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Short-term seasonal habitat facilitation mediated by an insect herbivore

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Abstract

In nature some organisms may facilitate others by creating shelter or other niches that they use for variable periods. We describe a natural multitrophic-species complex in the Netherlands involving a plant, the common hogweed (*Heracleum sphondylium*) a specialist chewing herbivore, the parsnip webworm (*Depressaria pastinacella*) and various arthropods associated with them. Larvae of *D. pastinacella* feed on *H. sphondylium* seeds and, after they have finished feeding, chew holes in the hollow stems where they pupate. In some areas of the country almost 50% of plants are attacked by webworms. The holes are used by other arthropods to gain access to the stems including herbivores, omnivores, predators and decomposers. The duration of plant occupancy varies between 3 and 4 months, until the plants die. Plants without moth-produced holes were always free of other arthropods, whereas plants with holes, in addition to pupae (and/or mummified-parasitized webworm larvae), often contained many woodlice, earwigs and/or spiders. Earwigs and woodlice perform important ecological functions as predators (in orchards) and decomposers respectively. Our results show that the simple biological activity of one herbivore species can have at least short-term effects on the local arthropod community.

Zusammenfassung

In der Natur können manche Organismen andere begünstigen, indem sie Refugien oder andere Nischen erschaffen, die sie für unterschiedliche Zeiträume nutzen. Wir beschreiben einen natürlichen multitrophischen Artenkomplex in den Niederlanden, der den Wiesen-Bärenklau (*Heracleum sphondylium*), die Pastinakmotte (*Depressaria pastinacella*) und verschiedene mit ihnen assoziierte Arthropoden umfasst. Die Larven der Pastinakmotte fressen an Bärenklausamen und beißen später Löcher in die hohlen Stengel, um sich darin zu verpuppen. Die Löcher werden von anderen Arthropoden genutzt, um Zugang ins

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Stengelinnere zu erhalten. Die Pflanze wird für etwa drei bis vier Monate besiedelt bis sie abstirbt. Pflanzen ohne Mottenlöcher wurden niemals von anderen Arthropoden besiedelt, während Stengel mit Löchern zusätzlich zu den Mottenpuppen bzw. parasitierten Larvenmumien häufig viele Asseln, Ohrwürmer und/oder Spinnen enthielten. Ohrwürmer und Asseln erfüllen wichtige ökologische Funktionen als Räuber in Obstplantagen bzw. als Zersetzer. Unsere Ergebnisse zeigen, dass die einfache biologische Aktivität einer Herbivorenart zumindest kurzfristige Auswirkungen auf die lokale Arthropodengemeinschaft haben kann.

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Introduction

Biotic interactions amongst species are known to play a primary role influencing the structure and function of ecological communities (Showalter 2000; Stachowicz 2001). These interactions may be mutualistic or antagonistic in nature and include important processes such as pollination, competition, herbivory, predation and parasitism (Schemske, Mittelbach, Cornell, Sobel, & Roy 2009). However, organisms can also directly or indirectly affect individuals of other species in space and time by altering structural aspects of the habitat that affect the behaviour, development and survival of the other organisms (Hastings et al. 2007; Gribben et al. 2009). When a species generates conditions that affect entire ecosystems at potentially large scales or which persist in time, the species driving these conditions is known as an ‘ecosystem engineer’ (Jones, Lawton, & Shachak 1994). For example, beavers (*Castor canadensis*) manufacture dams that create wetland habitats that are colonized by many other plants and animals (Wright, Jones, & Flecker 2002). Other mammals, such as armadillos, prairie dogs and marmots create refuges and alter nutrient cycles through the burrows they construct (Yoshihara, Ohkuro, Bayarbaatar, & Takeuchi 2009; Desbiez & Kluwyber 2013). Invertebrates with shorter life cycles nevertheless may also act as ecosystem engineers. For instance, ants and termites create mounds that facilitate nutrient cycling, enhance plant growth and thus attract various other types of herbivores (Jouquet, Dauber, Lagerlöf, Lavelle, & Lepage 2006; Sanders & van Veen 2011; Esmaili & Hemami 2013). Lill and Marquis (2003) reported that in spring caterpillars of *Pseudotelphusa* sp. tie leaves together with silk that act as shelters during feeding. These shelters are used by a diverse group of other insects later in the season after the caterpillars have abandoned them and pupated. The shelters presumably provide protection from natural enemies and heavy rainfall and reduce the risk of desiccation from exposure to direct sunlight (Greeney, Dyer, & Smilanich 2012).

