Evaluation of *Cyphocleonus trisulcatus* (Coleoptera: Curculionidae) as a potential biological control agent for *Leucanthemum vulgare* in North America

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Abstract

*Leucanthemum vulgare*, a perennial forb native to Eurasia, has become invasive in several other parts of the world. Since there is a lack of methods suitable for sustainable management of this plant across invaded landscapes, a biological control project has been initiated in North America and Australia. We evaluated the potential of the root-feeding weevil *Cyphocleonus trisulcatus* as a biological control agent for *L. vulgare* in North America by investigating its impact on *L. vulgare* and studying its larval host range under no-choice, multiple-choice cage and open-field conditions. Our impact experiment revealed that larval feeding by *C. trisulcatus* can severely damage and even kill plants. No-choice tests conducted with 41 non-target species showed that *C. trisulcatus* can develop on five closely related species. In a multiple-choice cage test established with three of these species, the medicinal plant *Matricaria chamomilla* and the native North American *M. occidentalis* were also attacked, but to a lower degree than *L. vulgare*. An open-field test conducted with four varieties of the ornamental Shasta daisy (*Leucanthemum × superbum* and *L. × maximum*) revealed similar attack on Shasta daisy as on *L. vulgare*. Due to the popularity of Shasta daisies, we suggest that *C. trisulcatus*, despite its potential to suppress *L. vulgare* populations, is not a suitable biological control agent for North America. However, *C. trisulcatus* may still be a potential biological control agent for *L. vulgare* in regions where Shasta daisy is less popular, such as Australia. Further host-range tests with species native to Australia as well as with additional species important for the horticultural industry in Australia are currently under way.

**KEYWORDS**

asteraceae, curculionidae, host-specificity testing, impact studies, oxeye daisy, weed biological control

1 | INTRODUCTION

*Leucanthemum vulgare* (Vaill.) Lam. (Asteraceae) (oxeye daisy) is a perennial forb native to Europe and western Asia. It has been introduced to many other parts of the world as an ornamental or a seed contaminant and can now be found on all continents except Antarctica (Holm, Pancho, Herberger, & Plunkett, 1979). In North America, it was reported to have naturalized in Québec and in the north-eastern United States by the eighteenth century (Fernald, 1903). It is now common in the north-eastern and north-western...
states of the United States and in the south-eastern and south-western provinces of Canada where it invades pastures, meadows, roadside areas and forest openings. More recently, it has also been reported to invade similar habitats in south-eastern Australia and in the Kashmir Valley in India (Khuroo, Malik, Reshi, & Dar, 2010; McConnachie et al., 2015). Leucanthemum vulgare can form dense, extensive populations in pastures, where it is generally avoided by grazing cattle and promotes soil erosion because of its shallow root system (Clements, Cole, Darbyshire, King, & McClay, 2004; Olson & Wallander, 1999). It also reduces plant species diversity and hay initiation in North America (McClay, Stutz, & Schaffner, 2013). The system (Clements, Cole, Darbyshire, King, & McClay, 2004; Olson & Wallander, 1999). Application of herbicides to suppress L. vulgare or of fertilizer to stimulate the growth of competing vegetation can reduce weed densities locally (Clements et al., 2004; Olson & Wallander, 1999), but these practices are not feasible for large-scale management. Hence, there is a lack of methods suitable for the sustainable management of this plant species across invaded landscapes (Clements et al., 2004).

In 2008, a biological control programme against L. vulgare was initiated in North America (McCoy, McClay, & Schaffner, 2013). The genus Leucanthemum is represented by 42 species in its native range in Eurasia (Greuter 2006+), but none of them is native to North America (Barkley, Brouillet, & Strother, 2006). In addition, the genus is phylogenetically relatively isolated from species native to North America, which is expected to further increase the probability to find sufficiently specific biological control agents of L. vulgare. Aside from L. vulgare, L. ircutianum DC. has also been introduced to North America, but it is far less abundant than L. vulgare (Fernald, 1903; Mulligan, 1958; Stutz, Štajerová, Hinz, Müller-Schärer, & Schaffner, 2016). The main non-target species of concern is the horticultural Shasta daisy (Leucanthemum × superbum), a hybrid of L. vulgare, L. maximum, L. lacustre and another Asteraceae species, that was introduced by the famous American plant breeder Luther Burbank in 1901 (Tahara, 1921). In North America, numerous varieties of Shasta daisy are widely grown as horticultural plants, mostly in home gardens (Anderson & Olsen, 2015; Hawke, 2007).

The root-feeding weevil Cyphocleonus trisulcatus Herbst (Coleoptera: Curculionidae) is one of the species that have been prioritized as potential biological control agents of L. vulgare. In the European literature, it is only reported from L. vulgare and the closely related L. ircutianum (Dieckmann, 1983; Rheinheimer & Hassler, 2010). In addition, root feeders in the family Curculionidae have proven to be among the most successful biological control agents of other weed species (Blossey and Hunt-Joshi, 2003). The congeneric Cyphocleonus achates Fahraeus is a successful biological control agent of knapweeds (Centaurea diffusa Lam. and C. stoebe L.) in North America (Bourchier & Van Hezewijk, 2013; Van Hezewijk & Bourchier, 2012; Story, Callan, Corn, & White, 2006). Cyphocleonus trisulcatus has been reported from different parts of Europe, including central and southern Europe, Scandinavia and Russia (Rheinheimer & Hassler, 2010). Our surveys in southern France revealed that C. trisulcatus can be locally quite common in this region, with up to 20% of the roots damaged by larvae (Stutz et al., 2016). The larvae of C. trisulcatus are reported to feed and pupate in the roots and adults are mostly found between May and August. No further information was available in the literature about the biology and the life cycle of this species (Dieckmann, 1983; Rheinheimer & Hassler, 2010).

