Bittersweet bugs: the Dutch insect community on the nightshade *Solanum dulcamara*

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The native Solanaceaous plant *Solanum dulcamara* occupies both dry and wet habitats in The Netherlands. During field examinations, a flourishing insect community was found on this plant species, including both generalist and specialist herbivores. The most abundant specialist herbivores belong to the flea beetles (Chrysomelidae). Surprisingly, we also found notable numbers of ants (Formicidae) and lady beetles (Coccinelidae) that were apparently foraging on sugar secretions at wounds caused by leaf herbivores. Since flea beetles are easily scared off by third trophic level insects, we suggest that sugar secretions may serve as an indirect defence strategy against herbivores.

Description of a new plant model

Solanum dulcamara (Linnaeus) (figure 1) is commonly known as bittersweet or woody nightshade. It belongs to the Solanaceae and is a close relative to potato, tomato, petunia and many other cultivated plant species (Van der Meijden 2005). *Solanum dulcamara* is a very widespread species: in The Netherlands it can be found in urban areas as well as in undisturbed natural sites. Its habitat ranges from relatively dry sandy areas to regularly inundated floodplains, illustrating its great capability to deal with various water conditions. This plant is native to greater parts of Eurasia and Northern Africa, but also occurs as an invasive species in Northern America, Australia and New Zealand (Weeda *et al.* 1988, Howell 2008). The species is an indicator of nutrient-rich soils and is frequently found at sites disturbed by human activities. Depending on the water and light conditions of the habitat, it grows either as a bush or a winding climber. Its strong nature and wide distribution were already noticed by the famous Dutch botanist Jac P. Thijsse who described different growth strategies and phenotypes in his Flora (Thijsse 1946). In Northern Europe *S. dulcamara*'s growing season ranges from early March until October, when it will drop its leaves and most of the branches will die off. Next spring the remaining woody stems will form new shoots. Bumblebees (*Bombus* spp.) are mostly responsible for pollination. Their buzzing behaviour is essential for releasing the pollen from the anther cone. The taxonomic relatedness of *S. dulcamara* to important crops and cultivars and its strong nature under various conditions, makes it a valuable plant model. Crop breeders may benefit by knowing the mechanisms that allow this plant to cope with herbivores, pathogens and dramatic changes in its abiotic environment.

Taxonomic sources

Unless mentioned otherwise, identifications of insects and basic characteristics were initially retrieved from the comprehensive series of 'Die Käfer Mitteleuropas' (Freude *et al.* 1964-1998), the handbook of Dutch biodiversity (Noordijk *et al.* 2010) and a descriptive study from Walter Steinhausen about European flea beetles (Steinhausen 2005). Most observations were done at the Experimental Botanical Garden of the Radboud University Nijmegen, where censuses were executed throughout the growth season of *S. dulcamara* in 2010 and 2011. Additional surveys were performed on natural field populations in Voorne's coastal region (province of Zuid-Holland), Brunssum and Pietersberg (both province of Limburg), the Frisian lakes (province of Friesland) and in the Ooijpolder near Nijmegen (province of Gelderland).

Solanum dulcamara's herbivore community

Coleoptera

Despite the fact that *S. dulcamara* contains various chemical defences, such as bitter alkaloids that can deter herbivores, the leaves of *S. dulcamara* in the field typically show many small holes, indicating a herbivore community that has adapted to *S. dulcamara*'s defences. The damage is mainly caused by the adults of Alticinid flea beetles (Coleoptera: Chrysomelidae). Flea beetles owe their name to their jumping capacity enabled by their greatly enlarged femora (hind legs). Disturbance easily scares them, causing them to jump off the leaf immediately. Even though it seems that flea beetles make random jumps, it has been found that at least some species are fairly good in controlling their jump resulting in a well coordinated feet-first landing (Brackenburry & Wang 1995). Unlike larger herbivores, such as Lepidopteran larvae that often consume entire leaves, flea beetles tend to make relatively small holes. This results in typical leaf damage that is often described as a 'shotgun pattern' (figure 2).

