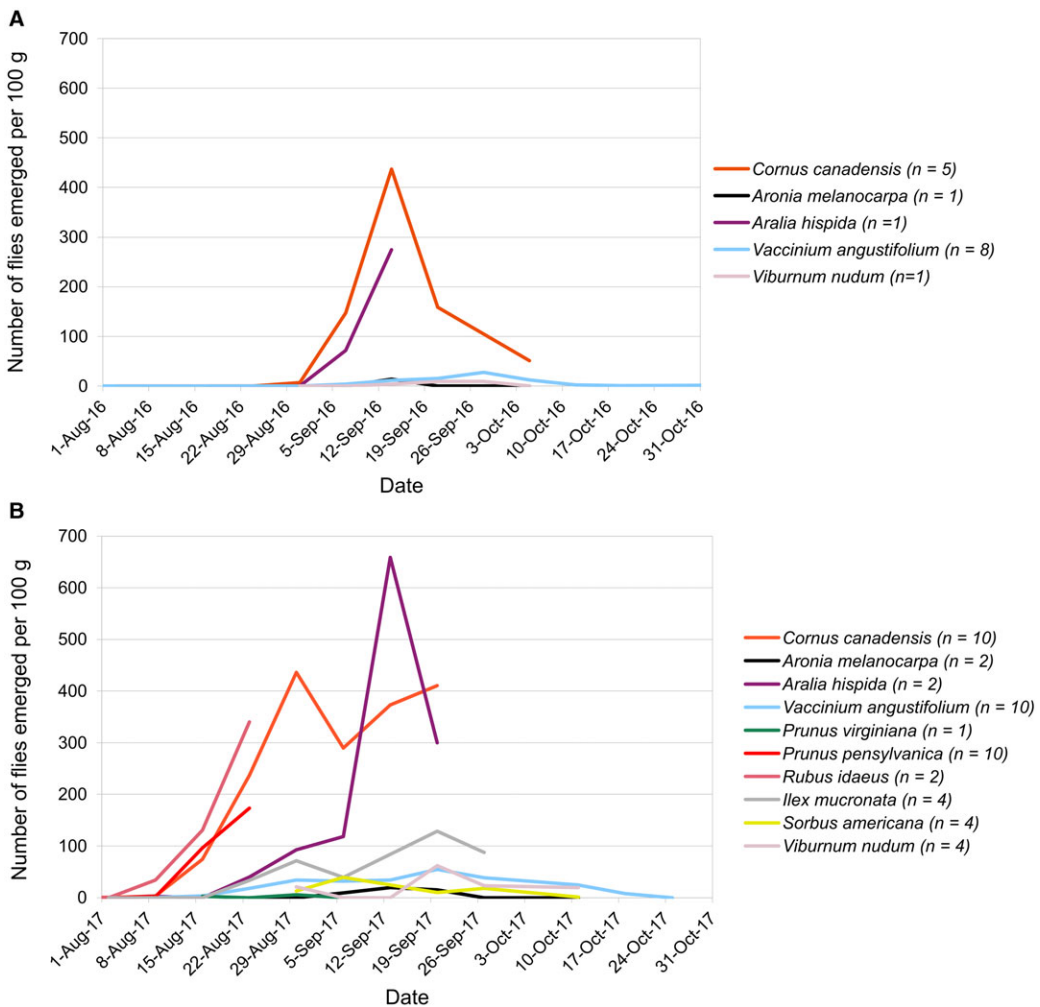


Fig. 2. Infestation levels of wild fruits, defined as the number of *Drosophila suzukii* flies produced in controlled conditions per 100 g of field-collected fruits in **A**, 2016 and **B**, 2017 in lowbush blueberry, in the Saguenay-Lac-Saint-Jean region, Québec, Canada. No flies emerged from fruit samples collected before August. The number of sampling sites where fruit species were available for sampling is indicated in parentheses.

