

Artificially perforated holes in stems of small hogweed mimic ecosystem engineering by a moth

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Abstract

Ecosystem engineers are species that manipulate the physical state of ecosystems and thereby affect the behaviour and ecology of other species. Mature larvae of the parsnip webworm, *Depressaria radiella* Goeze, chew holes in the hollow stems of *Heracleum sphondylium* L. into which they pupate. The stems are separated into several compartments that are separated by filamentous membranes. Holes excavated by webworm larvae attract several beneficial species of arthropods that use them for shelter in autumn, including the common earwig (*Forficula auricularia* L.) and the common rough woodlouse (*Porcellio scaber* Latreille). If artificially made holes mimic the engineering effect of *D. radiella*, they could be made to attract (local) communities of beneficial arthropods and perhaps facilitate overwintering habitat. We conducted a field experiment to determine whether artificial holes perforated into stem compartments of *H. sphondylium* mimic the natural situation with *D. radiella*. At five sites near the city of Leiden, the Netherlands, *H. sphondylium* plants were exposed to different treatments: a single hole perforated in the first, second or third stem compartment, or in all three compartments. After 3 weeks, arthropod numbers were counted inside and around hogweed stems. The arthropod community in the stems differed from that surrounding the stems; the latter consisted mainly of woodlice and wolf spiders, whereas in the stems, in addition to woodlice, many earwigs were found and no wolf spiders. Both artificial and webworm-excavated holes that were present at one site were used by woodlice and earwigs. The position of the holes along the stem did not affect the number of arthropods found in that segment, although the arthropods exhibited a tendency to move up the stems. The results show that artificial holes mimic webworm-excavated holes in that both attract the same species of beneficial arthropods.

KEYWORDS

Depressaria radiella, earwig, *Heracleum sphondylium*, pest control, spider, woodlouse

1 | INTRODUCTION

Ecosystem engineers are species that change the physical state of the environment over different scales and thus create or modify habitats in ways that directly or indirectly affect resource availability to other organisms (Jones et al., 1994). These changes can have rippling effects throughout ecological communities that affect the behaviour and ecology of many other species found in them (Daily et al., 1993). There are many examples of ecosystem engineers in the empirical literature, ranging from large mammals (e.g. beavers and elephants), birds (e.g. woodpeckers) to invertebrates (e.g. ants, termites and other insects) (Dangerfield et al., 1998; De Almeida et al., 2020; Wiebe, 2017; Wright et al., 2002). For example, African elephants shape and maintain savannahs by damaging and knocking down trees (Haynes, 2012). This creates optimal foraging habitat for other species such as antelopes and gazelles, which are unable to live there in the absence of elephants. Additionally, associated changes in biota, due to the impacts of elephants, can affect geomorphological processes (e.g. erosion; Haynes, 2012). There are many ecological processes that ecosystem engineers influence in nature, for instance by creating structural habitats which act as refuges when utilized by other species that reduce their exposure to abiotic stresses (i.e. heat) or the risk of predation (Wright & Gribben, 2017).

There are several ways in which ecosystem engineers create structural habitats for other species. Many species of mammals live in burrows excavated into the soil which benefit other species by providing them with shelter (Pike & Mitchell, 2013). For instance, the European rabbit is known to create large underground tunnel systems (warrens) that are utilized by a range of other vertebrate species, such as lizards, after being abandoned by the rabbits (Gálvez Bravo et al., 2008). There are also many insects that create temporary shelters with facilitating effects on other insects. For instance, the caterpillars of *Pseudotelphusa* sp. tie oak leaves into loops, thereby creating shelters in which they rest between feeding bouts (Lill & Marquis, 2003; Lill & Marquis, 2004; Wang et al., 2012). Vacated shelters or artificially created shelters are utilized by other species of leaf-chewing insects, and their removal significantly reduces the density and species richness of these herbivores (Lill & Marquis, 2003). Cornelissen et al. (2016) reviewed the effects of these shelters and found that they had facilitative effects on many species in the arthropod community. Larvae of the great Capricorn (*Cerambyx cerdo* L.), an endangered longhorn beetle, create galleries in dead oak trees that are important refuges for a wide diversity of saproxylic insects (Buse et al., 2008). In the Brazilian Cerrado savanna, wood-boring beetles create cavities with varying entrance-hole diameters thereby structuring ant communities occupying these cavities (Priest et al., 2021) and plants with galls formed by gall midges also attract higher numbers of insect herbivores than plants lacking them (Crawford et al., 2007; Uesugi et al., 2016).

Another shelter-building insect is the parsnip webworm, *Depressaria radiella* Goeze (Lepidoptera: Depressariidae), a specialist-feeding herbivore of the small hogweed, *Heracleum sphondylium* L. (Apiaceae) and related species, that is native to Eurasia

