

Consumption of fungi-infected fallen pear leaves by the common woodlouse

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ABSTRACT

Consumption of infected plant tissues by decomposing organisms is an important part of ecosystem services. We tested how the common woodlouse (*Porcellionides pruinosus*, Isopoda: Oniscidea) may contribute to the decomposition process in a laboratory experiment in which *Mycosphaerella pyri*-infected pear leaves with or without the aecia of *Gymnosporangium sabinae* were offered as food. We recorded the loss of healthy and infected leaf tissues. Isopod survival rate was also monitored. We found (1) a certain pattern of preference in the consumption of infected leaf material; and (2) that the presence of *G. sabinae* reduced leaf consumption but had no effect on the ingestion of *Mycosphaerella*-infected spots; and (3) the mortality of *P. pruinosus* was adversely influenced by *G. sabinae*, but the results were highly dependent on confinement conditions. Our results suggest that woodlice consume plant pathogenic fungi, and therefore offer the ecosystem service of neutralizing infective plant remnants during decomposition.

KEYWORDS

plant pathogen consumption, isopods, *Porcellionides pruinosus*, *Gymnosporangium sabinae*, *Mycosphaerella pyri*

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INTRODUCTION

Since the conception of ecosystem services (ES) emerged in the 1990s, the research to understand ecosystem functions, and the role of beneficial organisms is sustained (Zhang et al., 2007; Adhikari and Hartemink, 2015). ES include the natural suppression of pests, and agro-ecosystems on the long run benefit from having an ecological balance between pests and those organisms that control them (Zhang et al., 2007). At the same time, ecosystems also provide interactions and mechanisms that are considered harmful from the human perspective. Interestingly, while the concept of ecosystem disservices (EDS) was coined parallel with that of the beneficial ES, the volume of studies on weeds, invertebrate and vertebrate pests as providers of ecosystem disservices is definitely lower (von Döhren and Haase, 2015). Therefore, an integrated approach is needed to understand the complexity of ES and EDS (Herd-Hoare and Shackleton, 2020).

The role of terrestrial woodlice (Isopoda: Oniscidea) in agro-ecosystems is inconclusive. Since isopods are present in conventional and organic agricultural environments alike, they have been long used as indicator organisms (Paoletti and Hassall, 1999). Integrated management refers to them as non-targets, as their role as pests has not been confirmed, but neither have they been positioned as definite beneficials, either.

Woodlice are appreciated as decomposers, as they shred and disintegrate organic materials of diverse origin, with leaf litter being their main material of supply (Dickinson and Pugh, 1974; Sutton, 1980; Forró and Farkas, 1998; Otártics et al., 2014; Ferreira et al., 2016; Harvey et al., 2016). Their fragmenting activity increases the active surface of decomposing materials, so these are more easily available for further, microbial transformation by bacteria and fungi (Leclercq-Dransart et al., 2019). Decomposition depends on time and organic material available, and also on the species composition of both isopods and microorganisms involved (El-Wakeil, 2015).

From the agricultural perspective on the other hand, isopods were generally considered harmful (Vernon and Dennis, 1966; Schneider and Krczal, 1984; Gratwick, 1992), and many studies have investigated their role as pests of specific arable crops including soybean (Brody and Lawlor, 1984; Saluso, 2004; Alfaress, 2012), soybean and sunflower (Faberri et al., 2010, 2011), potato (Montesanto and Cividini, 2017), and in the protected production of squash, lettuce, broccoli, cabbage, strawberry and potato (Garland and Seaman, 1994; Martinez et al., 2014). At the same time, studies have shown that when allowed, isopods choose decaying plant material over fresh, due to the higher digestibility and possible palatability of the former (Zimmer, 2002).

While the movements of an active isopod community will inevitably involve the dissemination of fungal and bacterial agents, the notion that isopods were capable of transmitting diseases was rejected (Garland and Seaman, 1994).

Some studies acknowledge the role of isopods in controlling fungal bodies, the consumption of fungal plant pathogens is one of the lesser studied segments of ecosystem services (Ortiz and Rohlf, 2016). To understand the role of isopods more clearly, we set up a feeding experiment to find out (i) whether the tested isopod species consume any of the mycelia or propagules of the tested fungal pathogens and (ii) how this consumption influences the survival of isopods.

Our hypothesis was that *Porcellionides pruinosus* prefers leaves with *Gymnosporangium sabinae* and *Mycosphaerella pyri*.