In order to successfully control the target weed and to minimize indirect effects, biological control agents must impose a significant negative impact on the target weed (McCoy & Balcunias, 2005; Pearson & Callaway, 2005). In addition, the risk that a biological control agent attacks any non-target plants in the introduced range needs to be thoroughly evaluated through host-range studies. While the fundamental host range of a potential biological control agent can be determined by no-choice tests (Cullen, 1990), multiple-choice tests conducted under open-field conditions give a more realistic estimate of the range of species that might be attacked under natural conditions if the biological control candidate will be released into the target region (Briese 1999; Clement & Cristofaro, 1995; Schaffner, Smith, & Cristofaro, 2018).

The goal of this study was to evaluate the potential of C. trisulcatus as a biological control agent for L. vulgare in North America by gathering more information on its biology and experimentally assessing its impact on L. vulgare and its host range. For this, we assessed the impact of C. trisulcatus on growth and reproduction of L. vulgare using potted plants and investigated its host range under no-choice and multiple-choice cage and open-field conditions in its native range.

2 | MATERIALS AND METHODS

2.1 | Insect rearing

The C. trisulcatus adults used in this study originated from a rearing colony which had been established from larvae collected from eight populations of L. vulgare and one population of L. ircutianum in southern France (100 km east and north of Montpellier, see Table S1 in supporting information), in June 2012 and 2013. Plants infested with C. trisulcatus were collected in the field and half of them were transferred to pots, while the remaining plants were dissected for larvae which were then transferred onto healthy potted L. vulgare and L. ircutianum plants. All plants were individually covered with gauze bags, and emerging adults were subsequently either kept in transparent plastic cylinders (1.3 L) at ambient temperature or provided with rosettes of L. vulgare or L. ircutianum inserted in moist florist sponge, or on potted plants individually covered with gauze bags. To assess onset of oviposition, the cut rosettes and potted plants were regularly dissected and checked for eggs. During winter, the weevils were either kept in incubators set at 2–3°C or outdoors.

2.2 | Impact experiment

Plants of L. vulgare were grown from seeds collected in North America and sown in seedling trays in a greenhouse on 13 December 2013. In March 2014, 30 seedlings were potted in plastic pots (diameter 14 cm, height 17 cm) in a mixture of garden soil (Selmaterra, Eric Schweizer AG, Switzerland), sand and vermiculite (14:3:1) with
1 g/L of slow-release NPK fertilizer (Hauert Tardit 6M) added. The thirty plants were randomly allocated to two groups, and the number of rhizomes was estimated for each plant from above-ground as a proxy of initial plant size. There was no significant difference in the number of rhizomes per plant between the two groups \( (z = 0.4, p = 0.7) \). On 27 May, all plants were individually covered with gauze bags with a mesh size of 1 mm and two egg-laying females were released onto each of the 15 plants of the first group. The 15 plants of the second group were kept free of attack by *C. trisulcatus*. Six days later, the gauze bags were removed from all plants and the weevils retrieved. To protect the plants from other herbivory, they were moved to a gauze-covered field cage \( (2 \times 2 \times 1.6 \text{ m}) \) and positioned in a randomized design. From early August to mid-October 2014, all plants were again individually covered with gauze bags and regularly checked for adult emergence. In late October, when most of the shoots were dry and adult emergence had ceased, the number of shoots and flower heads was counted and all shoots removed, dried and weighed. After the flowering shoots had been removed, we measured the average height (from the soil surface to the top of the rosette leaves) and the diameter of each plant. All plants were overwintered outside where they were embedded in sawdust to protect them from harsh environmental conditions. To determine the potential long-term effect of *C. trisulcatus*, we re-measured all plants in July 2015, when they were flowering. The number of shoots and flower heads of each plant was counted, the length of the longest shoot measured, and above- and below-ground biomass were separately harvested, dried at 80°C for 24 hr and then weighed.

### 2.3 Test plant species

A general test plant list was developed based on the centrifugal phylogenetic approach proposed by Wapshere (1974) and revised by Briese (2003) and Kelch and McClay (2004). The selection of test plants was based on the phylogeny of the Anthemideae published by Oberprieler et al. (2009) and concentrated on species from this tribe, but representative members of other major tribes within the Asteraceae family, especially species native to North America as well as crops of economic importance, were also included. In addition, representative species from other families that contain polyacetylenes, a characteristic group of secondary metabolites found in *Leucanthemum vulgare* known to function as allelochemicals (Champagne, Arnason, Philogene, Morand, & Lam, 1986; Wrang & Lam, 1975), were incorporated in the list. The final list included some 50 species from which a subset of 41 plant species (including 21 species native to North America) were used in host-range tests with *C. trisulcatus*. The closely related ornamental Shasta daisy was represented by seven varieties (six varieties of *L. × superbum* and one variety of *L. × maximum*) and the garden Chrysanthemum (*Chrysanthemum × grandiflorum*) by three varieties. *Leucanthemum vulgare* grown from seeds collected from three populations in Canada and five populations in the United States as well as *L. ircutianum* grown from seeds collected from two populations in Canada were used as control plants. The majority of test plants were grown from seeds and sown three to six months before being used in tests. Some of the *L. vulgare* plants used in the multiple-choice cage tests and in the open-field test were sown one year earlier to ensure that they produced flowering shoots at the time the tests were conducted. The Shasta daisy varieties “Becky” and “Sunny Side Up” as well as all *Chrysanthemum* varieties were propagated from rhizomes or cuttings. All test plants were potted in pots (diameter 10-14 cm, height 17 cm) and grown in the same mixture of soil as the plants used in the impact experiment.