but is now introduced across much of the world (Berenbaum & Zangerl, 2006; Harvey et al., 2016; Harvey et al., 2019; Harvey et al., 2020; Ode et al., 2004). In the Netherlands, adult moths of *D. radiella* begin laying their eggs on leaves of *H. sphondylium* in early June. Newly hatched larvae move to the flowering umbels and developing fruits of *H. sphondylium* where they spin webs and feed exclusively on the fruits (Berenbaum & Zangerl, 2006). In early August, mature caterpillars abandon their webs and move down the stem, which is hollow and partitioned into several segments, each of which separated by a membrane. The larvae chew holes in one of the stem segments, enter them and pupate under a loose fold of silk. Several weeks later the adult moths emerge from the stems by exiting through the holes and then overwinter in the surrounding vegetation. In addition to providing a place to pupate to the caterpillars, these holes are also important habitat structures for secondary users such as other arthropods (Harvey et al., 2016). For example, woodlice, earwigs and sac spiders are often found in hogweed stems, but only in plants with holes chewed in the stem by *D. radiella* (Harvey et al., 2016). *Depressaria radiella* is therefore an ecosystem engineer that facilitates a multitrophic-species complex inside of hogweed stems. These transient seasonal habitats may enhance the survival of certain insects in autumn and perhaps even allow them to successfully overwinter, provided the plants remain intact (Harvey et al., 2016).

Stem habitats, created via holes chewed by mature *D. radiella* caterpillars, may have indirect effects on ecosystem functioning by facilitating various populations of arthropod decomposers and predators. For example, woodlice play an important role in decomposition and nitrogen release by moving litter deeper into the soil and dividing up litter to increase the surface area available for decomposition (Collison et al., 2013; Souty-Grosset et al., 2005). The cuticles of woodlice are rich in calcium, and their abundance in spring can benefit egg production and reproductive success in pied flycatchers (Bureš & Weidinger, 2003). Furthermore, earwigs are important omnivores that function as biological control agents in agroecosystems, by decreasing the abundance of woolly apple aphids in apple orchards while not damaging apples (Orpet et al., 2019). Additionally, some clubionid spiders are also important predators of pests in apple and citrus orchards (Kaspi, 2000).

Although holes created in hogweed stems by *D. radiella* enhances the local abundance of earwigs and woodlice (Harvey et al., 2016), it is not known if holes artificially created in the stems of this plant will have the same effect on arthropods. Other studies have reported that artificially created leaf shelters were shown to be colonized by arthropods (Cornelissen et al., 2016; Lill & Marquis, 2003; Romero et al., 2022; Vieira & Romero, 2013). In this study, we conducted a local experiment to determine whether artificial holes perforated into stem compartments of *H. sphondylium* by a steel perforator (used to make holes in leather) mimic the effects of holes created by *D. radiella* larvae. At five sites near the city of Leiden, the Netherlands, *H. sphondylium* plants were exposed to several treatments consisting of a single hole per stem in different stem compartments, or a three holes per stem, one in each compartment. Arthropod's colonization may be affected by the position of the holes along the stem due

to height differences. Arthropod numbers were counted inside the stem several weeks later. Moreover, arthropods were also counted in the stems of plants at one of the experimental sites where stems were naturally perforated by webworm larvae.

The main aims of the study are (1) to identify and determine the abundance of arthropods that use artificially created holes in stems of *H. sphondylium*, (2) to compare whether the placement of the hole (or holes) along the stems affects the diversity and abundance of arthropods that use them to enter the plant stem and (3) to compare these results with perforated stems naturally created by *D. radiella* larvae. Thus, we aim to determine whether artificially created holes in substrates mimic holes excavated by ecosystem engineers like *D. radiella* in hogweed stems in attracting the same species of arthropods.

2 | MATERIALS AND METHODS

2.1 | Study area

Five sites with *H. sphondylium* plants were selected near the Vliet canal in the South-Holland province in the Netherlands (Figure 1). The sites were in close proximity of each other with a minimum distance of 0.5 and a maximum of 4 km. Site 1 (52°14'94.57"N, 4°46'45.97"E) and 3 (52°14'63.06"N, 4°50'51.67"E) were located in the middle of an urban environment where *H. sphondylium* was growing close to the water and a bicycle path. Site 2 (52°13'42.22"N, 4°47'07.89"E) was located in a similar but less urbanized environment. Site 4 (52°14'18.04"N, 4°50'44.14"E) was located near the edge of polder park Cronesteyn, a 90-acre park within the municipal of Leiden. Different from the other sites, site 5 (52°12'23.67"N, 4°45'78.13"E) was located in close proximity of lake Vlietland, along a horse-riding path. Traces of the parsnip webworm *D. radiella*, such as silk webbing in the umbels and holes in the stem, were only found at site 3. *Heracleum sphondylium* were growing in (small) green

patches along walking/bicycle paths (Figure 1). At each sampling site, there were at least 100 plant individuals. The largest individuals at each site were chosen for sampling as the stems of these plants were firmer and remained upright after being treated. Smaller plants are also not regularly perforated by the webworm (personal observation).