Many other organisms may strongly influence others at much smaller spatial and/or temporal scales, rendering them as local or transient ‘facilitators’ rather than as more important ecosystem engineers. The exact type of facilitation depends on the biological activities of the facilitator and how

this positively affects other species in the vicinity. For example, woodpeckers excavate holes in trees that are later used as nesting sites or shelter by other vertebrates including cavity nesting birds and mammals (Aitken & Martin 2007). Abandoned burrows excavated by mammals such as woodchucks, pocket gophers and prairie dogs or reptiles such as tortoises are also used as overwintering sites, shelter or foraging routes by snakes, salamanders and small mammals (Vaughn 1961; Lips 1991). Many insects also create short-term refuges or nesting sites for other organisms. For instance, abandoned termite nests serve as nesting sites for a range of tropical birds (Brightsmith 2000). Thus far, only a few studies have shown that solitary-feeding insect herbivores can modify their food plants in ways that create small-scale habitats for a range of species across different trophic levels (e.g. Sigmon & Lill 2013). A pioneering study by Tischler (1973) found that hollow stems of European reeds and thistles are perforated by grazing deer in autumn which create winter refuges for hibernating insects, a form of facilitation he referred to as a “reaction chain”. Other studies have shown that insects can modify plant traits, such as growth or phenology, in ways that can either hinder or benefit other arthropods that share the plant with them (Crawford, Cruisinger, & Sanders 2007; Ohgushi 2008; Cornelissen, Cintra, & Santos 2016; Wetzel et al. 2016). However, these studies showed that ‘facilitators’ or ‘engineers’ may provide refuges other species, whereas studies showing that arthropods actually depend on the presence of a herbivore for refuges and/or shelter are scarce.

In this study we examine a multitrophic species complex involving an insect herbivore and several species of arthropods in three classes that benefit from it. Some of the species benefitting from the activity of the ‘facilitator’ are potentially important biological control agents or detritivores. The parsnip webworm, *Depressaria pastinacella* (Lepidoptera: Oecophoridae) lays its eggs on several closely related plants, including the common hogweed *Heracleum sphondylium* (Apiaceae). *D. pastinacella* adult moths become active in June and lay their eggs on the leaves of *H. sphondylium*. The eggs hatch and the neonate larvae move to the flowering umbels and developing fruit where they feed through all four instars in silken webs (Fig. 1A). Late final instar caterpillars emerge from the silken chambers, climb down the hollow