representation across sites. Infested fruits of Canadian bunchberry (*C. canadensis*) produced 8–11 times more *D. suzukii* flies than did lowbush blueberry, clearly making bunchberry the principal wild-fruit host species used in both years. In 2016, *C. canadensis* and *A. hispida* were the two most productive species, with more than 100 flies per 100 g of collected fruit on two or three sampling occasions in September. More diverse sampling in 2017 added *P. pensylvanica* and *R. idaeus* as highly productive wild-fruit species. Considering trends for both years, wild-fruit infestation levels peaked near mid-September, being greatest on *C. canadensis* in 2016 (Fig. 3A) and greatest on *A. hispida* in 2017 (Fig. 3B). *Prunus pensylvanica*, *R. idaeus*, and *C. canadensis* produced abundant *D. suzukii* flies about two weeks before *A. hispida* did, but this latter species then reached the highest weekly infestation level recorded, at about 650 flies per 100 g. All other wild fruits, and lowbush blueberry crop fruits, showed moderate (50–100 flies/100 g) to low (< 50 flies/100 g) levels of infestation. Aborted larvae and pupae were rare and were not included in infestation-level estimates.

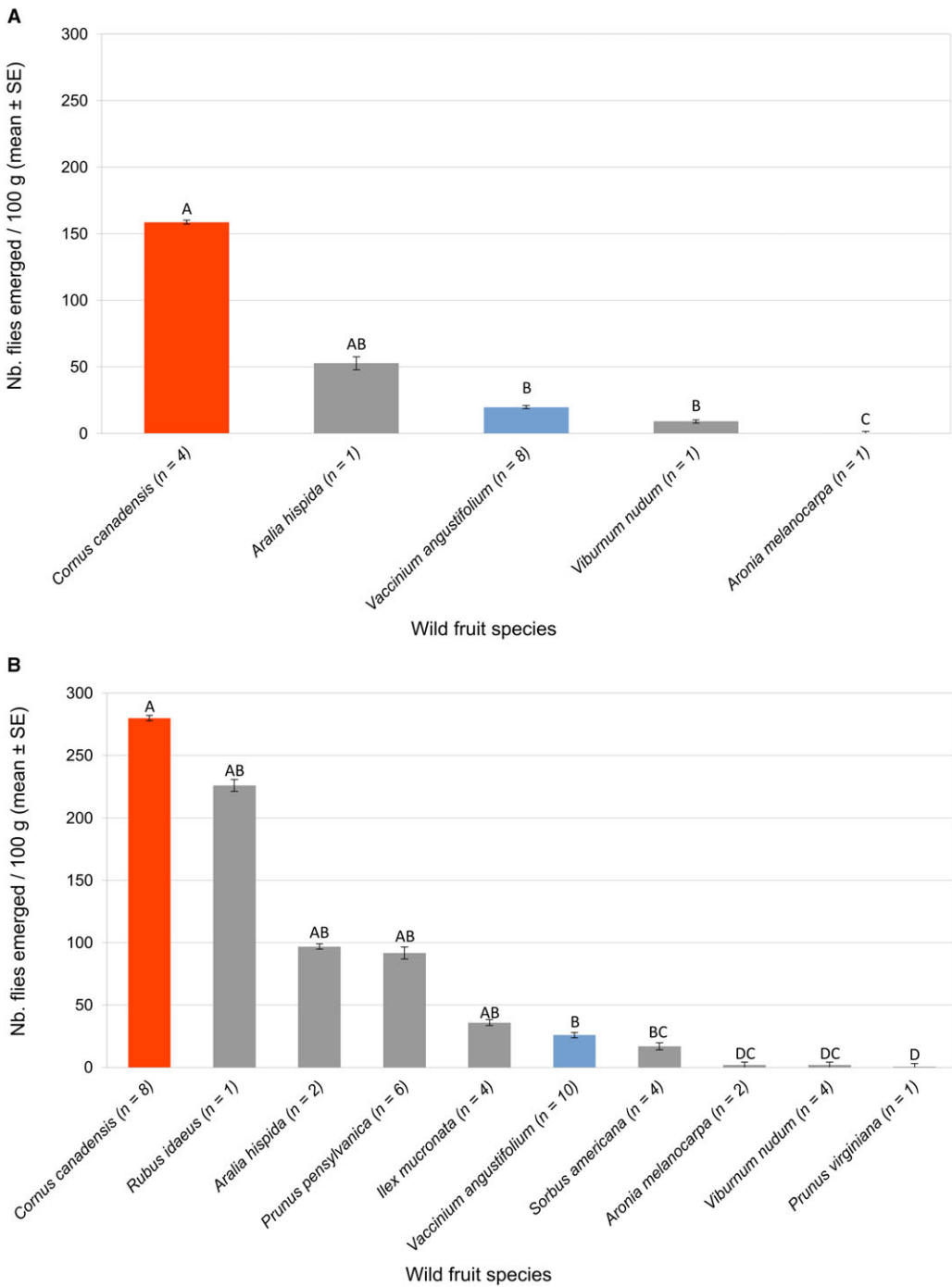


Fig. 3. Comparison of wild-fruit infestation by *Drosophila suzukii*, defined as the number of flies produced in controlled conditions per 100 g of field-collected fruit during lowbush blueberry harvest (mid-August to mid-September) in **A**, 2016 and **B**, 2017. Different letters indicate a significant difference between fruit species, at $\alpha = 5\%$. The number of sampling sites is indicated for each fruit species.

Table 2. Statistical modelling of per-fruit-infestation level for 10 common wild species of berry fruits available to *Drosophila suzukii* during the period of lowbush blueberry crop harvest, as a function of continuous variables as potential stimuli involved in host selection and taxonomically variable family.

Source	df	Mean square	F	Pr > F
Full model	8	1.64790	2.03	0.4971