2.2 | Sampling

Stems of *H. sphondylium* are hollow and partitioned; each stem segment is 20 to 40cm long and is separated by a filamentous membrane that prevents arthropods from moving between segments. Plants with *D. radiella* feeding damage can be infested by multiple caterpillars (Figure 2b,c), occasionally more than 20. Therefore, the number of holes per plant and compartment, and the number of larvae entering them, can vary among infested plants. However, entrance holes may be used by other webworm larvae as the number of holes does not necessarily correlate with the number of webworms in the stems. How this affects other arthropods is unknown. Hogweed plants were inspected for the presence of *D. radiella* to prevent natural and artificially created holes occurring in the same plant individual. The presence of *D. radiella* can be recognized by the dense silken webbing surrounding umbels that the caterpillars used as feeding chambers. Seeding umbels and stems were inspected, and when no traces of *D. radiella* were found, it was assumed that the stems were 'clean'. To closely mimic infestation with *D. radiella*, artificial holes were made using a hole punch for leather fabric. The holes were approximately similar in size ($\varnothing = 7$ mm) compared with those made by *D. radiella* (Figure 2a). As there is no movement possible between the segments of the stem, the selected plants were exposed to four different treatments to investigate the effect of the position of the holes along the stem. The four treatments were: (1) one hole in the bottom segment of the plant; (2) one hole in the second segment of the plant (3) one hole in the top segment of the plant; (4) one



FIGURE 1 Five hogweed (*Heracleum sphondylium*) sampling sites near the city of Leiden, in the Netherlands. (a) Site 1; (b) site 2; (c) site 5; (d) site 3 and (e) site 4



FIGURE 2 Indications of arthropod presence in hogweed stems (*Heracleum sphondylium*) that have been perforated naturally by *Depressaria radiella* or artificially. (a) Artificial hole; (b) naturally, heavily infested stem; (c) larvae of *D. radiella*; (d) stem without hole (empty)

hole in each of the three segments of the plant. Each treatment was replicated ten times resulting in 40 treated plants at each site and 200 treated plants in total.

Artificial holes were made in the second week of August 2021, which is when most mature caterpillars of *D. radiella* chew holes in the stem of *H. sphondylium* in which they pupate. The plants with artificial holes were labelled and left for approximately 3 weeks. To sample the plants for arthropod presence, the stems were excised at ground level using a paring knife and were carefully opened by slicing laterally along the stem using the knife. All arthropods inside the stem were collected in a glass bowl that was placed under the stem and immediately counted and identified in the field. In a previous study, the common rough woodlouse, *Porcellio scaber* Latreille (Isopoda: Porcellionidae), the European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae) and the reed sac spider, *Clubiona phragmitis* Koch (Araneae: Clubionidae) were the most common arthropods found inside stems of hogweed plants with holes chewed by *D. radiella* (Harvey et al., 2016). Therefore, we expected that these arthropods would also be most common in stems of plants with artificially perforated holes. All other species (including non-arthropods, such as slugs) that were recovered from hogweed stems were classified under 'other species'. Thus, collected organisms were assigned to one of four categories. Additionally, at site 3, 10 plants with holes perforated by *D. radiella* were sampled for arthropods and other invertebrates. Finally, to show that plants without holes are 'clean' and contain no invertebrates, 10 plants without any holes (control) were cut open as described above. After counting, the arthropods were released into the field.

We also wanted to compare the composition of arthropods on the ground surrounding the base of the stems with that of arthropods within perforated stems. To be able to do this, ground ($\varnothing = \pm 20$ cm) around the base of the stems of 10 randomly chosen plants (without holes) at each site was vacuumed using a handheld vacuum cleaner with an aperture of 5 cm. The vacuumed arthropods

were also placed into a glass bowl, identified and counted in the field and released afterwards.

2.3 | Data analysis

All analyses were performed in R (R Core Team, 2021). We first investigated whether the abundance of arthropods in artificially perforated stems differed depending on the location of the artificial hole along the stem. We used the accumulative arthropod abundance per stem and not abundances for each of the four arthropod categories as these data contained many zeros. Accumulative abundances were analysed using a general linear mixed model with a negative binomial distribution for errors and a log link function using `glmer.nb` function of the `lme4` package. Location of the hole along the stem (three levels) was entered as a fixed factor and site as a random factor. We further tested whether the number of arthropods per hole is independent of the number of holes per plant. The presence of other holes in the same plant, as well as their distance to the ground, could influence the abundance of arthropods. To do this, we calculated the mean abundances for each of the three single-hole treatments and totalled them and compared this value with the mean abundance of arthropods in stems of plants with three holes using a one-sample *t*-test.

In order to detect differences in arthropod community composition, we used non-metric multidimensional scaling (NMDS), a multivariate ordination method maximizing rank-order correlations between distance measures and distance in the ordination space. We used NMDS to compare the composition of the community in stems with artificial holes and the community on the ground surrounding the stems based on the vacuuming collections. For the within-stem community, we used the data collected for stems with three holes as stems of individual plants with *D. radiella* damage often have more than one hole. We also included site (5 levels) and the interaction with community type (2 levels)

as fixed factors in the statistical model. The distance matrix was based on pairwise Bray–Curtis dissimilarities between samples. We used the same four species categories as described before. We first determined whether the variation among the group centroids (stem and ground arthropod communities) were similar using the *betadisper* function (*vegan* package). We used the *metaMDS* and the *adonis2* function of the *vegan* package in R to perform NMDS and PERMANOVA tests for group differences using distance matrices. The number of permutations was set at 1000. To determine which species category characterized community composition within and around stems we used the *multipatt* function of the *idivspecies* package. Finally, we determined whether arthropod communities found in hogweed stems differed between artificially and naturally perforated stems. We did this for data obtained from site 3, the only site where plants were also naturally perforated by *D. radiella*. We determined whether the total abundance of species differed in stems with natural holes and in stems with 3 artificial holes in consecutive stem segments as described above and also compared the communities in naturally and artificially perforated stems using NMDS, followed by a PERMANOVA test.