MATERIAL AND METHODS

Tested isopod species

***P. pruinus* (Brandt, 1833).** The body colour of the common woodlouse (or plum woodlouse) may be brown or the blueish purple of the plum fruit. The outer layer of the cuticle is covered in a thin sheet of microscopic bubbles, giving *P. pruinus* its distinctive glossy surface (Gregory, 2009; Farkas and Vilisics, 2013; Vittori and Gantar, 2020). Its body length is usually not more than 12 mm. As all isopods, the plum woodlouse grows by a two-phase molting, with the new body being wider and longer than the original one. The minerals of the exuvia are usually regained for further use (Hornung, 2011). This synanthropic isopod species originates from the Mediterranean region, but now is abundant everywhere. It usually inhabits decaying or composted plant material, and as it plays an important ecological role in the decomposition process (Sutton et al., 1984). According to the eco-morphological types (Schmalfuss, 1984), the plum woodlouse belongs to the “runner” type.

Collection, identification and management of isopods before the experiment. Isopods were collected by hand at a Regional Waste Management Centre (Pusztázámor, Pest County, Hungary) and identified to species level according to Farkas and Vilisics (2013).

Individuals of *P. pruinus* were introduced into plastic containers at the Entomology and Plant Pathogen Laboratory of the Department of Integrated Plant Protection of MATE, Hungarian University of Agricultural and Life Sciences. The temperature measured between 22 and 25 °C, and there was a 0:24 (light:dark) regime before the experiment. Animals were fed ad libitum with a mixture of fallen leaves collected from a local orchard (Gödöllő, Pest County, Hungary), including leaves of maples (*Acer* spp.), oaks (*Quercus* spp.), planes (*Platanus* spp.), and various fruit trees (*Malus* spp., *Pyrus* spp., *Prunus* spp., *Juglans* spp.). Females with apparent signs of gravidity were excluded from the experiment, while those in their early, hardly detectable stage of gestation remained. No other gender-specific measurements were applied.

Tested plant pathogenic fungi

***G. sabinae* (Dickson) G. Winter.** The European pear rust belongs to division Basidiomycota, subdivision Pucciniomycotina, class Pucciniomycetes, order Pucciniales, family Gymnosporangiaceae, genus *Gymnosporangium* (Mycobank, 2021). *G. sabinae* causes leaf spots on pear foliage and has a distinctive set of protruding aecia when the fungus reaches the stage to release spores for further infection. With various junipers being the primary host and pear the secondary, this fungus is widespread in Europe, and its time of infection on pear varies according to location (Lâce, 2017). *G. sabinae* has only been reported from the United States in 2009 (Yun et al., 2009). Biological control options include agrotechnical measures, the use of resistant varieties, and there have been steps to use fungi to counteract the pathogen (Lâce, 2017).

***Mycosphaerella pyri* (Auerswald) Boerema (anamorph syn: *Septoria pyricola* Desm.).** The pear leaf spot belongs to division Ascomycota, subdivision Pezizomycotina, class Dothideomycetes, order Dothideomycetidae, family Mycosphaerellaceae, genus *Mycosphaerella* (Mycobank, 2021). The fungus causes brown lesions with definite margins on pear, its main host, and



is rarely detected on quince and apple, too (Horst, 2013). The most affected phenophase is when leaves and fruits are still young (Chatzidimopoulos and Pappas, 2016). The biological control of *M. pyri* is based on resistant cultivars (Verma and Sharma, 1999).

Collection and identification of plant pathogenic fungi. Infected pear (*Pyrus communis*) leaves were collected from the local orchard described above within the first week of October, 2016. Fungi present on the leaves were cultured and identified at the laboratory described above.

Experimental setup. The experiment lasted between 10 October and 24 October 2016.

We had 15 Petri dishes with a diameter of 8.5 cm layered with filter paper, and 15 plastic boxes measuring $7 \times 5 \times 5$ cm with 20 g of a general potting medium called Florimo[®] containing *Sphagnum* moss peat, low moor peat, organic humus, composted cattle manure, clay, fertilizer mixture, with a pH of 6.4 ± 0.5 in every box. To all Petri dishes and boxes, ten randomly selected pear leaves were added with or without signs of the European pear rust (*G. sabinae*). All offered leaves contained spots of *Mycosphaerella pyri*. Containers were labelled according to the type of environment (P for Petri dish; B for box with potting medium), and to the presence of the fungal bodies of *G. sabinae* (G+ for visible signs of infection; G- for no signs of the pear rust).