Colour band	1	2.25696	2.78	0.3437
° Brix	1	5.85656	7.22	0.2268
Diameter	1	0.38889	0.48	0.6144
Family	5	0.65653	0.81	0.6830

***Drosophila suzukii* sex ratios on wild fruits**

The overall sex ratio of adult flies emerging from Canadian bunchberry samples in 2016 was 0.52, not significantly different from 1:1 ($\chi^2_1 = 1.44$, $0.10 < P < 0.25$, $n = 669$). Data for other wild-fruit species were pooled based on nonsignificant heterogeneity chi-square ($\chi^2_2 = 1.44$; $0.25 < P < 0.50$, $n = 60$), the overall sex ratio (0.58) also not being different from 1:1 ($\chi^2_1 = 1.67$; $0.10 < P < 0.25$, $n = 60$).

In 2017, the sex ratio of larger numbers of emerging adults from Canadian bunchberry samples was 0.54 and was significantly female biased ($\chi^2_1 = 37.56$; $P < 0.001$, $n = 4652$). Pooled data for other wild-fruit species after checking for homogeneity ($\chi^2_7 = 8.14$, $0.25 < P < 0.50$, $n = 1025$) indicated that the sex ratio (0.56) was also female biased ($\chi^2_1 = 12.90$, $P < 0.001$, $n = 1025$). When the sex ratio of flies from wild fruits was compared to that from lowbush blueberry crop fruits, no significant difference in either year was shown (2016: $\chi^2_1 = 0.38$; $0.50 < P < 0.75$, $n = 1789$; 2017: $\chi^2_1 = 0.21$; $0.50 < P < 0.75$, $n = 6741$).

Field infestation levels in relation to wild-fruit characteristics

Supplementary material, Table S2 shows the measured quantitative variables of the 10 fruit species sampled (fruit diameter, sugar content, and colour bands) that were used in modelling field infestation level as a function of fruit characteristics. We also used Family as a taxonomic (nominal) variable in modelling, Family being the sole sufficiently replicated species diversity variable insuring that number of explanatory variables in model did not exceed number of observations. None of the nine variables considered could explain observed field infestation levels, the model as a whole clearly not being significant ($F_{8,1} = 2.03$, $P = 0.4971$; Table 2).