3 | RESULTS

Though the abundance of arthropods in artificially perforated stems tended to increase with the position of the hole along the stem, this was not statistically significant ($\chi^2 = 3.98$, $df = 2$, $p = 0.14$). The average number of arthropods in stem segments nearest to the ground was 1.9 ± 0.3 (mean $\pm$ SE), in the second segment 2.4 ± 0.3 , and in the third (and highest segment) 2.7 ± 0.3 . The abundance of arthropods varied among sites, in particular at site 5, where the number of arthropods found in the stems was more than three times higher than at any other sites. The abundance of arthropods in plants with three holes did not differ from the combined mean arthropod abundance found in plants with single holes (one sample *t*-test [$\mu = 7$], $t_{45} = 0.468$, $p = 0.64$).

In total 688 arthropods or slugs were collected from artificially perforated stems. Woodlice, *P. scaber*, were, by far, the most abundant inside perforated stems (Figure 3) at all sites, except for site 4. Earwigs, *F. auricularia*, were locally abundant (site 3 and 5) (Figure 3). The highest numbers of woodlice and earwigs found inside a single perforated stem segment were 16 and 8, respectively. Spiders (*Clubiona* sp.) were less common (12 out of 688) but were found in stems at each of the five sites. Often, hatching egg sacs were found with the spiders. Species in the category 'others' were mostly slugs, and a few coleoptera and chilopoda species (not further identified). The number of slugs found in perforated stems was highly variable and was highest at site 4. Overall, site 5 was by far the most productive, with approximately three times as many organisms collected from stems than at the other four sites. In samples vacuumed at the base of the plants, only a single earwig was collected at site 3. Woodlice were present in 37 out of the 50 ground samples. Although the number of spiders was higher in the ground samples, these were

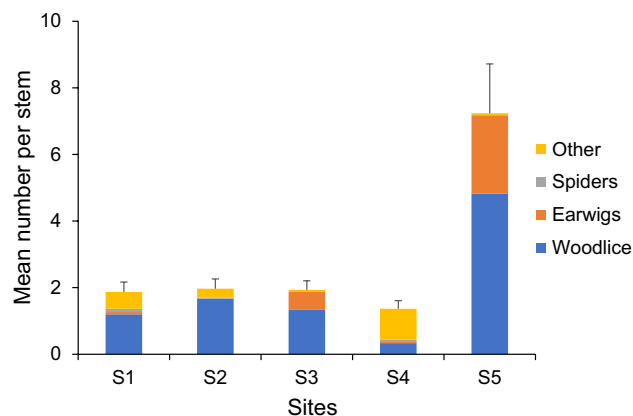


FIGURE 3 Mean number of invertebrates recovered per hogweed plant with one artificial hole at five different sites (S1–S5) near the city of Leiden, the Netherlands. Invertebrates recovered from the stems were categorized as woodlice, earwigs, spiders or others (mainly slugs). The number of plants per site was 30, except at site 5 where only 17 plants were found back 3 weeks after the holes were made. Error bars depict the standard error of the mean total number of all invertebrates

all wolf spiders (Lycosidae), whereas the only spider species found in the stem was *C. phragmitis*.

The multivariate version of the homogeneity of variance test showed that dispersion around the group centroids was variable, though not significantly ($F_{1,88} = 3.22$, $p = 0.07$). NMDS analysis of the arthropod species groups revealed differences among the sites ($F_{4,80} = 4.46$, $p = 0.001$, $R^2 = 0.13$), and between communities within and around the stem ($F_{1,80} = 24.4$, $p = 0.001$, $R^2 = 0.17$, Figure 4). However, the interaction term between site and community type was also significant ($F_{4,80} = 4.76$, $p = 0.001$, $R^2 = 0.13$). Performing separate NMDS analyses for each site showed that within-stem and ground communities differed at each location, but not to the same extent. Differences in community composition in stems and the area surrounding the stems (*multipatt* analysis) could be attributed to the presence of wolf spiders ($p < 0.001$) that were only found in samples collected by vacuuming around the stem. Moreover, earwigs, which were mainly found within the stems, as well as some other organism that were not further identified contributed to separation of the communities (both categories associated significantly with hogweed stems $p < 0.001$). Woodlice did not contribute to community differences between stem and vacuuming samples based on the *multipatt* analysis.

Only at site 3, stems were also naturally perforated by *D. radiella*; approximately one-third of the *H. sphondylium* plants were infested by *D. radiella*. The total abundance of species in naturally perforated stems did not differ from the abundance in stems with three artificial holes ($\chi^2 = 1.74$, $df = 1$, $p = 0.18$, Figure 5). The community was more variable in stems with 3 holes (one stem contained 6 slugs), and this largely explained the deviation in species composition compared with that of stems with single holes and stems that were naturally perforated. However, community composition did not differ between artificially (3 holes) and naturally perforated