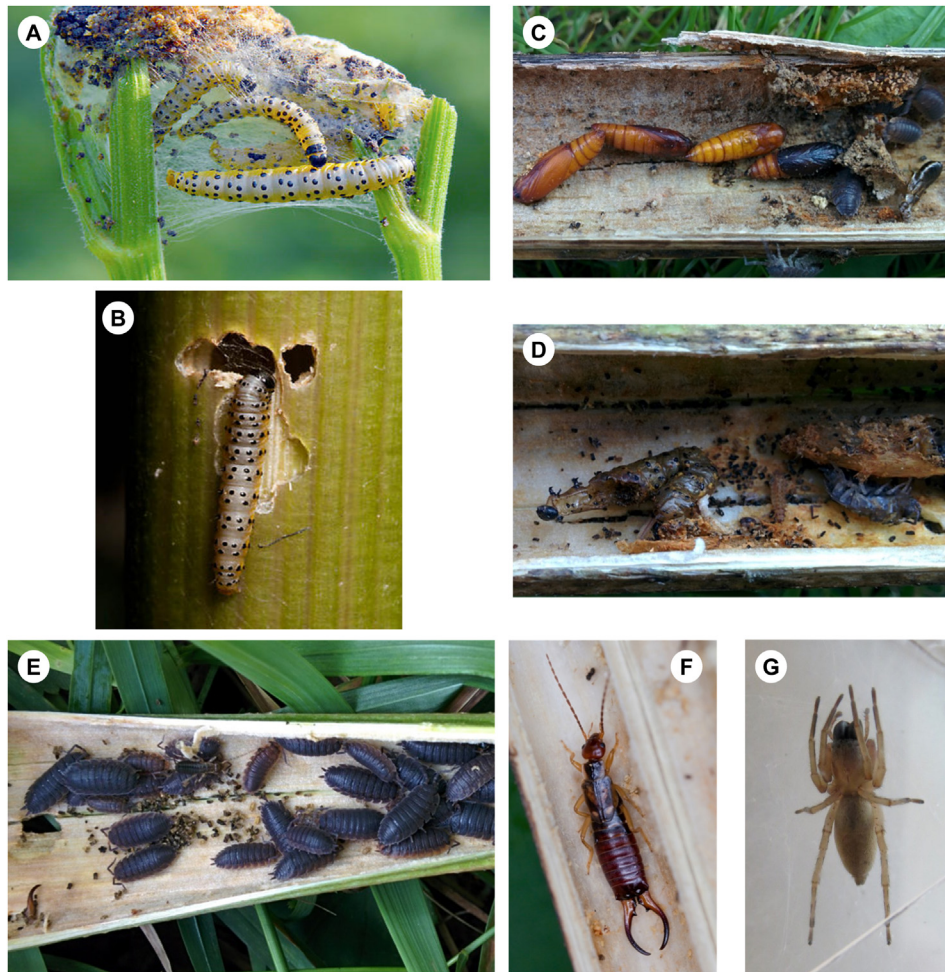


Fig. 1. (A) Feeding larvae of parsnip webworm *Depressaria pastinacella* and (B) a fully grown larva chewing into stem of food plant; (C) pupae of *D. pastinacella* in stem; (D) webworm mummy containing polyembryonic parasitoid *Copidosoma sosares* partially consumed by earwigs in stem (middle); (E) woodlice *Porcellio scaber*; (F) adult common earwig *Forficula auricularia*; (G) adult sac spider *Clubiona phragmitis*.

stems and chew a hole in them (Fig. 1B) through which they enter the stem and then pupate in a loosely constructed silken sac (Fig. 1C). The adult moths emerge approximately 1 week later through the entrance hole formed by the larvae, mate, and drop into surrounding leaf litter where they overwinter. The most important natural enemy of *D. pastinacella* is the egg-larval polyembryonic parasitoid *Copidosoma sosares* (Hymenoptera: Encyrtidae) which produces characteristic ‘mummies’ of the host caterpillar shortly before pupation (Fig. 1D). Here, we compared stems of *H. sphondylium* plants for the presence of other arthropods with or without holes excavated by *D. pastinacella* caterpillars at 6 different locations in The Netherlands. The main aim is to determine whether the presence of arthropods present in the stems depends upon holes in the stems chewed by *D. pastinacella* caterpillars. The different locations were selected on the basis of their distance from each other as well as their proximity to the rivers Rhein and Waal, which may influence the local community of arthropods. We hypothesize that access to the stems of hogweeds as temporary refuges and/or feeding

sites for other arthropods is dependent upon the presence or absence of *D. pastinacella*-excavated holes, and thus that the species acts as a facilitator at the scale of individual hogweed plants.

Methods and materials

Locations

Plants were sampled at six locations in five provinces in The Netherlands (Fig. 2) between August and October, 2014. The following locations were: Haaksbergen, Overijssel: 52°8′21.08″N, 6°42′56.92″E; Veenhuizen, Drenthe: 53°2′49.80″N, 6°23′30.80″E; Drimmelen, North Brabant: 51°42′11.98″N, 4°47′42.81″E; Heteren, Gelderland: 51°56′41.06″N, 5°45′21.06″E; Badhoevedorp, South Holland: 52°19′56.83″N, 4°48′11.88″E; Ooij, Gelderland: 51°51′46.61″N, 5°56′1.29″E (Fig. 2). The Haaksbergen and Veenhuizen locations are rural areas with patches of mixed



Fig. 2. Map of the Netherlands with the six main sites where *Heraclium sphondylium* plants were sampled in the mid-late summer of 2014. 1 = Veenhuizen; 2 = Haaksbergen; 3 = Ooij; 4 = Heteren; 5 = Badhoevedorp; 6 = Drimmelen.

forests and are situated in the north-eastern part of the country, Badhoevedorp is situated in a polder in the western part of the Netherlands which is primarily used for agriculture, whereas Heteren, Ooij, and Drimmelen are all located between the large Rhine and the Waal rivers which run through the middle of the Netherlands. This area is like the polder landscape: very open with agricultural fields and few trees.