Canadian bunchberry versus lowbush blueberry fruit preference experiments

No-choice experiment. The *Drosophila suzukii* females' daily egg-laying rate was similar in Canadian bunchberry and lowbush blueberry fruits ($F_{1, 21} = 0.58$, $P = 0.4553$; Fig. 4), with approximately two eggs laid per day in ripe fruits made available. There were no significant effects of time into the experiment ($F_{3, 58} = 2.24$, $P = 0.0935$) over the 12-day period of testing or of its interaction with fruit species ($F_{3, 58} = 2.27$, $P = 0.0896$).

Choice experiment. When given choice between a fruit of Canadian bunchberry or one of lowbush blueberry exposed simultaneously, female egg laying significantly differed ($F_{1, 77} = 9.24$, $P = 0.0032$), with about twice as many eggs being laid on lowbush blueberry than on Canadian bunchberry (Fig. 5A). Time (days) also significantly ($F_{3, 77} = 3.68$, $P = 0.0156$) affected egg laying (Fig. 5B), with no interaction of time and fruit species

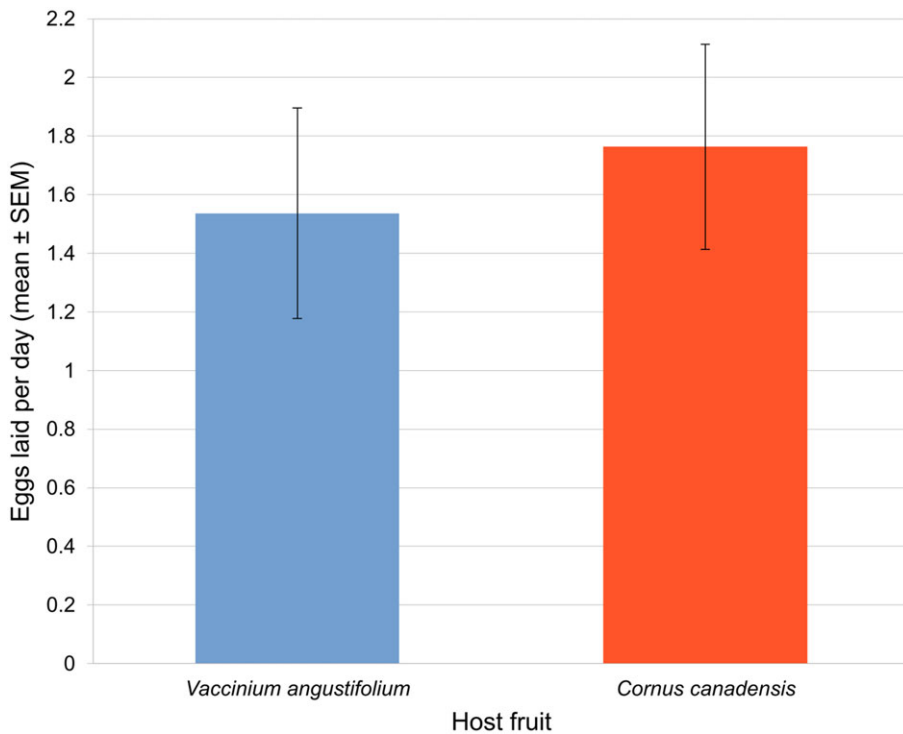


Fig. 4. Daily fecundity of *Drosophila suzukii* females in a no-choice test on host fruit species Canadian bunchberry, *Cornus canadensis*, and lowbush blueberry, *Vaccinium angustifolium*.

($F_{3, 77} = 0.47$, $P = 0.7045$), despite females apparently laying slightly more eggs earlier in the experiment.