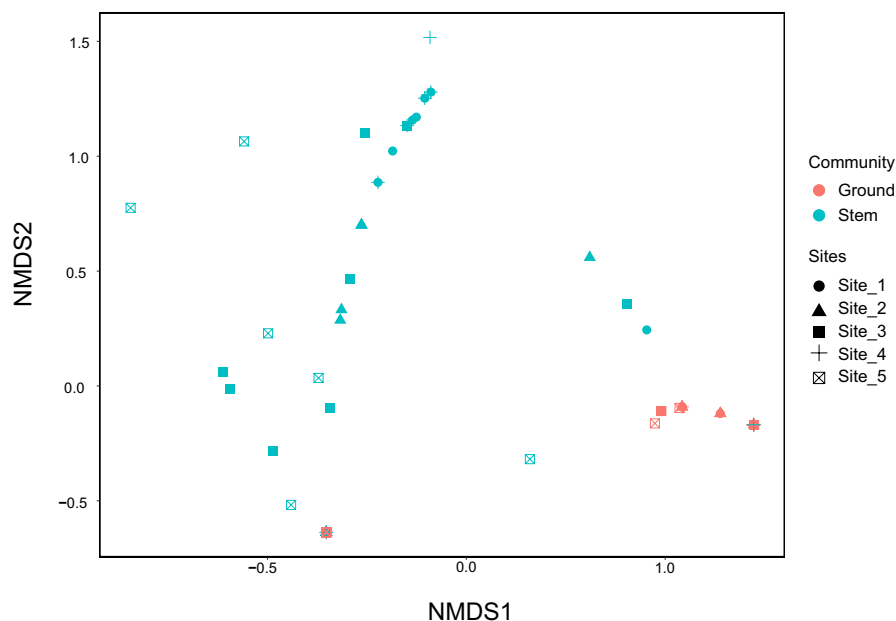


FIGURE 4 NMDS ordination plot of invertebrates found in artificially-perforated hollow stems of hogweed plants (red symbols) and those vacuumed around hogweed stems on the ground (green symbols). Stems were artificially perforated with one hole in each of three stem segments of a single plant. Ground samples were taken around randomly selected plants that had not been perforated. Invertebrates were sampled at five different sites, indicated by different symbols. Invertebrates were categorized as woodlice, earwigs, spiders or others. Each dot is a sample. There were 9 or 10 samples per community type at each site with the exception of site 5 where invertebrates could only be recollected from 6 plants. NMDS stress is 0.077, which is a measure for model fit, and is very good.

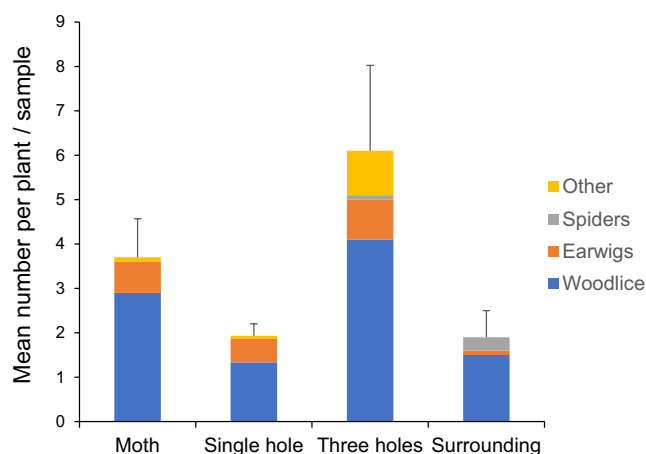


FIGURE 5 Mean number of invertebrates recovered per hogweed plant at site 3 according to sampling treatment. Invertebrates were recovered from stems naturally perforated with *Depressaria radiella* (moth), artificially (single hole or three holes) or from vacuuming samples around stems (surrounding). Invertebrates recovered from the stems were categorized as woodlice, earwigs, spiders or others (mainly slugs). The number of plants was 30 for single holes, and 10 for the other sampling treatments. Error bars depict the standard error of the mean total number of all invertebrates

stems ($F_{1,17} = 0.42$, $p = 0.76$, $R^2 = 0.04$). (A statistical model including all perforation treatments was also not significant). As expected, control non-perforated stems did not contain any arthropods. Thus, arthropods could only enter stems with holes.

4 | DISCUSSION

The results of this study demonstrate that mimicking the ecosystem engineering behaviour of *D. radiella* caterpillars in stems of *H. sphondylium*, by artificially perforating holes in them, attracts woodlice, earwigs and clubionid spiders, which use the stem as a refuge during autumn months. The position of the artificial holes did not affect arthropod abundance inside the stems, although there was a slight tendency for arthropods to move higher up the stem and to enter the holes there. Additionally, when holes were perforated in the first three plant segments closest to the ground, arthropod abundance increased approximately by the same factor (i.e. threefold). Therefore, providing artificial holes to multiple segments of the stem as opposed to single holes in one segment resulted in similar arthropod densities per segment. Whereas arthropod abundance was fairly uniform in four of the sampled hogweed sites, there were significantly higher abundances of arthropods at the fifth site. Thus, although the five sites were located in fairly close proximity, there is local variation in the degree of colonization of perforated hogweed stems.

Arthropods were attracted to the artificial holes in the absence of *D. radiella* which corresponds with previous studies where artificially rolled leaves that mimicked leaves rolled by the caterpillar *Pseudotephusa* sp. also had positive effects on the arthropod community (Lill & Marquis, 2003; Lill & Marquis, 2004). Furthermore, even at the relatively small spatial scales in which the experiment was conducted, there was a local hotspot (site five) where the abundance of woodlice and earwigs in perforated stems was significantly

higher than at the other four sites. At site 5, plants were growing adjacent to a small lake and a horse-riding path, which could explain the higher number of arthropods found there. Along the paths horses turn up soil with their hooves and also leave copious amounts of dung, which may facilitate arthropods via nutrient availability, and especially woodlice, which are important detritivores. Similarly, cattle dung in grasslands was found to increase Hemiptera species richness due to enhanced nutrient availability (Dittrich & Helden, 2012). Additionally, other studies have emphasized the importance of dung in ecological communities, as it increases organic matter content in the soil which in turn positively affects soil communities in tropical systems (Decaëns et al., 2004; Teutscherová et al., 2021).