Ten *P. prunosus* adults with an average body weight of 114.15 mg were introduced into every container, which were then covered and placed randomized on a tray and kept at room temperature, between 22 and 25 °C. During the experiment, we followed no special light regime, containers were left to have the natural light/dark rhythm of the laboratory, 11:13 (light:dark). Samples were taken two times a week, and at the same time every container was sprayed with water by pressing a hand-held vaporizer three times to avoid desiccation. We measured the loss in the size of the fungal spots, the loss in the number of acacia of *G. sabinae*. Loss of leaf material was detected regardless of the health status and the fungal cause of infection of pear leaves.

To evaluate loss of leaf and fungal material we made photographs using a Sony E5823 camera with the same setting throughout the experiment (resolution $5,520 \times 4,140$, 72 dpi, sRGB, 1/32s, ISO–100, focal length 4 mm, no flash), using the same station point. The print versions of these photographs were copied to a millimetre paper to quantify missing leaf and fungal matter to track and evaluate the rate and total value of consumption of leaf and fungus of isopods.

At the end of the experiment, we defined the acceptance rate of acacia, that is, how many of the acacia remained intact, how many showed signs of some consumption and how many were completely eaten.

The number of adult individuals were counted at the completion of the experiment, and survival rates were calculated.

Data were evaluated using one-way ANOVA with pairwise Tukey tests and with an Independent (Two Samples) *T*-test with PAST[®] program (Hammer et al., 2001).

RESULTS

It was our general observation that the consumption of leaf material was higher when the isopods were in boxes with the potting medium. In some cases, consumption was so intense that only the veins remained (Fig. 1).





Fig. 1. Typical progression pattern of leaf consumption observed on pear leaves spontaneously infected with *Mycosphaerella pyri* and *Gymnosporangium sabiniae* in a laboratory experiment testing the pathogen consumption of *Porcellionides pruinosus*. Gödöllő, Hungary, 2016

The highest consumption of leaves without *G. sabiniae* was noticed in boxes (BG-), while the lowest leaf material loss was recorded within Petri dishes with pear rust infection (PG+). More leaves were consumed in boxes even if the leaves were pear rust-infected (BG+) than when the leaves were free of pear rust, but the isopods were kept in Petri dishes (PG-). The comparison of treatment combinations revealed that there was a significant difference in the total loss of leaf material with pear rust-free leaves offered in boxes (BG-) having the highest amount of loss when compared to any other treatment (PG- $p = 0,02$; PG+ $p = 0,002$; BG+ $p = 0,04$). The total loss of leaf material was the highest in the (BG-) treatment and the lowest in the (PG+) treatment. Values of (BG+) and (PG-) were similar, and there were no significant differences among the three lowest values of total loss of leaf material (Fig. 2).

Although the loss of spots infected with *Mycosphaerella pyri* showed no significant difference among the various treatments, a clear tendency was visible that *M. pyri* spots were consumed in the largest amount in Petri dishes with the presence of rust (PG+), reaching nearly 100% loss. In boxes with potting medium however, the loss of mycosphaerella spots was similar in both pear rust-free (BG-) and pear rust-infected leaves (BG+) (Fig. 3).

Evaluating the acceptance of aecia we found that in Petri dishes, only 23% of the aecia remained intact, 45% was tasted and 32% was completely consumed. That translates to having 1, 3 and 11 Petri dishes with intact, tasted or consumed fungal bodies.

Isopods had different preferences in boxes: 43% of the aecia remained intact, 33% was tasted and 24% was completely consumed. That means that 3, 5 and 7 fungal bodies were left intact, were tasted or consumed in the boxes (Fig. 4).

The highest survival rate of isopods was found in boxes, where leaves did not contain the aecia of *G. sabiniae* (Fig. 5).