Discussion

The first objective of the present study was to determine the alternative wild-fruit hosts of *D. suzukii* in lowbush blueberry agroecosystems of the Saguenay-Lac-Saint-Jean region, Québec, Canada, based on wild fruits sampled over two seasons. *Drosophila suzukii* fly emerged from five species belonging to four families in 2016, to which six species were added in 2017 (Fig. 1). Three of these species are reported here for the first time as new hosts for *D. suzukii*: *Aralia hispida* Ventenat (Araliaceae), *Prunus pensylvanica* Linnaeus, and *Sorbus americana* Marshall (Rosaceae) (Table 1). Two of the species, *P. pensylvanica* and *S. americana*, had been sampled before as potential hosts of *D. suzukii* in the United States of America, where they were not found to be infested (Table 1). Two of three newly reported hosts, *Prunus* Linnaeus and *Sorbus* Linnaeus, belong to fruiting plant genera with species that have often been found to be used by *D. suzukii*. However, species belonging to genus *Aralia* Linnaeus (or to the Araliaceae in general) have rarely been reported as hosts of *D. suzukii* (Poyet *et al.* 2015; Maier 2021).

Five berry fruit species shown to be used by *D. suzukii* in the present study were well-known hosts of the pest in Canada, the United States of America, or Europe. Of these, the most notable is wild raspberry, *R. idaeus* (Table 1). This species was previously recorded to be suitable for *D. suzukii* in association with lowbush blueberry in Maine, United States of America by Ballman and Drummond (2017), who also found *C. canadensis* and *Ilex mucronata* (Linnaeus) Powell *et al.*