Sampling of plants for arthropods

Senescing plants were consecutively sampled along linear transects (for roadside collections) or in groups (for field-located plants). A fully grown plant was determined as one in which the plant was in senescence, all seeds were dried or had already fallen from the plant and the outer stem was no longer moist and green in colour but dry and brown (post-reproductive stage). Approximately 50 plants in each location were sampled using a paring knife to cut open the stems along their entire length. Each hollow stem contains several chambers that are separated by a membrane, and all of these were opened on the sampled plants. When a hole or holes were located on the plant stem, this was recorded. Once a stem was cut, it was carefully teased open and arthropods found in them were identified and counted. Counts were made visually *in situ*.

Data processing and statistical analyses

Logistic regression (generalized linear model (GLM) with a binomial distribution and a logit-link function) was used to investigate whether sampling location affected presence or absence of holes in hogweed stems. When the location effect was significant, Tukey–Kramer multiple comparison tests were conducted to determine which location differed from other locations.

The proportion of arthropods in plant stems was also determined at the location level. For the most abundant taxa we also determined whether the absolute number of individuals found in stems with holes varied with the sampling location using a general linear ANOVA on log-transformed species counts.

We used multivariate statistics (SIMCA-P+ 12.0, Umetrics AB, Umeå, Sweden), to elucidate differences in the proportion of the most abundant taxa collected from stems of hogweed plants at the different sampling locations in one analysis. This projection method determines whether the locations can be separated based on quantitative differences in invertebrate counts by a Y-data matrix of dummy variables which assigns the locations to groups. The PLS-DA (Projection to Latent Structures Discriminant Analysis) extension in the SIMCA software program then approximates the point ‘swarm’ in X (matrix with invertebrate counts) and Y in PLS components in such a way that maximum co-variation between the components in X and Y is achieved. The results of the analysis are visualized in score plots, revealing the location structure according to model components, and loading plots revealing the contribution of the variables to these components as well as the relationships among the variables. Data were log-transformed, mean-centred and scaled to unit variance before they were subjected to the analysis. The loadings on the first and second component axes were analysed using ANOVA followed by Tukey–Kramer multiple comparison tests to reveal which locations differed from others.

Results

An overview of arthropods found in hogweed stems

The most abundant arthropods found in stems of *H. sphondylium* plants were *Porcellio scaber* (Fig. 1E), *Forficula auricularia* (Fig. 1F) and *Clubiona phragmitis* (Fig. 1G). The presence and abundance of these species in hogweed stems was subsequently analysed statistically. However, other arthropod species were occasionally found in very small numbers at various sites but they were not quantified. One to several brown centipedes *Lithobius forficatus*, for example, were found in stems at the Heteren location, as well as an unidentified species of Heteroptera which was found in high numbers (>50) in the stems of two plants. Very small

