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# Shelters of leaf-tying herbivores decompose faster than leaves damaged by free-living insects: Implications for nutrient turnover in polluted habitats

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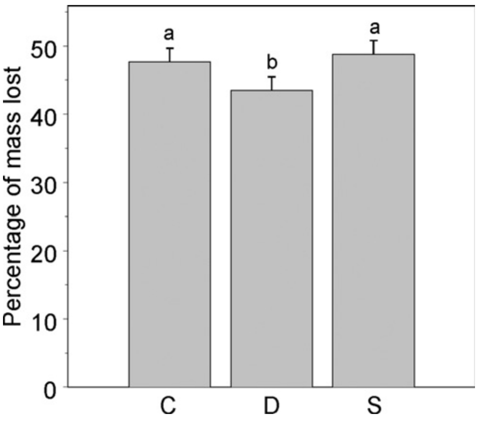
## HIGHLIGHTS

- Leaf eating insects can influence decomposition processes in different ways.
- Birch leaves damaged by insects decomposed slower than intact leaves.
- Shelters built by insects from birch leaves decomposed faster than untied leaves.
- Severe environmental pollution decreased decomposition rate of birch leaves.
- Pollution did not modify the effects of herbivory on leaf decomposition rate.

## GRAPHICAL ABSTRACT



Damage by free-living insects (D) reduces decomposition rates of mountain birch (*Betula pubescens* ssp. *czerepanovii*) leaves compared to intact leaves (C), but structuring of litter due to engineering activity of leaf-tying insects (S) counterbalances adverse effects of leaf damage on decomposition processes.

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## ABSTRACT

Leaf-eating insects can influence decomposition processes by modifying quality of leaf litter, and this impact can be especially pronounced in habitats where leaf-eating insects reach high densities, for example in heavily polluted areas. We hypothesized that the decomposition rate is faster for shelters of leaf-tying larvae than for leaves damaged by free-living insects, in particular due to the accumulation of larval frass within shelters. We exposed litter bags containing samples of three different compositions (shelters built by moth larvae, leaves damaged by free-living insects and intact leaves of mountain birch, *Betula pubescens* ssp. *czerepanovii*) for one year at two heavily polluted sites near the nickel-copper smelter at Monchegorsk in north-western Russia and at two unpolluted sites. The decomposition rate of leaves damaged by free-living insects was 91% of that of undamaged leaves, whereas the mass loss of leaves composing shelters did not differ of that of undamaged leaves. These differences between leaves damaged by different guilds of herbivorous insects were uniform across the study sites, although the decomposition rate in polluted sites was reduced to 77% of that in unpolluted sites. Addition of larval frass to undamaged leaves had no effect on the subsequent decomposition rate. Therefore we suggest that damaged leaves tied by shelter-building larvae decompose faster than untied damaged leaves due to a looser physical structure of the litter, which creates favourable conditions for detritivores and soil decomposers. Thus, while leaf damage by insects per se reduces litter quality and its decomposition rate, structuring of litter by leaf-

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tying insects counterbalances these negative effects. We conclude that leaf-tying larvae, in contrast to free-living defoliators, do not impose negative effects on nutrient turnover rate even at their high densities, which are frequently observed in heavily polluted sites.

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## 1. Introduction

Long-term and severe industrial pollution imposes profound impacts on terrestrial ecosystems (Kozlov et al., 2009). Although effects of pollution on biota are generally detrimental (Kozlov and Zvereva, 2011), pollution was found to favour plant-feeding insects (Zvereva and Kozlov, 2010). Among these, leaf-tying larvae clearly benefit from heavily polluted environments, and the increases in their densities were observed around various industrial polluters (Kozlov and Zvereva, 1992; Kozlov and Haukioja, 1993; Selikhovkin, 1995; Kozlov, 1997). Earlier we demonstrated that the density of shelters built by leaf-tying larvae feeding on mountain birch (*Betula pubescens* ssp. *czerepanovii* [Orlova] Hämet-Ahti) was more than four-fold greater in polluted habitats near the nickel-copper smelter at Monchegorsk, northwestern Russia, than in unpolluted forest sites (Zvereva et al., 2014) and attributed this effect to the impact of pollution-induced habitat deterioration on crown architecture of their host plants. Mountain birch trees persisting in industrial barrens have compact and dense crowns (Zverev et al., 2013), which facilitate leaf-tying larvae by reducing their mortality both inside and outside the shelter. This effect is persistent in time: the densities of leaf-tying larvae near Monchegorsk have remained high for decades (Kozlov, 1997; Kozlov et al., 2009; Zvereva et al., 2014). However, the consequences of the increased abundance of shelter-building caterpillars for structure and functions of polluted ecosystems have not been explored previously.