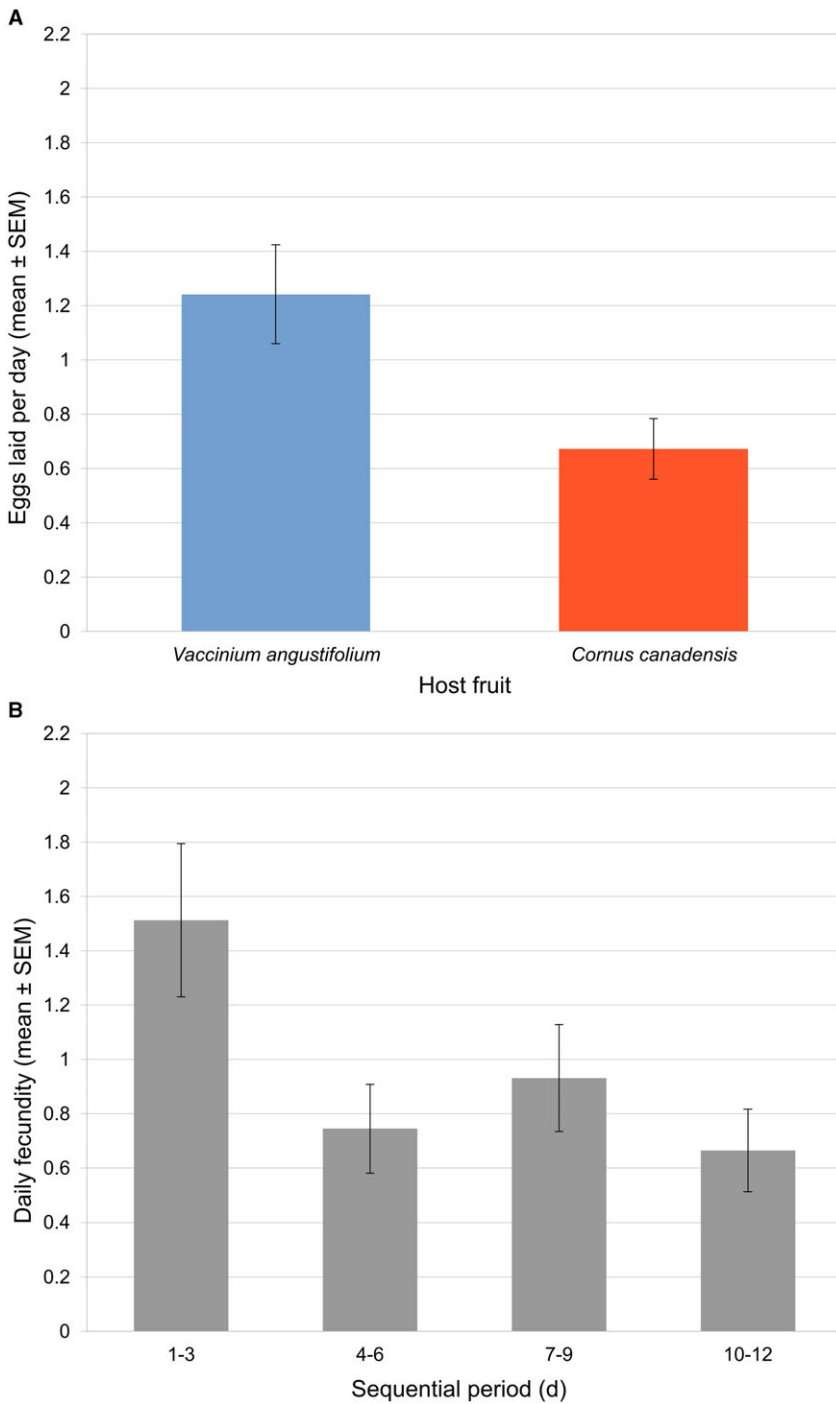


Fig. 5. Daily fecundity of *Drosophila suzukii* females in a binary-choice preference test on **A**, host fruit species Canadian bunchberry, *Cornus canadensis*, and lowbush blueberry, *Vaccinium angustifolium*, and **B**, according to time intervals into the experiment.

(Aquifoliaceae) to be exploited by *D. suzukii* in their study. Bunchberry, *C. canadensis*, is a common weedy species in reduced-management lowbush blueberry (Desjardins 2014; Ballman and Drummond 2017, and references therein; Champagne-Cauchon *et al.* 2020). Being common in blueberry field borders on humid soils, mountain holly, *I. mucronata*, is also a weedy nuisance in lowbush blueberry (Desjardins and Néron 2010). Previously reported hosts in Table 1 also include white rod, *V. nudum* var. *cassinoides* (wild raisin). It was found to host *D. suzukii* in Canada's Atlantic provinces (Little *et al.* 2019) but not in neighbouring Maine in a concomitant survey (Ballman and Drummond 2017). Black chokecherry, *A. melanocarpa*, a suboptimal host in laboratory assays in Wisconsin, United States of America in 2015 (Hietala-Henchell *et al.* 2017), was found to not be infested in Atlantic provinces in 2017 (Little *et al.* 2019). A last mention in the category of previously known hosts is the widespread chokecherry, *P. virginiana*. It was reported as a wild host of *D. suzukii* in British Columbia, Canada in early 2010s (Thistlewood *et al.* 2019) and in New York State in 2013 (Elsensohn and Loeb 2018), but *P. virginiana* was not infested near blueberry fields in 2015–2016 in Maine (Ballman and Drummond 2017). Chokecherry is also a common wild host of *D. suzukii* in southern New England, United States of America (Maier 2021) and is known to support *D. suzukii*'s fly development (Little *et al.* 2017).

Wild-fruit species from which no *D. suzukii* flies emerged (five species; Table 1) could be inherently unsuitable hosts for *D. suzukii*, despite its opportunistic polyphagy (Lee *et al.* 2015; Poyet *et al.* 2015; Briem *et al.* 2016; Little *et al.* 2020; Winkler *et al.* 2020). Alternatively, they might be suitable potential hosts that were insufficiently collected in the present study because they were uncommon in our sites. Red osier dogwood, *C. sericea* (only one fruit sample), was likely insufficiently collected; Lee *et al.* (2015) found it to be infested by *D. suzukii* in Oregon, United States of America. This was likely also the case with wild strawberry, which Gong *et al.* (2016) reported as being suitable for *D. suzukii* fly development.