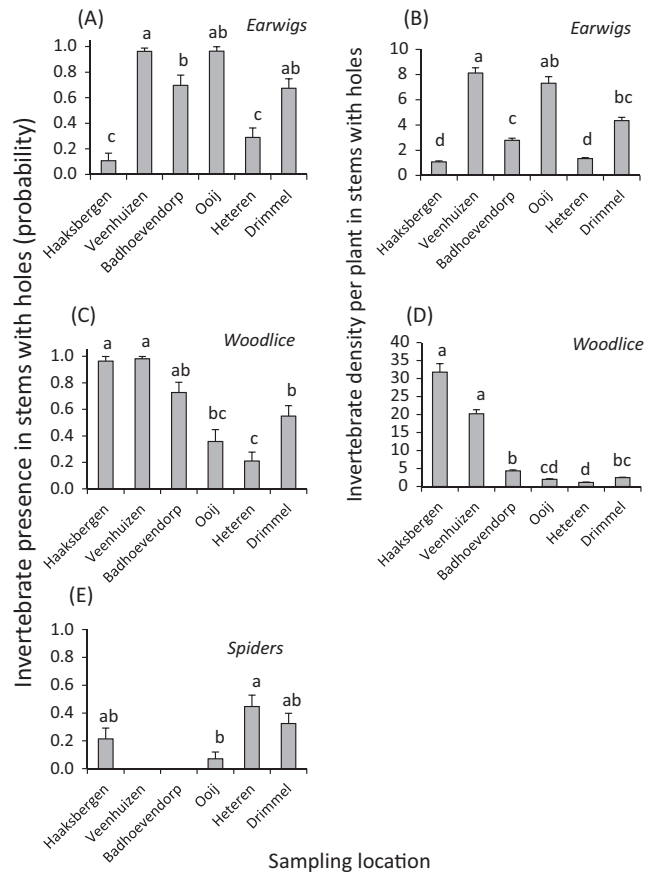


Fig. 3. Proportion (A, C, E) and the absolute numbers (B, D) of earwigs (A, B), woodlice (C, D) or spiders (E) in stems of *Heracleum sphondylium* plants with holes at six locations in The Netherlands (see Fig. 2). Letters above the bars depict differences between locations (Tukey–Kramer multiple comparison tests).

numbers of Collembola, Carabidae, and other spiders were also found in a few stems at the various sites.

Parsnip webworm cavities and stem colonization

The presence of arthropods in the stems (or not) depended on holes chewed by the final instar caterpillars. Every plant containing a hole ($n = 221$) contained at least one moth pupa and/or mummy; plants without holes ($n = 429$ from all locations combined) were never found to contain any invertebrate species. In addition to *D. pastinacella* and *C. sosares*, most plants (200 out of 221) contained spiders, earwigs and/or woodlice. At the Heteren location 71% of the stems contained at least one of the other colonizer species whereas at the other five locations this percentage varied between 88 and 100%.

The proportion of earwigs, woodlice or spiders in hogweed plants with holes in their stems was also location-dependent (GLM, earwigs $\chi^2_5 = 105.5$, $P < 0.001$, woodlice, $\chi^2_5 = 97.8$, $P < 0.001$; spiders, $\chi^2_5 = 56.65$, $P < 0.001$; Fig. 3A, C and E). In addition, the absolute densities of earwigs and woodlice

varied with sampling location (GLM, earwigs $\chi^2_5 = 34.8$, $P < 0.001$, woodlice, $\chi^2_5 = 77.9$, $P < 0.001$, Fig. 3B and D). Spiders were only present in 38 out of the 221 stems with holes and the majority of these stems (58%) had one spider, 24% had two spiders and there was one stem with 6 spiders. The proportion of earwigs in hogweed stems with holes was highly variable from one location to another. There were large differences in the proportion of earwigs in hogweed stems between Haaksbergen and Veenhuizen, and between Heteren and Drimmelen. At locations where the proportion of earwigs in stems with holes was high, there also tended to be more earwigs per stem than at locations where the proportion was low (Fig. 3A and B).

Woodlice were omnipresent in the non-riverine locations, Haaksbergen, Veenhuizen and Badhoevendorp (between 70 and 98% of the plants that had holes also contained woodlice), whereas the likelihood of woodlice presence in stems with holes was much lower at the riverine locations (between 20 and 60% of the plants with holes contained woodlice) (Fig. 3C). The number of earwigs per stem was significantly higher at the Haaksbergen and Veenhuizen location than at the other four locations (Fig. 3D). At the latter four locations woodlice densities were never higher than 15 per stem with the exception of one stem containing 25 woodlice at Badhoevendorp, whereas at Haaksbergen and Veenhuizen several stems contained more than 100 woodlice.

The likelihood of finding spiders was lower than the other two species, but more spiders were found at the three river locations, Drimmelen, Ooij and Heteren, than at the other locations with the exception of Haaksbergen (Fig. 3E). No spiders were found in hogweed stems in Veenhuizen and Badhoevendorp.

Multivariate analysis including the counts of invertebrates summarizes the patterns above and clearly separated the locations (Fig. 4A). The first component explaining 34.3% of the variation separated the locations into three groups Heteren (group1), Drimmelen, Ooij and Badhoevendorp (group 2) and Haaksbergen and Veenhuizen (group 3) ($F_{5,212} = 37.2$, $P < 0.001$). At the Heteren location hogweed stems had relatively larger numbers of spiders and lower numbers of the other two invertebrates. To a lesser extent this was also true for the locations in group 2. Haaksbergen and Veenhuizen on the other hand had higher numbers of woodlice and earwigs. The second component explaining an additional 33.3% of the variance separated Haaksbergen from the other locations and Ooij from Heteren ($F_{5,212} = 20.6$, $P < 0.001$; Fig. 4B). At Haaksbergen more woodlice and fewer earwigs were found, whereas at the other locations this pattern was reversed.