The leaf damage caused by plant-feeding insects has variable effects on subsequent decomposition of leaf litter, including retardation, acceleration or no change in decomposition relative to undamaged leaves (Choudhury, 1988; Chapman et al., 2006; Kurokawa and Nakashizuka, 2008; Silfver et al., 2015; Cárdenas et al., 2015). These differences arise primarily due to changes in leaf chemistry following insect damage (Grime et al., 1996; Wardle et al., 2002; Butenschoen and Scheu, 2014). In particular, increases in the concentrations of plant secondary compounds can be responsible for the slower decomposition rates observed in damaged leaves (Findlay et al., 1996; Schweitzer et al., 2005). On the other hand, fragmentation of leaf tissues due to herbivory and higher edge availability in damaged leaves may enhance leaf decomposition (Cárdenas and Dangles, 2012). The accumulation of undecomposed plant litter was reported from several industrial barrens (Kozlov and Zvereva, 2007), and therefore the increased damage of plant leaves by insects may have far-reaching consequences for nutrient turnover in these heavily polluted habitats.

Insect feeding guilds often impose differing impacts on their host plants (Welter, 1989; Zvereva et al., 2010; Zvereva and Kozlov, 2012; Moreira et al., 2015), but this source of variation is only rarely considered in studies on leaf litter decomposition. Researchers either combine leaves damaged by different herbivores (Cárdenas et al., 2015; Silfver et al., 2015) or consider only leaves damaged by free-living defoliators (Schowalter et al., 2011; Cárdenas and Dangles, 2012) or by gall-forming insects (Frost et al., 2012; Künkler et al., 2013). At the same time, the impacts of herbivores on litter quality and on subsequent litter decomposition rate may differ even within the feeding guild. For example, leaves damaged by lace bugs decomposed more slowly than undamaged leaves, whereas aphid damage had no effect on the leaf decomposition rate (Kay et al., 2008).

Shelter-building is a common behaviour among leaf-eating insects. The shelters can be made of leaves that are rolled, folded or tied with silk. These shelters are of different shapes, from simple folded leaf fragments to complex silk tunnels and structures involving multiple leaves sewn together and/or attached to twigs (Abarca et al., 2014). This shelter-building behaviour, which is one of the well-studied examples of ecosystem engineering, has multiple effects on communities of arboreal arthropods (Lill and Marquis, 2007; Wang et al., 2012; Cornelissen et al., 2016). Nevertheless, to our knowledge, the use of abscised shelters by epigeic arthropods has not been studied, nor have the impacts of abscised shelters on leaf litter decomposition processes been evaluated.

Healthy larvae inhabiting leaf shelters usually eject faecal pellets from the shelters (Weiss, 2003); however, a total of 17% of the abandoned shelters on birches in the Kola Peninsula still contained substantial amounts of frass (i.e. exceeding five faecal pellets), ranging from 0.44 to 5.73 mg dry weight per shelter (Zvereva et al., 2014). Insect frass contains high amounts of nitrogen and is comprised mainly of labile organic material that decomposes quickly (Lovett and Ruesink, 1995), so frass can enhance microbial growth (Frost and Hunter, 2004) and, in turn, accelerate the litter decomposition rate (Zimmer and Topp, 2002).

We hypothesized that the presence of faeces in leaf shelters would facilitate leaf decomposition relative to that observed for untied leaves damaged by free-living defoliating insects. On the other hand, adverse effects of industrial pollution on soil biota (Bååth, 1989; Rusek and Marshall, 2000) and on decomposition processes (Freedman and Hutchinson, 1980; Kozlov and Zvereva, 2015) may be expected to modify the effects of herbivory on leaf decomposition rate in heavily polluted industrial barrens relative to unpolluted forests; however, the direction of this effect is hard to predict. We tested these hypotheses in field experiments, conducted in heavily polluted and unpolluted sites, by comparing the decomposition rates of intact leaves, untied leaves damaged by free-living defoliators and shelters made by leaf-tying larvae (i.e. tied leaves, often with insect frass inside), as well as the decomposition rates of intact leaves with realistic amounts of frass added. We predicted that (1) untied damaged leaves would decompose more slowly than intact leaves due to the adverse effects of plant defensive chemistry induced by insect feeding on the activity of decomposers; (2) shelters built by plant-feeding insects would decompose more rapidly than untied damaged leaves; (3) insect frass, alone or within a shelter, would increase the decomposition rates of both intact and damaged leaves; and (4) all these effects will be differently expressed in unpolluted than in heavily polluted habitats.

## 2. Materials and methods

### 2.1. Study area and study sites

The study was conducted near the town of Monchegorsk (67°56′ N, 32°49′ E) in north-western Russia, about 150 km south of the tree line. The nickel-copper smelter located at Monchegorsk was one of the largest polluters in the Northern hemisphere for decades. The smelter began production in 1937–1938 and had no air-cleaning facilities until 1968. The annual emissions of sulphur dioxide ($SO_2$) reached a maximum of 278,000 metric tons (t) in 1983, steadily declined to about 100,000 t by the mid-1990s, dropped to 45,000 t in 1999 and have remained at about this level since then. Metal emissions during the 1980s–1990s were 3000–8000 t of nickel and 1000–6000 t of copper annually and then declined in concert with declines in $SO_2$. For the history of pollution impacts on the study region and the levels of

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