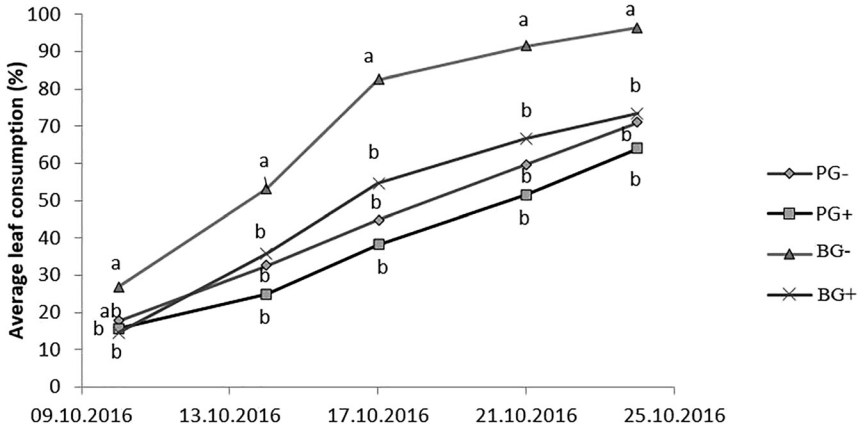


Fig. 2. Cumulated loss of fallen pear leaf material due to isopod consumption according to treatments where *Porcellionides pruinosus* individuals were fed with pear leaves with or without *Gymnosporangium sabinae* infection. All leaves contained spots of *Mycosphaerella pyri*. Different letters indicate significant differences (ANOVA, Tukey's post hoc test). (P = Petri dish; B = Box with potting medium; G refers to the presence of *G. sabinae*)

DISCUSSION

Fragmentation, dispersal of decaying plant material, and contribution to decomposition and nutrient recycling (Leclercq-Dransart et al., 2019; Vařutová et al., 2019) are what makes

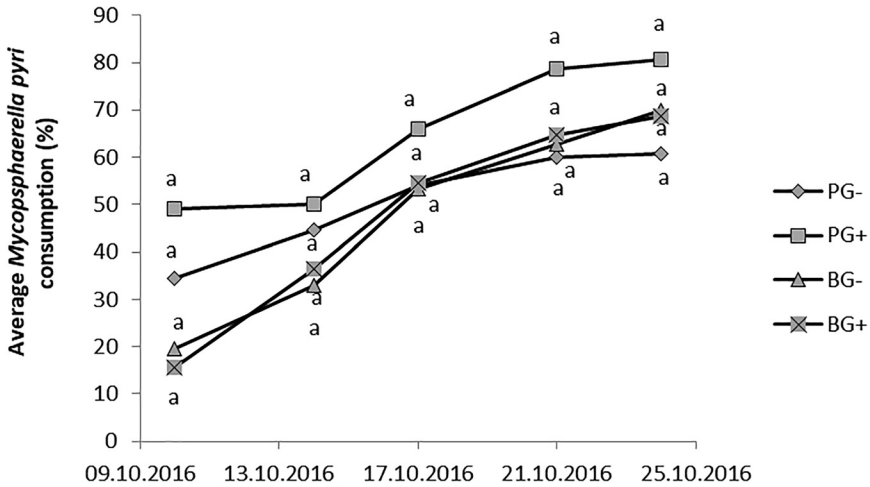


Fig. 3. Cumulated loss of *Mycosphaerella pyri*-infected spots due to consumption by isopods over the course of an experiment where *Porcellionides pruinosus* individuals were fed with fallen pear leaves with or without *Gymnosporangium sabinae* infection. Different letters within the same sampling date indicate significant differences (ANOVA, Tukey's post hoc test). (P = Petri dish; B = Box with potting medium)



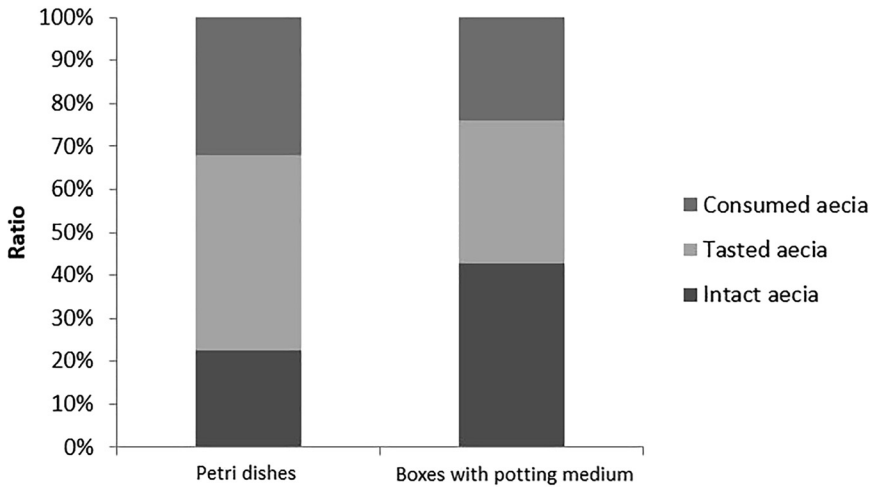


Fig. 4. Loss in the number of aecia of *Gymnosporangium sabinae* due to isopod consumption at the end of an experiment where *Porcellionides pruinosus* individuals were fed with infected or pear roset-free leaves in Petri dishes and in boxes with potting medium