Discussion

Our results unambiguously show that *D. pastinacella* caterpillars are important small-scale habitat facilitators through the holes the larvae chew in the stems of *H. sphondylium* plants. These holes facilitate access to the hollow

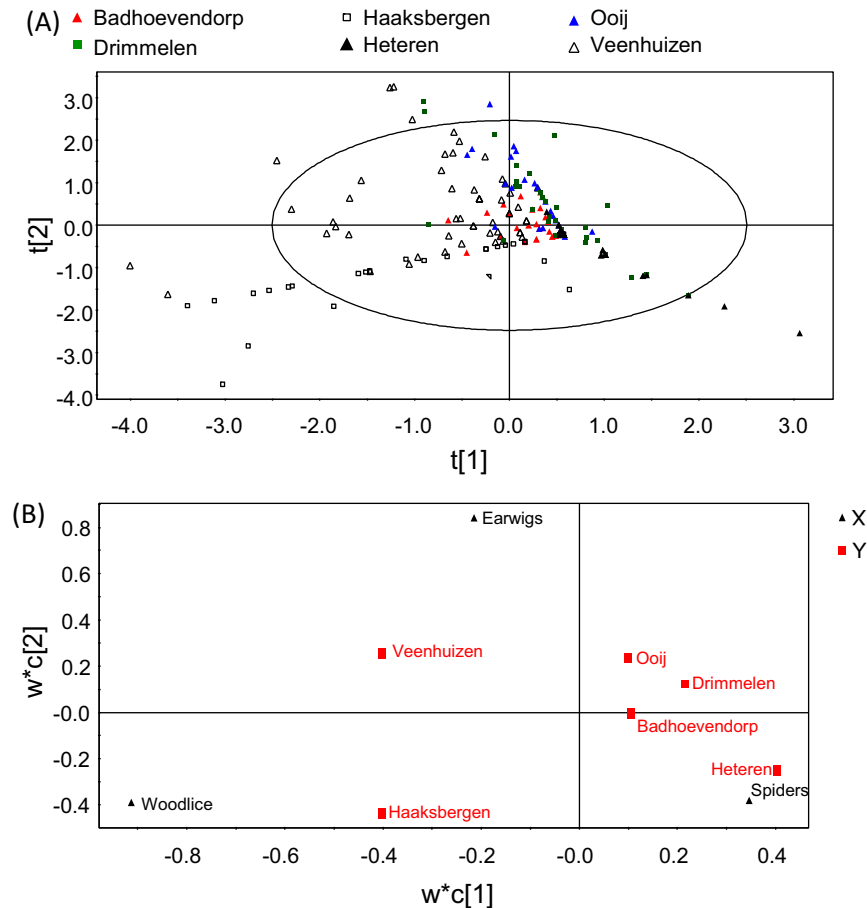


Fig. 4. Results of PLS-DA (Projection to Latent Structures Discriminant Analysis) of invertebrate counts in stems of *Heracleum sphondylium* plants with holes at six locations in the Netherlands (see Fig. 2). The score plot (A) depicts the location structure of each of the sampled plants (each symbol represents an individual plant) according to the first two significant model components and the loading plot (B) depicts the contribution of the invertebrate counts to these components as well as the relationships among these variables (fraction of explained variance; $R^2(X) = 0.68$, $R^2(Y) = 0.15$). The ellipse defines the Hotelling's T2 confidence region (95%). The red squares represent the centroids of the locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

stems by a range of other arthropods. The most frequently observed were the woodlouse *P. scaber*, an important detritivore that eats decaying plant tissue inside of the stems (Fig. 1), an omnivore, the common earwig *F. auricularia* (Dermaptera: Forficulidae, Fig. 1), and a predator, the sac spider *C. phragmitis* (Arachnida: Clubionidae, Fig. 1). The earwig is considered to be an important biological control agent of several aphid species in orchards (Moerkens, Leirs, Peusens, & Gobin 2009; Romeu-Dalmau, Piñol, & Agustí 2012; Monteiro et al. 2013) whereas woodlice are important macro-detritivores that enhance decomposition or organic matter (Souty-Grosset, Badenhausser, Reynolds, & Morel 2005; Vos, van Ruijven, Berg, Peeters, & Berendse 2011; Crowther et al. 2013).