In line with previous studies (i.e. Harvey et al., 2016; Harvey et al., 2019), stems of plants at site 3 that were naturally perforated by *D. radiella* caterpillars also contained woodlice and earwigs in numbers similar to those found in stems with artificially perforated holes. Species composition of the arthropod community within hogweed stems and in the vegetation surrounding the stems differed; although woodlice were omnipresent, earwigs were mainly found within perforated stems and wolf spiders were only found in the surrounding vegetation and did not enter the stems. This result confirms that *D. radiella* functions as an 'ecosystem engineer' and not simply as a 'facilitator'. The role of *D. radiella* as an ecosystem engineer was previously unclear because the earlier studies did not include ground sampling adjacent to hogweed stems. This new insight endorses the importance of shelter-building arthropods (e.g. insect herbivores) in stimulating local arthropod communities. Several other arthropod species have also been shown to alter the physical state of ecosystems at small scales resulting from their engineering activities (Lill & Marquis, 2007; Novais et al., 2017; Novais et al., 2020).

Spiders were the only arthropod group with higher abundances on the ground surrounding the stems than inside the stems. However, all of the spiders collected around the stem bases were wolf spiders (Lycosidae) that were never found inside the stems and remain on or very close to the ground as motile predators. By contrast, the only spider species found inside the stems was the reed sac spider, *Clubiona phragmitis*, a species that habitually makes its webs in vegetation such as grasses. Harvey et al. (2016) also found that this was also the only spider species found in stems of hogweed infested by *D. radiella*. After winter cutting of *Phragmites australis* (Poaceae) *Clubiona* spiders were found to enter the cut stems and to deposit their eggs sacs in them (Schmidt et al., 2005).

We also found that, without webworm-perforated or artificial holes, plants were always 'clean' and thus never contained any arthropods inside them. As an ecosystem engineer, *D. radiella* potentially influences the ecology and other organisms in four main ways. First, it provides herbivores and detritivores with the inner tissues of hogweeds stems that may be more palatable due to feeding and defecation of woodlice inside them. The holes also allow water to enter, which further breaks down the inner stem walls and facilitates the growth of fungi on them. Second, omnivores (earwigs) and predators (sac spiders) feed on other invertebrates in the stem. For instance, mummies of the parasitoid *Copidosoma sosares*, which is the

main natural enemy of webworms, are frequently consumed by earwigs inside of hogweed stems (J.A. Harvey, personal observation). Slugs are reportedly also used as prey by earwigs (Buxton, 1974), and thus earwigs may also have been attracted to stems with slugs inside them. Third, the stem provides a micro-refuge that is buffered against climatic extremes and the presence of many arthropods in close proximity generates warmth (Cornelissen et al., 2016). Studies with other arthropods also show that crowding positively affects parameters like thermoregulation and disease resistance (Li et al., 2021; Podhorna et al., 2018). Earwigs, for example, are highly susceptible to cold winters (Moerkens et al., 2012). Finally, it may provide arthropods with protection against a broad range of natural enemies that are living in the habitats adjacent to the plants. Earwigs possess chemical defences that are effective against ants but not against spiders, so structural shelter in hogweed stems may greatly enhance their survival against wolf spiders that are abundant on the ground (Gasch & Vilcinskis, 2014). Woodlice are also important prey of ground-dwelling arthropod predators including the centipede, *Lithobius forficatus* (Sunderland & Sutton, 1980). Therefore, occupancy of hogweed stems may greatly reduce predation risk, to both species of arthropods.

In North America, *D. radiella* was introduced from Europe where their larvae feed upon seeds of the naturalized plant species *Pastinaca sativa* and, more recently, the native plant species *H. maximum* (Ode et al., 2004). Moreover, both *P. scaber* and *F. auricularia* were also introduced into North America and are now widely distributed. A previous study conducted in the Rocky Mountains of Colorado and New Mexico found that native populations of the cow parsnip, *H. maximum*, that had been infested with *D. radiella* larvae also harboured variable numbers of earwigs (but not woodlice) that similarly entered the stems through the holes chewed by mature webworm caterpillars Harvey et al. (2019). Remarkably, the authors even found a native North American *Clubiona* species inside several *D. radiella*-perforated stems of cow parsnip *H. maxima* plants. This reveals that the ecosystem engineering activities of *D. radiella* have been re-established across different continents utilizing different (but closely related) plant species, and that the arthropods primarily utilizing the stems are the same or closely related to those in the native range.