### 2.4 Host-range testing

Host-range testing was conducted at CABI in Delémont, Switzerland, in 2014 and 2015. All 41 test plant species were first exposed to *C. trisulcatus* under no-choice conditions to eliminate all non-target species on which *C. trisulcatus* cannot complete its life cycle from further tests. To collect additional information about which species within the fundamental host range would be accepted for oviposition when females were given a choice between target and non-target species, multiple-choice cage tests were then conducted with *L. vulgare* and three of the non-target species that supported adult development under no-choice conditions. In addition, an open-field test was conducted to further estimate the likelihood that the closely related Shasta daisy, which was found to be heavily attacked under no-choice conditions, would be attacked by *C. trisulcatus* if released as a biological control agent.

### 2.5 No-choice oviposition and larval development tests

No-choice oviposition and larval development tests were set up between 28 May and 24 July 2014 and between 15 May and 17 July 2015, using a total of approximately 150 females. Two egg-laying females each were placed onto individually potted, gauze-covered test and control plants. After 3-7 days (depending on prevailing temperature), the females were retrieved from the plants and individually placed into small cups together with a male and leaves of *L. vulgare* or *L. ircutianum* for at least two days to ensure that they were able to feed on their natural hosts between tests. Only females that continued laying eggs were reused for additional tests. A total of 1-13 replicates were set up per test plant species (Table 1). Three to eight weeks after the plants had been exposed to *C. trisulcatus*, the roots and rhizomes of all plants were dissected, the soil was checked for larvae, and the total number of larvae found per pot was recorded. As soon as larvae were found in one replicate of a test plant species, dissection was stopped and the remaining replicates were kept for adult emergence. All retained plants were individually covered with gauze bags and regularly checked for adult emergence. Only replicates where more than 50% of the simultaneously exposed control plants were attacked were considered as valid replicates.
TABLE 1 Results of no-choice oviposition and larval development tests conducted with Cyphocleonus trisulcatus in 2014 and 2015

| Plant species | Plants dissected for larvae | Plants kept for adult emergence |
|---------------|----------------------------|---------------------------------|
|               | No. of replicates | % plants with larvae | No. of larvae/ plant (mean ± SE) | No. of replicates | % plants with adult emergence | No. of adults/ plant (mean ± SE) |
| Family Asteraceae |                          |                                |                                    |                    |                                |                                    |
| Tribe Anthemideae |                          |                                |                                    |                    |                                |                                    |
| Subtribe Leucantheminae |                          |                                |                                    |                    |                                |                                    |
| Leucanthemum vulgare (Vaill.) Lam. | 3 | 100.0 | 11.7 ± 5.2 | 57 | 94.7 | 6.2 ± 0.8 |
| Leucanthemum × maximum (Ramond) DC | 16 | 87.5 | 5.4 ± 1.2 |
| Leucanthemum × superbum (Bergmans ex J. Ingram) Kent “Alaska” | 7 | 85.7 | 5.0 ± 1.9 |
| Leucanthemum × superbum “Becky” | 1 | 0 | 0 | 4 | 100.0 | 5.3 ± 2.7 |
| Leucanthemum × superbum “Crazy Daisy” | 7 | 100.0 | 3.7 ± 0.4 |
| Leucanthemum × superbum “Marconi Double” | 5 | 80.0 | 4.2 ± 1.7 |
| Leucanthemum × superbum “Silver Princess” | 5 | 100.0 | 3.0 ± 0.9 |
| Leucanthemum × superbum “Sunny Side Up” | 1 | 100.0 | 1.0 |
| Subtribe Anthemidinae |                          |                                |                                    |                    |                                |                                    |
| Anthemis arvensis L. | 7 | 0 | 0 |
| Anthemis cotula L. | 6 | 0 |
| Tanacetum huronense Nutt. | 8 | 0 |
| Tanacetum vulgare L. | 7 | 0 |
| Tripleurospermum inodorum (L.) Sch. Bip. | 6 | 0 |
| Subtribe Artemisiinae |                          |                                |                                    |                    |                                |                                    |
| Artemisia californica Less. | 6 | 0 |
| Artemisia campestris L. | 7 | 0 |
| Artemisia cana Pursh | 7 | 0 |
| Artemisia filifolia Torr. | 2 | 0 |
| Artemisia frigida Willd. | 9 | 0 |
| Artemisia ludoviciana Nutt. | 7 | 0 |
| Arctanthemum arcticum (L.) Tzvelev | 13 | 0 |
| Chrysanthemum × grandiflorum (Ramat.) Kitam. “Garden Mums” | 7 | 0 |
| Chrysanthemum × grandiflorum “Canary Mum” | 5 | 0 |
| Chrysanthemum × grandiflorum “Morden Delight” | 5 | 0 |
| Leucanthemella serotina (L.) Tzvelev | 7 | 0 |
| Subtribe Glebionidinae |                          |                                |                                    |                    |                                |                                    |
| Argyranthemum frutescens (L.) Sch. Bip. | 6 | 0 |
| Glebionis coronarius (L.) Cass. ex Spach | 1 | 100.0 | 2 | 4 | 25.0 | 0.5 ± 0.5 |
| Ismelia carinata (Schousb.) Sch.Bip. | 7 | 0 |

(Continues)
Multiple-choice oviposition and larval development tests in field cages