One of the most abundant flea beetle species on *S. dulcamara* is *Epitrix pubescens* (Koch) (figure 3). This species is also capable of feeding on the closely related *Solanum nigrum*, but it is much

1. Typical flower of *S. dulcamara* with anther cone. Photo: Onno W. Calf
1. De typische bloemvorm van *S. dulcamara* met kegelvormige meeldraden.

2. *Psylliodes affinis* and the typical shotgun wounding pattern. Photo: Onno W. Calf
2. *Psylliodes affinis* en de typische schade waarbij het lijkt alsof het blad getroffen is door een hagelschot.

3. Mating couple of *Epitrix pubescens* on *S. dulcamara* leaf. Photo: Onno W. Calf
3. Parend koppel van *Epitrix pubescens* op bitterzoet.

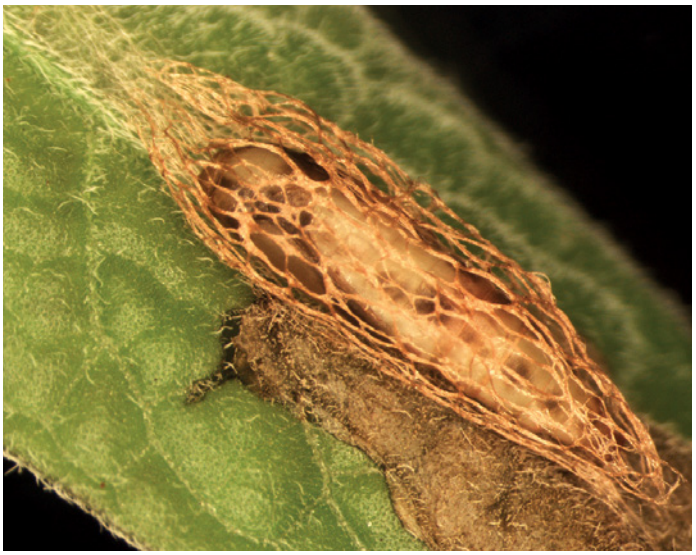
less abundant on this plant species. The adults overwinter in the soil and leaf litter layer on the base of the plant from where they emerge in spring, mate and oviposit. The larvae feed by chewing on the roots and the small (length: 1.5-2 mm) black adults emerge from the soil to feed on the foliage. They generally have two generations each year with peak densities in June and September, but their abundance is fairly high throughout the season. One plant can be colonized by dozens of beetles.

Another abundant flea beetle is *Psylliodes affinis* (Paykull) (figure 2). This beetle is less monophagous and also feeds on congeneric plant species such as potato *(S. tuberosum)*. This flea beetle is a little bigger (length: 2-2.6 mm) and less abundant than *E. pubescens*, but it has the same life history strategy for overwintering, reproduction and feeding. On calm days with stable weather it is fairly easy to find at least two or three of these beetles on a single plant. Like *E. pubescens*, *P. affinis* also has two generations, though the peaks in their abundance are slightly earlier. They have a pale yellow-golden appearance and in contrast to *E. pubescens* it is fairly easy to see the greatly enlarged femora protruding from underneath the body.

The third and last flea beetle species that can be found on *S. dulcamara* is less commonly observed. *Psylliodes dulcamarae* (Koch), with a length of 3-4 mm, is much bigger than *P. affinis* and about four times the size of *E. pubescens*. It is monophagous on *S. dulcamara* but is much less abundant than the previously mentioned flea beetles and clearly has two main generations in May and September. The adults seem to be almost absent from June to August, whereas *E. pubescens* and *P. affinis* are present throughout the entire season. The larvae of *P. dulcamarae* feed and develop inside the stem of *S. dulcamara*. Their presence can be noticed by small holes in the stem (figure 4). It is unclear whether the larvae or adults make these holes, but most likely

4. Hole in *S. dulcamara* stem caused by *Psylliodes dulcamarae* larva. Photo: Onno W. Calf
4. Een gaatje in de stengel van bitterzoet veroorzaakt door een larve van *Psylliodes dulcamarae*.

5. Larva of *Leptinotarsa decemlineata*. This species is an important pest on potato, but has also found its host in *S. dulcamara*. Photo: Onno W. Calf
5. Een larve van *Leptinotarsa decemlineata*. Deze soort is een bekende plaag op aardappel, maar heeft ook bitterzoet als waardplant.