Our results reveal that holes artificially perforated into stems of hogweeds functionally mimic holes chewed in the stems by mature larvae of *D. radiella*. Although the stems of hogweeds can occasionally contain large numbers of woodlice and earwigs, they tend to be relatively transient habitats, lasting only during the autumn months, because the stems rapidly decompose after seed fall and are blown over by the wind. It would be interesting to use other hollow substrates—such as sections of bamboo or hogweed stems externally treated with preservatives—that would persist over the course of a winter and to see if they could similarly attract beneficial arthropods. Artificial holes could be placed in them as a tool to attract woodlice and earwigs, which, as described earlier, provide important ecological services including litter decomposition and pest control, respectively (Collison et al., 2013; Orpet

et al., 2019; Souty-Grosset et al., 2005). Previous work has shown that refuges (boxes containing straw) constructed to reduce exposure to thermal extremes can enhance winter survival (Solomon et al., 1999). Similarly, given the attraction of earwigs to the interior of hogweed stems, these stems or structures like them, may be a useful tool in enhancing overwintering survival in orchard habitats where their pest control activities are considered important. These refuges could also enhance habitat heterogeneity in agricultural habitats which benefits many invertebrates, including a range of beneficial species (Benton et al., 2003).

AUTHOR CONTRIBUTIONS

All authors conceived the research and contributed to the writing of the manuscript. SB conducted all experiments. SB and RG analysed data and conducted statistical analyses. All authors read and approved the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data have been made publicly available at the Zenodo repository (<https://doi.org/10.5281/zenodo.6389728>).

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REFERENCES

- Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18, 182–188.
- Berenbaum, M. R., & Zangerl, A. R. (2006). Parsnip webworms and host plants at home and abroad: Trophic complexity in a geographic mosaic. *Ecology*, 87, 3070–3081.
- Bureš, S., & Weidinger, K. (2003). Sources and timing of calcium intake during reproduction in flycatchers. *Oecologia*, 137, 634–641.
- Buse, J., Ranius, T., & Assmann, T. (2008). An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conservation Biology*, 22, 329–337.
- Buxton, J. H. (1974). *The biology of the european earwig forficula auricularia l. with reference to its predatory activities on the damson-hop aphid phorodon humuli (schrunk)*. University of London.
- Collison, E. J., Riutta, T., & Slade, E. M. (2013). Macrofauna assemblage composition and soil moisture interact to affect soil ecosystem functions. *Acta Oecologica*, 47, 30–36.
- Cornelissen, T., Cintra, F., & Santos, J. (2016). Shelter-building insects and their role as ecosystem engineers. *Neotropical Entomology*, 45, 1–12.
- Crawford, K. M., Crutsinger, G. M., & Sanders, N. J. (2007). Host-plant genotypic diversity mediates the distribution of an ecosystem engineer. *Ecology*, 88, 2114–2120.
- Daily, G. C., Ehrlich, P. R., & Haddad, N. M. (1993). Double keystone bird in a keystone species complex. *Proceedings of the National Academy of Sciences of the United States of America*, 90, 592–594.
- Dangerfield, J., McCarthy, T., & Ellery, W. (1998). The mound-building termite *macrotermes michaelsoni* as an ecosystem engineer. *Journal of Tropical Ecology*, 14, 507–520.
- De Almeida, T., Mesléard, F., Santonja, M., Gros, R., Dutoit, T., & Blight, O. (2020). Above-and below-ground effects of an ecosystem engineer ant in mediterranean dry grasslands. *Proceedings of the Royal Society B-Biological Sciences*, 287, 20201840.
- Decaëns, T., Jiménez, J. J., Barros, E., Chauvel, A., Blanchart, E., Fragoso, C., & Lavelle, P. (2004). Soil macrofaunal communities in permanent pastures derived from tropical forest or savanna. *Agriculture, Ecosystems & Environment*, 103, 301–312.
- Dittrich, A. D. K., & Helden, A. J. (2012). Experimental sward islets: The effect of dung and fertilisation on hemiptera and araneae. *Insect Conservation and Diversity*, 5, 46–56.
- Gálvez Bravo, L., Belliure, J., & Rebollo, S. (2008). European rabbits as ecosystem engineers: Warrens increase lizard density and diversity. *Biodiversity and Conservation*, 18, 869–885.
- Gasch, T., & Vilcinskis, A. (2014). The chemical defense in larvae of the earwig *forficula auricularia*. *Journal of Insect Physiology*, 67, 1–8.
- Harvey, J. A., Ode, P. J., Malcicka, M., & Gols, R. (2016). Short-term seasonal habitat facilitation mediated by an insect herbivore. *Basic and Applied Ecology*, 17, 447–454.
- Harvey, J. A., Gols, R., Smith, B., & Ode, P. J. (2019). Invasive moth facilitates use of a native food plant by other native and invasive arthropods. *Ecological Research*, 34, 659–666.
- Harvey, J. A., Ode, P. J., & Gols, R. (2020). Population-and species-based variation of webworm-parasitoid interactions in hogweeds (*heracelum* spp.) in The Netherlands. *Environmental Entomology*, 49, 924–930.
- Haynes, G. (2012). Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology*, 157–158, 99–107.
- Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.
- Kaspi, R. (2000). Attraction of female *chiracanthium mildei* (araneae: Clubionidae) to olfactory cues from male mediterranean fruit flies *ceratitis capitata* (diptera: Tephritidae). *BioControl*, 45, 463–468.
- Li, H., Dai, C., Zhu, Y., & Hu, Y. (2021). Larvae crowding increases development rate, improves disease resistance, and induces expression of antioxidant enzymes and heat shock proteins in *mythimna separata* (lepidoptera: Noctuidae). *Journal of Economic Entomology*, 114, 1808–1816.
- Lill, J. T., & Marquis, R. J. (2003). Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology*, 84, 682–690.
- Lill, J. T., & Marquis, R. J. (2004). Leaf ties as colonization sites for forest arthropods: An experimental study. *Ecological Entomology*, 29, 300–308.
- Lill, J. T., & Marquis, R. J. (2007). 6 - microhabitat manipulation: Ecosystem engineering by shelter-building insects. In K. Cuddington, J. E. Byers, W. G. Wilson, & A. Hastings (Eds.), *Theoretical ecology series* (pp. 107–138). Academic Press.
- Moerkens, R., Leirs, H., Peusens, G., Belien, T., & Gobin, B. (2012). Natural and human causes of earwig mortality during winter: Temperature, parasitoids and soil tillage. *Journal of Applied Entomology*, 136, 490–500.
- Novais, S., Aguirre-Jaimes, A., Quesada, M., & Hernández-Ortiz, V. (2020). Ecosystem engineering by leaf-rolling mites enhances arthropod diversity. *The Science of Nature*, 107, e45.
- Novais, S. M. A., DaRocha, W. D., Calderón-Cortés, N., & Quesada, M. (2017). Wood-boring beetles promote ant nest cavities: Extended effects of a twig-girdler ecosystem engineer. *Basic and Applied Ecology*, 24, 53–59.
- Ode, P. J., Berenbaum, M. R., Zangerl, A. R., & Hardy, C. W. (2004). Host plant, host plant chemistry and the polyembryonic parasitoid *copidosoma sosares*: Indirect effects in a tritrophic interaction. *Oikos*, 104, 388–400.