Multiple-choice cage tests were conducted with three of the species that supported adult development under no-choice conditions, that is the native North American *Matricaria occidentalis* and the commercially grown *M. chamomilla* and *Glebionis coronaria*. We were not able to include *Achillea ptarmica* in these tests because attack under no-choice conditions for this species became only apparent when the multiple-choice tests had already been set up. The tests were

| Plant species                        | Plants dissected for larvae | Plants kept for adult emergence |
|--------------------------------------|-----------------------------|---------------------------------|
|                                      | No. of replicates | % plants with larvae | No. of larvae/plant (mean ± SE) | No. of replicates | % plants with adult emergence | No. of adults/plant (mean ± SE) |
| Matricaria chamomilla L.             | 1                          | 100.0                  | 5                                 | 3                          | 100.0                  | 1.7 ± 0.3                      |
| Matricaria occidentalis Greene       | 1                          | 100.0                  | 1                                 | 3                          | 66.7                   | 0.7 ± 0.3                      |
| Achillea alpina L.                   | 8                          | 0                      |                                   |                            |                        |                                |
| Achillea borealis Bong.              | 9                          | 0                      |                                   |                            |                        |                                |
| Achillea ptarmica L.                 | 7                          | 14.3                   | 1.0 ± 1.0                         |                            |                        |                                |

Subtribe santolininae

| Plants kept for adult emergence |
|----------------------------------|
| Santolina chamaecyparissus L.     | 7                          | 0                      |
| Chamaemelum nobile (L.) All.      | 8                          | 0                      |

Subtribe cotuliniae

| Plants kept for adult emergence |
|----------------------------------|
| Cotula coronopifolia L.          | 2                          | 0                      |

Tribe astereae

| Plants kept for adult emergence |
|----------------------------------|
| Solidago nemoralis Aiton         | 9                          | 0                      |

Tribe cardueae

| Plants kept for adult emergence |
|----------------------------------|
| Carthamus tinctorius L.          | 6                          | 0                      |
| Cirsiurn flodmanii (Rydb.) Arthur | 3                          | 0                      |
| Cynara scolymus L.               | 6                          | 0                      |

Tribe coreopsideae

| Plants kept for adult emergence |
|----------------------------------|
| Coreopsis tinctoria Nutt.        | 5                          | 0                      |

Tribe eupatorieae

| Plants kept for adult emergence |
|----------------------------------|
| Eutrochium maculatum (L.) E.E.Lamont | 2                          | 0                      |

Tribe gnaphalieae

| Plants kept for adult emergence |
|----------------------------------|
| Anaphalis margaritacea (L.) Benth. | 7                          | 0                      |

Tribe helenieae

| Plants kept for adult emergence |
|----------------------------------|
| Ehelium autumnale L.             | 6                          | 0                      |

Tribe heliantheae

| Plants kept for adult emergence |
|----------------------------------|
| Helianthus annuus L.             | 7                          | 0                      |

Tribe lactuceae

| Plants kept for adult emergence |
|----------------------------------|
| Cichorium intybus L.             | 6                          | 0                      |
| Lactuca sativa L.                | 7                          | 0                      |

Tribe madieae

| Plants kept for adult emergence |
|----------------------------------|
| Arnica chamissonis Less.         | 6                          | 0                      |

Tribe senecioneae

| Plants kept for adult emergence |
|----------------------------------|
| Senecio eremophilus Richardson   | 4                          | 0                      |

Family apiaceae

| Plants kept for adult emergence |
|----------------------------------|
| Daucus carota L.                 | 6                          | 0                      |

Family campanulaceae

| Plants kept for adult emergence |
|----------------------------------|
| Lobelia cardinalis L.            | 5                          | 0                      |

Note: Each plant was exposed to two egg-laying females for 3–7 days.

*Plant species native to North America.

Plants grown from seeds of a commercially available cultivar of *Arctanthemum arcticum* were used.
conducted in four large gauze-covered field cages (2 × 2 × 1.6 m) each containing three potted plants of each of the three non-target species and of L. vulgare as controls. At the time the experiment was set up, all test plants had shoots while the L. vulgare plants of the same age were still in the rosette stage. We therefore used a total of three L. vulgare plants with shoots that had been sown in the previous year and a total of nine L. vulgare plants in the rosette stage as controls (Table 2). The plants were randomly distributed within the field cages and buried into sawdust so that the upper edge of the pot was level with the surface of the sawdust. The plants did not touch each other, nor did they touch the net of the field cages. Eleven egg-laying females each were released into two of the cages on 28 May 2015 and into the two remaining cages on 15 June. Ten days after the release of the females, all plants were removed from the cages and checked for females. Once all the females were retrieved, the plants were individually covered with gauze bags. On 9 and 10 July (for plants from cages set up on 28 May) and between 15 and 17 July (for plants from cages set up on 15 June), roots and rhizomes of all plants were dissected, the soil was checked for larvae, and the total number of larvae per pot recorded.

2.7 Multiple-choice oviposition and larval development tests in the open-field

An open-field test was set up with four different Shasta daisy varieties (L. × superbum “Alaska,” L. × superbum “Becky,” L. × superbum “Crazy Daisy” and L. × maximum) on a meadow at CABI, Delémont, Switzerland. To investigate whether females of C. trisulcatus were actively searching for Shasta daisy, we arranged experimental patches of L. vulgare and Shasta daisy at various distances from the point where we subsequently released the weevils. If C. trisulcatus is not attracted to Shasta daisy, we would expect that non-target attack would only occur close to the release point, but that L. vulgare is also attacked when placed further away. Twelve potted plants of each of the four Shasta daisy varieties (all except the variety “Becky” were in the rosette stage) and 48 plants of L. vulgare (36 plants in the rosette stage and 12 older plants with shoots) were arranged in patches of four plants each. Each patch consisted of four Shasta daisies (one of each variety) or four L. vulgare (either four without shoots or two without and two with shoots), and the patches were set up at 2.5, 5 and 10 m radially from a central release point (Figure 1). The potted plants were buried into the soil so that the upper edge of the pot was level with the surface of the soil. Between 16 and 18 June 2015, a total of 50 egg-laying females of C. trisulcatus were released at the central point. One month later, all plants were removed, carefully checked for C. trisulcatus adults and individually covered with gauze bags. All plants were regularly checked for adult emergence.