6. Pupa of *Acrolepia autumnitella* in its 'golden' cage. Photo: E.S. Pierson, General instruments RU
6. De pop van *Acrolepia autumnitella* in zijn 'gouden' kooi.

7. The swollen flower bulb receptacle (gall) indicates infestation by *Contarinia solani* gall midges. Photo: Onno W. Calf
7. De verdikte bloembodem (gal) van de bloemknoppen geeft aan dat deze knoppen zijn geïnfesteerd door *Contarinia solani* galmuggen.

the adults lay their eggs in the stem and after hatching the larvae create the mine including the hole in the stem through which the larva disposes of its faeces. At the end of the larval development the larvae crawl out of the stem in order to pupate in the soil. The adults only feed on *S. dulcamara* foliage. *Psylliodes dulcamarae* is easily confused with beetles from the common genus *Altica* that feed on various herbs. These *Altica* beetles generally are much more abundant in the overall insect community and are frequently observed on *S. dulcamara*, even though they do not feed on it. They can be distinguished by the eye based on their colour and puncturing patterns on the elytra. *Altica* has a slightly green gloss and their elytra are sparsely punctured, whereas *P. dulcamarae* clearly has a blue shine with punctures arranged in longitudinal rows over the elytra (Freude *et al.* 1964-1998). Using a binocular the distinction is even clearer, as the antennae of *Altica* species have eleven segments and beetles belonging to the genus *Psylliodes* have ten.

In addition to these three flea beetle species, we frequently found a specialist beetle belonging to the family Nitidulidae. *Pria dulcamarae* (Scopoli) is a flower beetle, feeding on pollen and flower buds as both adult and larva. These small beetles (length: 1.6-1.8 mm) are excellent flyers, going from bud to bud to feed. Occasionally they visit other plant species to feed on but they only reproduce on *S. dulcamara*. Their abundance seems to rely much on the weather conditions. During the dry spring and summer of 2010 only few individuals were observed, but after the first heavy showers in August their numbers were exploding and hundreds of individuals were found flying around a single *S. dulcamara* bush. During the wetter summer of 2011 this species was continuously observed in large numbers.

Table 1. The less common herbivore insects on *S. dulcamara*.
Tabel 1. De minder algemene herbivore insecten op bitterzoet (*S. dulcamara*).

Family and species	Short description
Agromyzidae: *Liriomyza bryoniae* (Kaltenbach)	Polyphagous Diptera with leaf mining larvae
Aleyrodidae: *Trialeurodes vaporariorum* (Westwood) (figure 8)	White fly, common greenhouse pest
Aphididae: *Myzus persicae* (Sulzer)	Aphid, common greenhouse pest
Gelechiidae: *Phthorimaea operculella* (Zeller)	Lepidoptera with leaf mining larvae in Solanaceous plants
Noctuidae: *Ceramica pisi* (Linnaeus)	Uncommon Lepidoptera with polyphagous larvae
Noctuidae: *Lacanobia oleracea* (Linnaeus)	Lepidoptera, generalist
Sphingidae: *Acherontia atropos* (Linnaeus)	Uncommon Lepidoptera in The Netherlands with larvae feeding on Solanaceous plants.
Thripidae	Thrips, common greenhouse pest
Tortricidae: *Adoxophyes orana* (Fischer v. Röslerstamm)	Lepidoptera with polyphagous leaf-rolling larvae

The last specialized beetle we found feeding on *S. dulcamara* leaves are the adults and larvae of *Leptinotarsa decemlineata* (Say) (figure 5). This invasive specialist on *Solanum* species was first recorded in The Netherlands in 1937. It originates from the Rocky Mountains in the United States of America. After the introduction of potato (*S. tuberosum*) in its host range it rapidly became a pest in the USA after which is has spread to Western Europe during the First World War (Hare 1990). After its arrival on this side of the Atlantic Ocean it has caused serious damage, mainly to potato fields, forcing farmers to take drastic control measures. Despite the former obligation to control these beetles and the provision of free pesticides in the past, these measures have failed to prohibit the establishment of the beetles in The Netherlands. Nowadays, *L. decemlineata* very common in The Netherlands and since 1995 there is no legal obligation anymore to report or control this species (Ministerie van LNV 1995). In 2010 about ten adults of *L. decemlineata* were found in *S. dulcamara* patches at the Radboud University's Experimental Botanical garden in Nijmegen. These individuals were all caught and destroyed to prevent further spreading. Nevertheless, in 2011 we caught about 75 adults from the same patches and the number of larvae that was feeding on the plants exceeded 500. As there were no potato plants in the close proximity, it is safe to say that this beetle indeed reproduces successfully on *S. dulcamara* as was found earlier in the USA (Hare 1983).