- Orpet, R. J., Goldberger, J. R., Crowder, D. W., & Jones, V. P. (2019). Field evidence and grower perceptions on the roles of an omnivore, european earwig, in apple orchards. *Biological Control*, 132, 189–198.
- Pike, D. A., & Mitchell, J. C. (2013). Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Animal Conservation*, 16, 694–703.
- Podhorna, J., Aubernon, C., Borkovcova, M., Boulay, J., Hedouin, V., & Charabidze, D. (2018). To eat or get heat: Behavioral trade-offs between thermoregulation and feeding in gregarious necrophagous larvae. *Insect Science*, 25, 883–893.
- Priest, G. V., Camarota, F., Powell, S., Vasconcelos, H. L., & Marquis, R. J. (2021). Ecosystem engineering in the arboreal realm: Heterogeneity of wood-boring beetle cavities and their use by cavity-nesting ants. *Oecologia*, 196, 427–439.
- R Core Team. (2021). *A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Romero, G. Q., Gonçalves-Souza, T., Roslin, T., Marquis, R. J., Marino, N. A., Novotny, V., Cornelissen, T., Orivel, J., Sui, S., & Aires, G. (2022). Climate variability and aridity modulate the role of leaf shelters for arthropods: A global experiment. *Global Change Biology*, 28, 3694–3710.
- Schmidt, M. H., Lefebvre, G., Poulin, B., & Tscharrntke, T. (2005). Reed cutting affects arthropod communities, potentially reducing food for passerine birds. *Biological Conservation*, 121, 157–166.
- Solomon, M., Fitzgerald, J., & Jolly, R. (1999). Artificial refuges and flowering plants to enhance predator populations in orchards. *IOBC WPRS Bulletin*, 22, 31–38.
- Souty-Grosset, C., Badenhassner, I., Reynolds, J., & Morel, A. (2005). Investigations on the potential of woodlice as bioindicators of grassland habitat quality. *European Journal of Soil Biology*, 41, 109–116.
- Sunderland, K. D., & Sutton, S. L. (1980). A serological study of arthropod predation on woodlice in a dune grassland ecosystem. *The Journal of Animal Ecology*, 49, 987–1004.
- Teutscheroová, N., Vázquez, E., Sotelo, M., Villegas, D., Velásquez, N., Baquero, D., Pulleman, M., & Arango, J. (2021). Intensive short-duration rotational grazing is associated with improved soil quality within one year after establishment in Colombia. *Applied Soil Ecology*, 159, 103835.
- Uesugi, A., Morrell, K., Poelman, E. H., Raaijmakers, C. E., & Kessler, A. (2016). Modification of plant-induced responses by an insect ecosystem engineer influences the colonization behaviour of subsequent shelter-users. *Journal of Ecology*, 104, 1096–1105.
- Vieira, C., & Romero, G. Q. (2013). Ecosystem engineers on plants: Indirect facilitation of arthropod communities by leaf-rollers at different scales. *Ecology*, 94, 1510–1518.
- Wang, H. G., Marquis, R. J., & Baer, C. S. (2012). Both host plant and ecosystem engineer identity influence leaf-tie impacts on the arthropod community of *Quercus*. *Ecology*, 93, 2186–2197.
- Wiebe, K. L. (2017). Northern flickers only work when they have to: How individual traits, population size and landscape disturbances affect excavation rates of an ecosystem engineer. *Journal of Avian Biology*, 48, 431–438.
- Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, 132, 96–101.
- Wright, J. T., & Gribben, P. E. (2017). Disturbance-mediated facilitation by an intertidal ecosystem engineer. *Ecology*, 98, 2425–2436.

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