2.8 Statistical analyses

To investigate the impact of C. trisulcatus on L. vulgare, quasi-Poisson generalized linear models (i.e. Poisson models with a dispersion parameter added to account for overdispersion) were used for the number of shoots and number of flower heads and linear models were used for all other parameters. To meet normality assumptions, square-root-transformed data were used to compare below-ground biomass of plants attacked by C. trisulcatus and control plants. To determine whether the proportion of plants attacked by C. trisulcatus differed between individual test plant species and L. vulgare, Fisher’s exact tests were conducted. To analyse whether the number of larvae or adults found per plant differed between individual test plant species or varieties and L. vulgare, quasi-Poisson generalized linear models (for the majority of the tested species) or Wilcoxon

| Plant species | No. of plants exposed | % plants with larvae found | No. of larvae (mean ± SE) |
|---------------|-----------------------|---------------------------|---------------------------|
| Cages 1 and 2 (set up on 28 May) | | | |
| Leucanthemum vulgare (rosettes) | 5 | 100.0 | 15.6 ± 1.9 |
| Leucanthemum vulgare (with shoots) | 1 | 100.0 | 2.0 |
| Glebionis coronaria | 6 | 0 | |
| Matricaria chamomilla | 6 | 50.0 | 1.7 ± 0.8 |
| Matricaria occidentalis | 6 | 33.3 | 0.5 ± 0.3 |
| Cages 3 and 4 (set up on 15 June) | | | |
| Leucanthemum vulgare (rosettes) | 4 | 100.0 | 17.8 ± 2.5 |
| Leucanthemum vulgare (with shoots) | 2 | 100.0 | 1.5 ± 0.5 |
| Glebionis coronaria | 6 | 0 | |
| Matricaria chamomilla | 6 | 0 | |
| Matricaria occidentalis | 6 | 0 | |

Note: Eleven egg-laying females were released in each of four cages. Half of the plants were exposed from 28 May to 9 June and the other half from 15 June to 25 June. Leucanthemum vulgare with shoots were 18 months old, and all other plants were six months old. All test plants had shoots at the time the tests were set up.

*Plant species native to North America.*
signed-rank tests (for the comparison of the number of adults that emerged from *L. vulgare* and *G. coronaria, M. chamomilla* and *M. oc-cidentalis* under no-choice conditions and for the comparison of the number of larvae found on *L. vulgare* rosettes compared to *L. vulgare* with shoots under multiple-choice conditions) were conducted. To investigate whether the number of adults that emerged from the plants exposed in the open-field test differed between *L. vulgare* rosettes and Shasta daisy and whether this potential difference varied with increasing distance from the release point, a quasi-Poisson generalized linear model that included plant species, distance from release point and their interaction was conducted. All analyses were performed with the software R version 3.4.3 (R Core Team 2017).

3 | RESULTS

3.1 | Biology

After emergence, adults of *C. trisulcatus* fed until November, when they went into hibernation until March. Mating was primarily observed in spring and females started to lay eggs between end of April and mid-June. Females laid eggs for approximately 2–2.5 months. Eggs were found externally on the roots or rhizomes. Most of the larvae were observed feeding externally on the roots and rhizomes, but occasionally larvae were also found feeding inside the central part of the main root and inside larger rhizomes. Pupation took place in the soil. Development from egg to adult took approximately 2.5–3.5 months and the first adults emerged in July. Some of the weevils of the rearing colony survived over several years. No parasitoids emerged from any of the developmental stages of *C. trisulcatus* collected in France or reared at CABI Switzerland.

3.2 | Impact experiment

An average (± SE) of 7.2 ± 0.8 adults emerged from all the plants exposed to *C. trisulcatus* while no adults emerged from any of the control plants not exposed to *C. trisulcatus*. After the first growing season, the number of shoots and flower heads and the biomass of the flowering shoots were similar for control and infested plants (all *p > .1*, Table 3). However, the diameter and height of the vegetative parts of the infested plants were on average 24% and 51% lower, respectively, compared with control plants (*t = 4.8, df = 28, p < .001* and *t = 4.9, df = 28, p < .001*, respectively, for mean and SE of the traits, see Table 3). One of the plants that had been infested with *C. trisulcatus* died during winter, and all other plants survived until the end of the experiment. During the second growing season (i.e. one year after the exposure to *C. trisulcatus*), plants infested
TABLE 3  Effect of larval feeding by Cyphocleonus trisulcatus on potted Leucanthemum vulgare

| Measurements taken       | Control plants | Infested plants |
|--------------------------|----------------|-----------------|
| Number of flower heads   | 7.5 ± 2.5      | 7.3 ± 1.9       | n.s.           |
| Number of flowering shoots| 4.3 ± 1.3      | 5.6 ± 1.4       | n.s.           |
| Biomass of flowering shoots (g) | 3.7 ± 2.4   | 2.8 ± 1.8       | n.s.           |
| Diameter of plant (cm)   | 17.8 ± 0.7     | 13.5 ± 0.5      | ***            |
| Height of plant (cm)     | 6.5 ± 0.6      | 3.2 ± 0.4       | ***            |

Note: Means (± SE) of 15 potted plants exposed to two egg-laying females for six days and of 15 control plants are shown. Plants were exposed in May 2014, and data were collected in October 2014.