A total of four other species (nonhosts) appear to be unsuitable for *D. suzukii*, with no flies emerging from multiple collections covering one or both years (Table 1). These results confirm a nonhost status for bearberry (*A. uva-ursi*, three sample-years). In British Columbia, bearberry was also negative for *D. suzukii* emergence, despite being common (Thistlewood *et al.* 2019, 15 sample-years). Similarly, in Nova Scotia, Canada, no emergence occurred from bearberry fruits (Little *et al.* 2019). No flies emerged either from eastern wintergreen fruits (*G. procumbens*, seven sample-years) in Little *et al.*'s (2017) Atlantic Canada survey. Its nonhost status was confirmed by Poyet *et al.* (2014), who observed eggs laying but hatching failure. Our data on *Maianthemum canadense* (eight sample-years) suggest that these fruits are not suitable, consistent with Ballman and Drummond's (2017) limited results (1 site, 2016). Furthermore, Lee *et al.* (2015) reported no infestation of fruits of *M. stellatum* in Michigan, United States of America (2 sites, 2011), which suggests that species of *Maianthemum* F.H. Wiggers are unsuitable hosts for *D. suzukii*. Finally, mountain serviceberry, *A. bartramiana* (five sample-years), most clearly came out as a nonhost in the present study. This is not surprising as fruit species belonging to the genus *Amelanchier* Medikus did not support *D. suzukii* in several other surveys. Some nonhost *Amelanchier* spp. that have been sampled elsewhere include *A. bartramiana*, *A. canadensis*, and *A. laevis* in Atlantic Canada (Little *et al.* 2019); *A. canadensis* in Maine (Ballman and Drummond 2017); and *Amelanchier* Medikus, *A. alnifolia*, and *A. cusickii* in British Columbia (Thistlewood *et al.* 2019).

Seasonal variation

Wild-fruit exploitation by *D. suzukii* extended for about nine weeks from mid-August to late October 2016 (Fig. 1A) and for 10 weeks from early August to mid-October 2017 (Fig. 1B). From

August onwards, lowbush blueberries near field borders most consistently supported *D. suzukii* emergence throughout the crop production season in both years. In addition, fruits of bunchberry *C. canadensis* in 2016 and of *S. americana*, *A. hispida*, and *V. nudum* var. *cassinoides* in 2017 were the most consistently available fruits in late summer through early fall. Thus, in addition to blueberry, these wild fruits appeared to be the most likely to contribute to *D. suzukii*'s abundance in lowbush blueberry crop fields during harvest. Note, however, that *A. hispida* fruits were no longer available for sampling in our sites in September 2016, weeks earlier than in 2017, which hypothetically might be explained by frugivore competition.

Despite being an early season fruit species suitable for *D. suzukii* (Gong *et al.* 2016), the wild strawberry (*F. virginiana*) appears insufficiently common in or near lowbush blueberry fields to contribute to local *D. suzukii* abundance. Mountain serviceberry (*A. bartramiana*) also matures its fruits relatively early in summer, but its fruits are likely to be resistant to *D. suzukii*, as discussed above. Three ericaceous plant species broadly available at either end of the season – bearberry (*A. uva-ursi*), eastern wintergreen (*G. procumbens*), and Canada mayflower (*M. canadense*) – also did not contribute to local *D. suzukii* dynamics due to fruit resistance, possibly at the genus level and consistent with other studies (Poyet *et al.* 2015; Ballman and Drummond 2017; Thistlewood *et al.* 2019).

Seasonal infestation and fruit quantitative and taxonomic properties

No evidence was found that observed field infestation levels of wild fruits by *D. suzukii* (number of flies emerged per 100 g of fruit) might directly depend on the potential oviposition stimuli that we measured (fruit size, visible colour spectra, and sugar content as °Brix) or on other undetermined specific traits that might vary at the host plant taxonomic family level among sampled fruit species. We conclude that traits known to influence female oviposition among the common wild berry fruits in peripheral forest habitats near blueberry crop fields are unlikely to directly contribute to the local dynamics of wild-fruit exploitation. This is consistent with results of several other studies addressing fruit polyphagy or preference in *D. suzukii* (Poyet *et al.* 2015; Kenis *et al.* 2016; Ballman and Drummond 2017; Thistlewood *et al.* 2019; Little *et al.* 2020). Wild-host availability and density, among other factors involved in the dynamics of fruit exploitation in similar agroecosystems (Ballman and Drummond 2017; Elsensohn and Loeb 2018; Drummond *et al.* 2019), should be examined in future work.