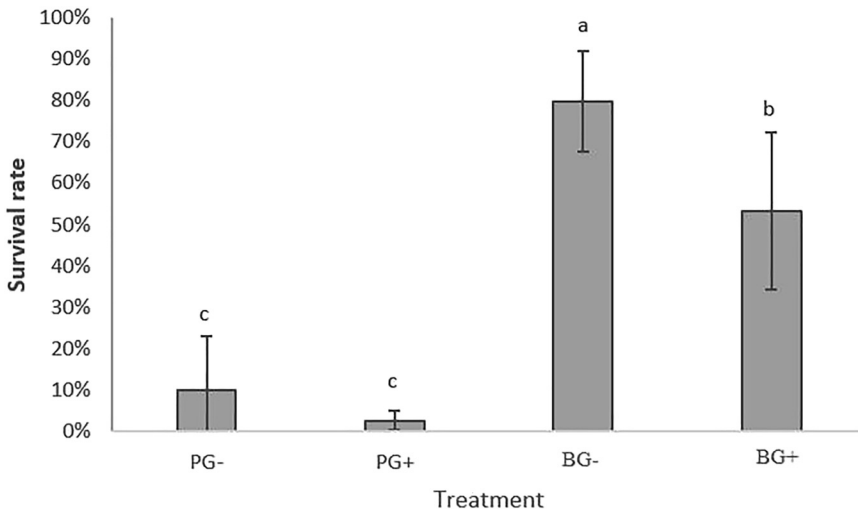


Fig. 5. Survival rate of isopods at the end of the feeding experiment according to treatments where *Porcellionides pruinosus* individuals were fed with pear leaves with or without *Gymnosporangium sabinae* infection. All leaves contained spots of *Mycosphaerella pyri*. Different letters indicate significant differences (ANOVA, Tukey's post hoc test; error bar: CI 95%). (P = Petri dish; B = Box with potting medium; G refers to the presence of *G. sabinae*)



woodlice important in the matrix of ecosystem services with special regard to soil quality (Ferreira et al., 2016). Their foraging behaviour was found to induce changes in the composition of plant material, so that the debris that has been ingested and egested by isopods are more suitable for further microbial breakdown and transformation (Kayang and Sharma, 1999).

Our hypothesis was based on the observation that the presence of a fungal and bacterial coat has a positive influence on the food choice of isopods, because as Zimmer and Topp (1997) found in a study examining the palatability of fresh and decomposed leaves in various stages of decomposition, the presence of microbes on the surface of and within the plant material has a greater influence on the suitability of a plant material as a fodder for isopods than the properties of the plant material itself.

Based upon the notion that microorganisms, including bacteria and fungi present on the surface of decaying plant material also constitute a part of the diet of detritivores including isopods (Hornung, 1981; Rabatin and Stinner, 1985; A'Bear et al., 2014), we wanted to find out whether isopods consume the mycelia, propagule, and resting body of fungal pathogens and if they do, is there a preference in their consumption towards any of the two used fungal species. By recording mortality, we examined how the survival rate of adult isopods was affected by the consumption of fungal bodies in this setting. Besides its simple availability and synanthropic lifestyle, *P. pruinus* became our test species because it responds well to various environmental circumstances and is easy to rear among artificial conditions.

In a laboratory feeding experiment using the leaf litter of *Alnus nepalensis* (Kayang et al., 1994) fungi were found not only to serve as food for terrestrial isopods but were preferred over bacterial material. In fact, isopod communities of caves regularly feed on algae and fungal matter to obtain their polyunsaturated fatty acids (Šustr et al., 2005). By massively feeding on fungi, isopods controlled fungal communities in a semi-natural experimental setting (Crowther et al., 2013). The low efficiency of crustacean digestion suggests that spores of microorganism may leave the gut system, which may alter the microbial species composition of the habitat (Hornung, 1981).