*a*Excluding flowering shoots.

**p < .001, quasi-Poisson generalized linear models (for number of shoots and flower heads) and linear models (for all other variables).

with C. trisulcatus produced on average 44% fewer shoots (*t* = 3.0, *df* = 28, *p* = .006, 21.3 ± 9.9 vs. 12.1 ± 6.9) and 44% fewer flower heads (*t* = 3.0, *df* = 28, *p* = .007, Figure 2) than non-infested control plants. Above-ground biomass and below-ground biomass were reduced by 44% (*t* = 4.1, *df* = 28, *p* < .001; Figure 2) and 68% (*t* = 5.8, *df* = 28, *p* < .001, Figure 2), respectively. The length of the longest shoot did not differ between plants infested with C. trisulcatus and control plants (*t* = 1.0, *df* = 27, *p* = .3, Figure 2).

3.3 | No-choice oviposition and larval development tests

Neither the proportion of plants with successful adult development nor the average number of emerging adults differed between L. vulgare and L. ir Curtianum (*p* = .3, Fisher’s exact test and *t* = 0.7, *df* = 71, *p* = .5, respectively, Table 1). Adult development was successful on a similar proportion of Shasta daisies and L. vulgare (89% vs. 95%, *p* = .4, Fisher’s exact test), but on average fewer adults emerged from Shasta daisies than from L. vulgare (3.7 ± 0.6 vs. 6.2 ± 0.8; *t* = 2.8, *df* = 107, *p* = .006).

Adults emerged from a similar proportion of the two annual plants M. chamomilla and M. occidentalis as from L. vulgare (both *p* > .1, Table 1) but from a significantly lower proportion of the annual plant Glebionis coronaria than of L. vulgare (*p* = .02, Fisher’s exact test, Table 1). Significantly fewer adults emerged from G. coronaria (*W* = 15, *p* = .003, Table 1), M. chamomilla (*W* = 26, *p* = .04, Table 1) and M. occidentalis (*W* = 11.5, *p* = .01, Table 1) than from L. vulgare.

Larvae were also found on one plant of the perennial Achillea ptarmica, but no adults emerged from any of the other four A. ptarmica plants that were not dissected. No larvae were found on any of the other 35 test plant species exposed.

3.4 | Multiple-choice test in field cages

In all four field cages, larvae were found on all of the L. vulgare plants. However, on average ten times more larvae were found on L. vulgare rosettes than on the older L. vulgare with shoots (*W* = 0, *p* = .02, Table 2). In the two field cages set up on 28 May, larvae were found on 50% of the M. chamomilla and on 33% of the M. occidentalis plants, but no larvae were found on these two species in the two field cages set up on 15 June. No larvae were found on any of the G. coronaria plants exposed. In the two field cages set up on 28 May, nine and 31 times more larvae were found on L. vulgare rosettes compared to M. chamomilla and M. occidentalis, respectively (both *p* < .05, Table 2), but a similar number of larvae were found on the two test plant species as on L. vulgare with shoots (both *p* > .05, Table 2).

3.5 | Multiple-choice test in the open-field

One month after C. trisulcatus was released in the open-field test, adults started to emerge from L. × superbum “Becky.” Since the development from egg to adult takes at least 2.5 months, this Shasta daisy variety must have been infested with C. trisulcatus prior to the experiment. Before being exposed in the open-field test, these plants had been kept apart from the other plants in a separate field cage and it was later observed that this cage had been contaminated.
with C. trisulcatus. Data obtained for L. × superbum “Becky” are therefore not reported here.

Adults emerged from all 12 L. vulgare patches and from all except one Shasta daisy patch. Adults emerged from a similar proportion of Shasta daisy plants as from L. vulgare rosettes (83% vs. 89%, \( p = .3 \), Fisher’s exact test, Table 4), but adults emerged from only one (i.e. 8%) of the L. vulgare plants with shoots. A similar number of adults emerged from all three Shasta daisies varieties (\( F = 0.2, df = 33, p = .8 \), Table 4). The number of adults that emerged decreased with increasing distance from the release point (\( t = 2.4, df = 68, p = .02 \), Table 4), but was similar for Shasta daisies as for L. vulgare rosettes (4.1 ± 0.7 vs. 4.9 ± 0.8, \( t = 0.2, df = 68, p = .8 \), Table 4), and there was no significant interaction between the two factors (\( t = 0.7, df = 68, p = .5 \)). A similar number of adults emerged from Shasta daisies as from L. vulgare rosettes at all three distances (all \( p > .1 \)).

4 | DISCUSSION

4.1 | Biology and impact of Cyphocleonus trisulcatus on Leucanthemum vulgare

Our impact study showed that larval feeding by C. trisulcatus severely damages the roots and rhizomes, which resulted in a significant reduction of the above- and below-ground biomass and the number of flower heads of L. vulgare in the year after attack. We also observed that one of the plants that was exposed to C. trisulcatus during the impact experiment and several L. vulgare plants that were exposed to C. trisulcatus during the host-range tests died. These results indicate that C. trisulcatus has the potential to kill individual plants and to suppress invasive L. vulgare populations by preventing or slowing down vegetative spread by rhizomes and reducing sexual reproduction. A closely related species, the root-feeder Cyphocleonus achates, was introduced as a biological control agent of Centaurea stoebe and C. diffusa in North America (Story et al., 2006). A pot experiment with this species had revealed that larval feeding reduced above- but not below-ground biomass of C. stoebe, indicating that the plants were able to compensate for the root damage (Steinger & Müller-Schärer, 1992). Nevertheless, under field conditions in the introduced range C. achates was found to not only reduce above-ground biomass and reproduction of C. stoebe (Knochel & Seastedt, 2010; Wooley, Smith, King, Seastedt, & Knochel, 2011), but also below-ground biomass (Corn, Story, & White, 2006). Similarly, C. achates was also shown to reduce plant density, plant height and the number of seed heads of the closely related C. diffusa (Van Hezewijk & Bourchier, 2012). Interestingly, in our study there were no signs that L. vulgare would compensate for attack by C. trisulcatus even one year after attack when attacked plants had 44% and 68% lower above- and below-ground biomass, respectively, compared to control plants. However, compensatory growth of L. vulgare might have been partly prevented.