Host choice in controlled conditions

Bunchberry, a highly suitable alternative host fruit, is ubiquitous in reduced management lowbush blueberry fields. Ripe fruits of blueberry and bunchberry were simultaneously available in blueberry fields in the present study during much of August and September (Fig. 1). Their relative abundance was not determined but is likely to be higher for blueberry than bunchberry in crop fields. Our controlled no-choice preference tests indicated that ripe fresh fruits of both species were equally acceptable to *D. suzukii*, allowing similar daily rates of progeny production – that is, of 1–2 hatched larvae per day per fruit – for up to approximately 12 days into adult female life in laboratory tests. This is consistent with data on *D. suzukii* fecundity, as modelled by Ryan *et al.* (2016). In binary-choice tests, however, blueberry was consistently preferred, with twice as many larvae hatched per fruit. This suggests that, in the context of pest management, bunchberries as alternative host fruits in blueberry fields are unlikely to reduce blueberry infestation by acting as a trap wild host

(Alnajjar *et al.* 2017). However, its high infestation level means that its overall abundance can increase *D. suzukii* pressure on the crop, which warrants further study.

Pest management implications for lowbush blueberry producers

The proximity of wild fruits such as bunchberry in natural wooded habitats surrounding lowbush blueberry fields or growing within the fields as weeds may contribute to the infestation of the blueberry crops. This is consistent with results of Champagne-Cauchon *et al.* (2020; see also Drummond *et al.* 2019), showing that *D. suzukii* captures and crop-fruit infestation decrease with distance from field borders. Wild-fruit species in forested borders cannot be realistically controlled, as might be possible in the borders of row fruit crops (*e.g.*, Urbaneja-Bernat *et al.* 2020), notwithstanding that movement dynamics of *D. suzukii* between blueberry fields and field borders is unknown. However, efficient control of directly competing bunchberry as a weed within fields might help lowbush blueberry growers; this potential should be investigated experimentally.

Conclusions

The present study's results are generally consistent with *D. suzukii*'s broad generalism as a key ecological trait of the species but indicate exceptions to its polyphagy for some berry fruit taxa. This generally agrees with previous reviews of its ecology, trophic relations, behaviour, and invasive history (Cini *et al.* 2012; Hamby *et al.* 2016; Ørsted and Ørsted 2019; Winkler *et al.* 2020; Cloonan *et al.* 2021). In the lowbush blueberry cultivation region of Saguenay-Lac-St-Jean, *A. hispida*, *P. pensylvanica*, and *S. americana* are reported here for the first time as suitable hosts for *D. suzukii*. Based on the data, four other sufficiently sampled berry fruit species, *A. uva-ursi*, *S. americana*, *M. canadense*, and *G. procumbens*, were not infested, with the last of those species being acceptable for oviposition but unsuitable for development. None of the wild fruits locally available in or near lowbush blueberry fields reached fruit maturity early enough to be used as hosts for flies that might be locally active in late spring to early summer in Québec. We know that *D. suzukii* can survive local winter conditions despite substantial sex-biased mortality and resume reproduction after prolonged winter diapause (Cloutier *et al.* 2021, 2022). We found no evidence that infestation of wild fruits during blueberry harvest was directly influenced by physical and visual egg-laying stimuli used for oviposition by *D. suzukii* or by any attractants that might differ among fruit species at the plant taxonomic family level. In preference tests comparing blueberry, *V. angustifolium*, and bunchberry, *C. canadensis*, fruits, both species appeared equally suitable for larval development, but blueberries were preferred for oviposition by females over bunchberries in binary-choice tests.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.4039/tce.2022.42>.

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Competing interests. The authors declare no competing interests.

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