

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 & Kluyber 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

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