| Plant species               | No. of replicates | % plants with adult emergence | No. of adults found/plant (mean ± SE) |
|-----------------------------|-------------------|-------------------------------|---------------------------------------|
| 2.5 m from release point    |                   |                               |                                       |
| L. vulgare (rosettes)       | 12                | 91.7%                         | 5.9 ± 1.6                             |
| L. vulgare (with shoots)    | 4                 | 0.0%                          |                                       |
| L. × maximum                | 4                 | 100.0%                        | 6.0 ± 3.7                             |
| L. × superbum "Alaska"      | 4                 | 100.0%                        | 7.3 ± 1.9                             |
| L. × superbum "Crazy Daisy" | 4                 | 100.0%                        | 6.3 ± 3.0                             |
| 5 m from release point      |                   |                               |                                       |
| L. vulgare (rosettes)       | 12                | 91.7%                         | 5.6 ± 1.3                             |
| L. vulgare (with shoots)    | 4                 | 25.0%                         | 2.5 ± 2.5                             |
| L. × maximum                | 4                 | 100.0%                        | 5.0 ± 1.5                             |
| L. × superbum "Alaska"      | 4                 | 100.0%                        | 2.5 ± 0.9                             |
| L. × superbum "Crazy Daisy" | 4                 | 75.0%                         | 3.0 ± 1.6                             |
| 10 m from release point     |                   |                               |                                       |
| L. vulgare (rosettes)       | 12                | 83.3%                         | 3.2 ± 1.0                             |
| L. vulgare (with shoots)    | 4                 | 0.0%                          |                                       |
| L. × maximum                | 4                 | 75.0%                         | 3.3 ± 2.3                             |
| L. × superbum "Alaska"      | 4                 | 50.0%                         | 1.5 ± 0.9                             |
| L. × superbum "Crazy Daisy" | 4                 | 50.0%                         | 2.3 ± 1.3                             |

Note: Patches of potted Leucanthemum vulgare and Shasta daisy (Leucanthemum × maximum and L. × superbum) were arranged at three distances from a central point where fifty egg-laying females were released (Figure 1). Plants were exposed for one month. Leucanthemum vulgare with shoots were 18 months old, and all other plants were six months old. All test plants had shoots at the time the test was set up.
by the fact that the plants were grown in pots where nutrients and space become limited with time. In summary, our results indicate that at least a similar impact of *C. trisulcatus* on *L. vulgare* should be expected if it were released as a biological control agent than what has been observed for *C. achates* on *C. stoeb* and *C. diffusa*.

In contrast to Dieckmann (1983) who reported that the larvae of *C. trisulcatus* develop and pupate in the roots of *L. vulgare*, we observed that the larvae almost exclusively feed externally on the roots and rhizomes and that pupation takes place in the soil. This behavior also differs from *C. achates* whose larvae feed, overwinter and pupate inside the central vascular tissue of the tap root of *C. stoeb* where they cause a gall-like enlargement (Stinson, Schroeder, & Marquardt, 1994). The differences in the feeding habitat between the two species are most likely adaptations to the architecture of the roots of their host plant: in contrast to *C. stoeb*, *L. vulgare* has no large tap root and most of the main roots and rhizomes are too small to support complete internal development of *C. trisulcatus* larvae.

4.2 | Host range of *Cyphocleonus trisulcatus*

Our no-choice tests revealed that *C. trisulcatus* is able to develop on the congeneric ornamental Shasta daisy (*L. × maximum* and *L. × superbum*) as well as on four plant species outside the genus *Leucanthemum*, that is the North American native *Matricaria occidentalis* and the commercially grown *M. chamomilla* (a medicinal plant), *Glebionis coronaria* (used as a leaf vegetable in Asian cuisine) and *Achillea ptarmica* (an ornamental), all belonging to closely related subtribes within the tribe Anthemideae (Oberprieler et al., 2009).

Interestingly, we found that in multiple-choice tests conducted in field cages and under open-field conditions *L. vulgare* plants with shoots were less often attacked by *C. trisulcatus* than rosette plants. Plants with shoots were sown 18 months and rosette plants 6 months before exposure and it was generally observed that, if grown in pots, *L. vulgare* plants grow much more vigorously in the first compared to the second year, probably due to the limited space and nutrients available in the pots. Our results may therefore indicate that *C. trisulcatus* has a preference for healthy, vigorously growing plants (Price, 1991), rather than a general preference for rosette plants compared to plants with shoots.