Of the many hundreds of plants that were sampled that had not been attacked by *D. pastinacella*, not a single stem contained an entrance hole and thus the hollow compartments of these plants were always unoccupied. *H. sphondylium* has very potent chemical defences – furanocoumarins – that inhibit the colonization and attack of many herbivores

(Sheppard 1991; McGovern, Zangerl, Ode, & Berenbaum 2006). *D. pastinacella* is probably the most important insect herbivore of *H. sphondylium* and is the only one that perforates holes in the stem in order to seek a pupation site. Plants with holes in the stems very often contained one to several species of other arthropods across a broad trophic spectrum. The most abundant were the woodlouse, *P. scaber*, the earwig *F. auricularia* and the spider *C. phragmitis*. However, stems were also occasionally found to harbour other spiders, centipedes, millipedes, ground beetles, collembolids and bugs, revealing that the ability to ascend plant stems to access the holes was not an impediment to their use by generally ground-dwelling arthropods.

Our data also show that populations farther away from the rivers were dominated by woodlice, whereas populations closer to the rivers were more often colonized by sac spiders. This may simply be due to habitat preferences exhibited by the various taxa. For instance, the sac spider *C. phragmitis* is common throughout much of Europe in marshy habitats where it constructs silken retreats in the fronds of perennial

species such as the common reed, *Phragmites australis* where it stays during the day; at night it is an active predator. These habitats are frequent in the great river floodplain of The Netherlands. Most of the arthropods collected in the stems of hogweed plants also were of variable age. Thus, there were both juveniles and adults among the woodlice, earwigs and spiders. In several cases spider egg sacs were hatching inside the stems as well.

Earwigs, woodlice and sac spiders all contribute to different supporting ecological services. Earwigs, for instance, are important predators of pests, especially aphids, in orchards (Nicholas, Spooner-Hart, & Vickers 2005; Romeu-Dalmau et al. 2012; Lordan, Alegre, Gatiús, Sarasúa, & Alins 2015) and because of this sustained efforts have been made at enhancing their overwintering survival (Carroll & Hoyt 1984; Gobin, Marien, Davis, & Leirs 2006; Moerkens, Leirs, Peusens, Belien, & Gobin 2012). They also readily attack mummies of *C. sosares* when they are available and this may sustain the earwigs in the stems, making the parasitoids important as supplemental nutrition. Woodlice also play an important role as macro-detritivores by affecting leaf litter quality, often in synergism with the activities of microbes and earthworms (Zimmer, Kautz, & Topp 2005; Vos et al. 2011). Some sac spiders are important predators of pests in crops (Pfannenstiel & Yeorgan 2002; Kruse, Toft, & Sunderland 2008). Moreover, along with several other species of spiders, *C. phargmitis* has been shown to be an ecological indicator of heavy metal toxicity in wetland habitats in Belgium (Maelfait & Hendrickx 1997).

In summary this study has reported how the presence of *D. pastinacella* facilitates access to hollow stems of hogweed plants by a range of arthropods across a broad trophic spectrum. This study has focused on arthropods, but during the process of sampling plants it was found that whereas unperforated stem chambers were always 'dry', damaged stems also contained abundant evidence of fungi and mildew. The stem chambers were often very moist and filled with frass from the various species occupying them, which may in turn attract microbes and fungi, adding further complexity to the system. Moreover, given the importance of *F. auricularia* as a biological control agent of various aphids in orchards, the manipulation of *H. sphondylium* stems by artificially perforating holes in them may enhance the ability of this predator to survive the winter season. In the field, wild hogweed plants die, fall over and rapidly decompose in late autumn and early winter, making the stem only a transient refuge for arthropods. However, it is possible that stems can be collected, artificially perforated and placed close to orchards where they could act as important overwintering sites for earwigs and spiders.

Further studies are planned in which arthropod abundance is examined in different species of closely related plants (*H. mantegazzianum*, *Pastinaca sativa*) that also host *D. pastinacella* and *C. sosares* as well as in plants where holes are manipulated e.g. artificially drilled, mimicking *D. pastinacella*. Furthermore, plants attacked by *D. pastinacella* are also

known to be invasive pests in various parts of the world e.g. New Zealand, North America, and therefore it would be interesting to compare the complex of species that exploit holes made by the larvae in both the native and invasive ranges.

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