Lepidoptera

Even though the most abundant specialist herbivores on *S. dulcamara* are beetles, we also found a specialist belonging to the order Lepidoptera. *Acrolepia autumnitella* (Curtis) is a small moth which is mining in the leaves of *S. dulcamara* as a larva. It feeds only on the leaf's mesophyll, which results in clear blotch mines. The larva disposes of its faeces outside the blotch mine and in the last stadia of feeding it usually needs to migrate to fresh leaves. When the larva is fully grown, it crawls out of the mine and pupates in a delicate silk net cage ('golden cage') that is usually attached to the lower part of the stem (figure 6). *Acrolepia autumnitella* has two generations per year and larvae can be found from June to September.

Another moth with leaf mining larvae on *S. dulcamara* in The Netherlands is *Scrobipalpa costella* (Humphreys & Westwood) from the family Gelechiidae. Similar to *A. autumnitella* this moth is monophagous on *S. dulcamara*. *Scrobipalpa costella* is restricted to the coastal region, found on plants growing in marshes in the dunes and along sea dikes (Jansen 1999). Usually the larva bores into the stem after leaving the mine and changes its residence a few times before pupation. Pupation takes place outside the mine in a loose silk cocoon. This species only has one generation a year and hibernates as larva. Adults have been collected from July till late September and larvae were found from mid September to May (Jansen 1999).

8. *Trialeurodes vaporariorum* feeds on *S. dulcamara* and is a persistent greenhouse pest. Photo: Onno W. Calf
8. *Trialeurodes vaporariorum* komt voor op bitterzoet en is een vervelende plaag op kasgewassen.

Other species

From July to the end of the season deformed buds of flowering *S. dulcamara* can be found. The flowers do not open and the receptacle is greatly enlarged. This phenomenon is the result of infestation by the gall midge *Contarinia solani* (Rübsaamen) (Diptera, Cecidomyiidae) (figure 7). Infestation causes gall formation and dropping of buds that may house dozens of larvae. The larvae crawl out of the gall to pupate in the soil and most likely stay there to overwinter. The taxonomic classification of this species and its host plant range are still unclear, as was already mentioned by Jensen (1946).

In addition to the abovementioned main specialist herbivores, we also found several generalists and specialists that were less common. Insects from this group are listed in table 1.

Third trophic level insects

Both in the field and the experimental garden we frequently recorded the presence of ants (Hymenoptera: Formicidae) and lady beetles (Coleoptera: Coccinelidae) on *S. dulcamara* plants (see table 2 and figure 9). Remarkably, we observed that both ants and lady beetles were foraging at the edges of the wounds caused by flea beetle feeding. Our observations were confirmed by our colleagues at the Free University of Berlin, Germany.

Table 2. Ant and ladybug species found on *S. dulcamara* during our two year examinations. Note that this not a complete list of all third trophic level insects that can be found on this plant.
Tabel 2. Aangetroffen mieren en lieveheersbeestjes op bitterzoet gedurende twee seizoenen. Dit is echter niet een volledige lijst van alle insecten van het derde trofische niveau die op deze plant kunnen worden aangetroffen.

Scientific name
Formicidae:
Formica fusca (Linnaeus)
Lasius brunneus (Latreille)
Lasius niger (Linnaeus)
Myrmica rubra (Linnaeus)
Coccinellidae:
Anisosticta novemdecimpunctata (Linnaeus)
Calvia decemguttata (Linnaeus)
Coccinella quinquepunctata (Linnaeus)
Coccinella septempunctata (Linnaeus)
Exochomus quadripustulatus (Linnaeus)
Harmonia axiridis (Pallas)
Hippodamia tredecimpunctata (Linnaeus)
Propylea quatuordecimpunctata (Linnaeus)

9. *Formica fusca* patrolling on *S. dulcamara*. Photo: Onno W. Calf
9. *Formica fusca* op patrouille op bitterzoet.