Under multiple-choice cage conditions, a few larvae were found on *M. chamomilla* and *M. occidentalis* in the two field cages set up at the end of May, but not in the two cages that were set up two weeks later. Both species are early flowering and die after seed production. It is therefore likely that the plants in the second two cages were already too old to be accepted for oviposition and/or to support larval development. Although the impact of larval feeding on these two species was not experimentally measured, we did not observe any evident impact above-ground. Further studies would be needed to evaluate whether the life cycles of these two non-target species are sufficiently synchronized with *C. trisulcatus* in the introduced range to support complete larval development and whether the relatively low attack rates have an impact on the number of flower heads produced (for the medicinal herb *M. chamomilla*) or on seed production (for the North American native *M. occidentalis*). Our multiple-choice cage tests revealed that the exposed *G. coronaria* plants, which already started to produce flowering heads, were not attacked by *C. trisulcatus*. However, it remains to be shown whether younger plants of this annual leaf vegetable would be attacked in cage tests and whether attack would have an impact on the plants above-ground. In addition, open-field tests would be necessary to elicit whether the species attacked by *C. trisulcatus* under field-cage conditions would also be attacked under natural conditions because exposure in field cages may have led to the acceptance of test plant species that would not be selected in the field (Marohasy, 1998). Additional studies would also be needed with *Achillea ptarmica* to further clarify whether *C. trisulcatus* can complete its development on this perennial species and whether it would attack it under multiple-choice conditions.

Although our results indicate that non-target species outside the genus *Leucanthemum* are suboptimal hosts for *C. trisulcatus*, this may not be the case for the congeneric ornamental Shasta daisies (*L. × maximum* and *L. × superbum*). All of the tested Shasta daisy varieties were heavily attacked under open-field conditions and similar numbers of adults emerged from them as from *L. vulgare* up to 10 m from where the weevils were released. Our results therefore indicate that *C. trisulcatus* would likely also attack Shasta daisy under natural conditions in North America. To our knowledge, *C. trisulcatus* has not been reported as a pest of Shasta daisies in its native range, which could be due to a lack in overlap of the habitats occupied by *C. trisulcatus* and Shasta daisy. In addition, the probability that *C. trisulcatus* encounters Shasta daisy is likely to be low in Europe, because the weevil is considered as rare (Rheinheimer & Hassler, 2010). This would likely change once *C. trisulcatus* is released in North America, where it is expected to build up high population densities, and Shasta daisies are very popular garden flowers (Anderson & Olsen, 2015). We did not experimentally measure the impact of larval feeding on Shasta daisy but our observations indicate that the damage caused by *C. trisulcatus* on Shasta daisy is comparable to the damage observed on *L. vulgare*.

4.3 | Implications for the biological control of *Leucanthemum vulgare*

In summary, our study provides evidence that, despite its considerable impact on *L. vulgare*, *C. trisulcatus* is not a suitable biological control agent for *L. vulgare* in North America because the risk of non-target attack and damage of Shasta daisies is considered to be too high. In North America, Shasta daisies are among the most beloved garden flowers and of significant value to the ornamental nursery industry (Anderson & Olsen, 2015), which is also evidenced by a study that evaluated 36 cultivars for their suitability to grow them in the northern parts of North America (Hawke, 2007). Nevertheless, *C. trisulcatus* may be a suitable biological control agent of *L. vulgare* on continents where Shasta daisy is not as popular as in North America. In Australia, *L. vulgare* is widespread in Victoria and Tasmania and it is becoming more abundant in New
South Wales. In New South Wales, L. vulgare has become one of the most alarming invasive plants in the Kosciuszko National Park and a programme to investigate the prospects for the biological control of L. vulgare was recently initiated (McConnachie et al., 2015; McDougall, Wright, & Peach, 2018). Investigations on the value of Shasta daisy for the flower industry in Australia are currently ongoing, but it seems that Shasta daisies are much less common than in North America and mainly grown for the cut flower industry (A. McConnachie, personal communication). Studies on the host range of C. trisulcatus are therefore being continued by conducting further tests with the horticultural test plant species supporting larval development (A. ptarmica, G. coronaria and M. chamomilla), and additional species important for the horticultural industry in Australia as well as species native to Australia. The latter is a relatively small group of test plant species, since in Australia the genus Leucanthemum is even more phylogenetically isolated than in North America and only a total of eight native species from the two genera Leptinella and Cotula are placed within the tribe Anthemideae (Thompson, 2007).

The absence of closely related native and/or economically important species in one country compared to another resulted in the release of several biological control agents that have been judged as not sufficiently specific in countries where these closely related species are present. For example, Epiblema strenua (Walker) has been introduced as a biological control agent for Parthenium hystaphorus L. and Ambrosia artemisiifolia L. in Australia and China, but not in India and South Africa because it develops on Guizotia abyssinica (L.f.) Cass, an oilseed crop cultivated in Ethiopia and India (McConnachie, 2015). Similarly, two biological control agents (Oxystilus pilosellae Zeller and Macrolabis pilosellae (Billie)) have been released against invasive hawkweeds (Pilosella spp.) in New Zealand but are not suitable biological control agents against invasive hawkweeds in North America, due to the presence of native hawkweeds (Hieracium spp.) (Grosskopf, Wilson, & Littlefield, 2008).

The close relatedness of L. vulgare and Shasta daisy and the popularity of the latter make it a challenge to find natural enemies that are sufficiently specific to be considered for field release in North America. Nevertheless, ongoing host-range tests conducted with two other potential biocontrol agents, that is the root-mining torricid moth Dichromapha aeratana Pierce & Metcalfe and the root-galling tephritid fly Oxyna nebulosa Wiedemann, revealed that these two species have a strong preference for L. vulgare and only occasionally attack Shasta daisies, making them promising candidates for potential release in North America.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS’ CONTRIBUTIONS

SS, HH and US conceived research. SS conducted experiments. SS analysed data and conducted statistical analyses. SS, HH and US wrote the manuscript. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study can be found in the Data S1.

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