The grazing pressure by fungivorous macroarthropods including isopods altered the genetic material of *Aspergillus nidulans* (Ortiz and Rohlfs, 2016). And while conventional feeding experiments typically involve inoculating a known strain or species of fungus over a sterilized, dehydrated and rehydrated mass of leaves (Kayang and Sharma, 1999), in our choice tests, animals were offered naturally available plant materials, with the pathogenic fungi occurring within plant tissues in various stages of decay. In our test *P. pruinus* individuals consumed fungal pathogens, and regarding preference between fungal species, we found that while both fungi are potential food sources for the isopod species, *Mycosphaerella pyri* was preferred over *G. sabinae*. The literature on the preference among microorganisms by isopods is limited, but our finding matches to that by Ihnen and Zimmer (2008) who observed that *Porcellio scaber* was able to select between microorganisms, and to meet their nutritional demand, the animals chose to consume specific types and species of microorganisms found in leaf litter.

Following the perception that the survival rate of woodlice are influenced by nutrition (Rushton and Hassall, 1983; Kautz et al., 2000; Zimmer, 2002), we examined what effect the consumption of fungal pathogens may have on their mortality. We found that *P. pruinus* had a definitely lower preference towards *G. sabinae*, but only in boxes with potting medium, the presence of the fungus did not adversely influence isopod survival which we attribute to the



presence of alternative food sources provided by the medium itself. It means that survival figures in this experimental setting were not directly influenced negatively or in any other way, by the presence of the fungus, but instead, there is an indirect and positive correlation with the presence of alternative, potentially nutrient-rich food sources within the medium. This is supported by the fact that the same fungal pathogen exerted no significant effect on isopod survival to populations kept in Petri dishes. Furthermore, we proved in a previous study that the entomopathogen *Beauveria bassiana* positively influenced the reproduction of *P. pruinosus* (Póss et al., 2017a, 2017b).

As a natural part of decomposition, the surface of leaves in leaf litter is usually covered by a biofilm, a coat made of bacteria and fungi. This is a preferred food source of isopods (Zimmer and Topp, 1997), and has its advantages: isopods feeding on leaves coated with biofilm showed a higher increase in body weight than those fed with leaves without the coating (Horváthová and Bauchinger, 2017).

One possibility is that in the case of pear rust-infected leaves the main deterrent was the lack of biofilm. In pear leaves, the presence of the pear rust (*G. sabinae*) induces the excretion of polyphenol compounds. This is a stress response from the plant to remove microorganisms from its surface (Kalisz et al., 2015), and polyphenols reduce the thickness and vigor of biofilm. Since phenolic compounds influence the food choice of isopods (Zimmer et al., 2002a, 2002b), the reduced isopod appetite for infected leaves we experienced may have been explained.

Population growth was the most noticeable in the more complex environment provided in boxes filled with potting medium. This finding may indicate that for certain type of studies, the all-artificial circumstances of Petri dishes and similar settings may result in misleading results, and that isopods seem to have a preference toward habitat conditions.

The most intensive mycelial loss was also recorded in boxes with potting medium. The behaviour of the animals was also different: isopods hid under leaves in the Petri dishes, while they rested either under the leaves or within the medium.

The findings of our experiments suggest that confinement type influences the responses and behaviour of isopods, as the tested species consumed more leaves, healthy and infected alike, in the more complex environment than in the Petri dishes that proved to be unusually harsh habitats for the tested isopod species, so their feeding and survival dropped. But we must keep in mind that the dietary choice of isopods sometimes is unpredictable (Gerlach et al., 2014). One may argue that to obtain realistic impressions on the role of isopods in the consumption of plant pathogens, one may have to create experimental settings that resemble the natural settings better. Crowther et al. (2013) for example created and used the so-called mesocosms to investigate the role of isopods in their natural environment.

This resonates with Alfaress (2012) noticing that isopod communities need the lack of disturbance to function properly, while Hornung et al. (2009) state that certain isopods are well adapted to the presence of human intervention. When semi-natural environmental conditions are provided, we have to take losses due to cannibalism into account as well (Sutton, 1980).

We assume that woodlice offer the ecosystem service of neutralizing infective plant remnants during decomposition. Further studies are needed to test how different woodlice species may dis-inoculate other plant pathogens of orchards and vegetable crops, and what effect the consumption of infected plant tissues may have on crop and woodlice health.



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