10. Sugar secretion at a leaf wound caused by a herbivore. We are investigating whether third trophic level insects are attracted by these sugar secretions to scare off herbivores. Photo: Onno W. Calf
10. Suikeruitscheiding bij bladschade. We onderzoeken of deze suikeruitscheiding insecten van het derde trofische niveau aantrekt om zo schadelijke herbivoren af te schrikken.

Usually, the occurrence of these third trophic level insects is closely correlated with the presence of aphids. Aphids either serve as prey or are tended by ants that receive honeydew as a reward. As aphids are uncommonly seen on *S. dulcamara* in the field, the frequent occurrence of ants and ladybeetles raises the question what attracts them to this plant.

The active secretion of sugars by plants via extrafloral nectaries in order to facilitate ants that deter herbivores is a well known defence strategy of plants (Wäckers 2002). *Solanum dulcamara*, however, is not known to possess extrafloral nectaries. Instead, we observed that droplets of sugar are secreted at the edges of wounds caused by herbivores (figure 10). Analyses indicate that these sugars originate from the phloem. Currently, we are studying whether *S. dulcamara* uses these secretions to recruit third trophic level insects such as ants and lady beetles. These insects may serve as bodyguards providing protection against the damaging herbivores.

Conclusion

In conclusion, *S. dulcamara* hosts an intriguingly diverse insect community that is 'caught' between the bitter (chemical defence) and sweet (sugar) defences of this plant species.

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Samenvatting

Bitterzoete beestjes: de Nederlandse insectenfauna op bitterzoet (*Solanum dulcamara*)
Bitterzoet (*Solanum dulcamara*) is in Nederland een algemene inheemse plantensoort die kan worden aangetroffen op zowel heel droge als op natte standplaatsen. Bij nadere bestudering bleek zich een opvallende gemeenschap van insecten te handhaven op deze plant. Dit artikel beschrijft de insecten die zijn aangetroffen tijdens onze veldstudies. Het meest talrijk zijn vijf soorten kevers, waaronder twee aardvlooien – *Epitrix pubescens* en *Psylliodes affinis* – die zich als larve voeden met de wortels van bitterzoet en als volwassen insect met de bladeren. Een derde aardvlo, *Psylliodes dulcamarae*, voedt zich als volwassen insect eveneens met de bladeren, maar mineert als larve in de stengels van deze plant. *Pria dulcamarae* is een glanskever die zich alleen richt op de bloemen en het stuifmeel. De laatste keversoort is de uit Noord-Amerika afkomstige Coloradokever (*Leptinotarsa decemlineata*), die zich niet alleen op aardappel, maar ook op bitterzoet goed lijkt te kunnen handhaven. Twee mineermotten, *Acrolepia autumnitella* en *Scrobipalpa costella*, die als larve mineren in de bladeren van bitterzoet kunnen eveneens worden aangetroffen, de tweede soort echter opvallend genoeg voornamelijk langs de Nederlandse kust. De laatste specialist is een galmug, *Contarinia solani*, die galvorming in de bloembodem veroorzaakt en zich daarmee voedt. Deze bloemen gaan daarmee verloren. Naast de echte specialisten is er ook een levendige populatie van mieren en lieveheersbeestjes aanwezig die patrouilleert over de plant. Doorgaans vindt men deze insecten samen met bladluizen, welke in het veld echter nauwelijks worden aangetroffen op bitterzoet. Op de plaatsen waar bladeren aangevreten zijn door insecten zijn uitscheidingen van suikers waargenomen die wellicht insecten van het derde trofische niveau aantrekken, zoals mieren en lieveheersbeestjes. Momenteel onderzoeken wij of dit zo is, want in dat geval heeft bitterzoet een nog niet eerder beschreven afweersysteem ontwikkeld om natuurlijke vijanden van herbivoren aan te trekken door middel van suikeruitscheiding bij verwonding.

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