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Diversity of macro-detritivores in dead wood is influenced by tree species, decay stage and environment

Juan Zuo [a, *], Myrthe Fonck [a], Jurgen van Hal [a], J. Hans C. Cornelissen [a], Matty P. Berg [b, c]

[a] Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
[b] Animal Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
[c] Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands

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ABSTRACT

Diplopoda (millipedes) and Isopoda (woodlice) are among the most abundant macro-detritivores in temperate forests. These key regulators of plant litter decomposition are influenced by habitat and substrate quality, including that of dead wood. Dead wood provides shelter and resources to macro-detritivores, but the relative effects of tree species, wood decay stage, forest environment and their interactions on macro-detritivore communities are poorly known. To unravel these effects, we combined a reciprocal field incubation experiment and direct field sampling to compare the Diplopoda and Isopoda communities in logs of silver birch (*Betula pendula*) and Norway spruce (*Picea abies*) in two contrasting sites in terms of soil texture, pH, fertility and microclimate. We found: (1) a curvilinear relationship between wood decay stage and abundance of Diplopoda and Isopoda, by using wood density as a measure for the decay stage; (2) the pH of dead wood was a good predictor of wood decay stage in a site with pH close to neutrality but not in an acidic site; (3) Diplopoda and Isopoda community composition on different tree species converged during the decay process, consequently tree species are more important in the substrate selection of macro-detritivores at the beginning of their dead wood decomposition; (4) tree species, the growing environment of the trees and the decomposition environment of the logs strongly determined Diplopoda and Isopoda community composition in dead wood, these drivers of macro-detritivore communities interacted with each other and with the wood decay stage. Thus, when trying to understand and predict future patterns of macro-detritivore diversity under regimes of changing land-use and climate, these interactions should be taken into account. An important next step will be to quantify the feedback of macro-detritivore community composition to dead wood decomposition itself. This feedback may be better understood from the combination of (1) the complex interactions of tree species, wood decay stage and forest environment on the macro-detritivore community and (2) the functional traits of these macro-detritivore species. A better knowledge about these feedbacks can help in predicting carbon storage and nutrient cycling functions of dead wood in forests differing or changing in tree species composition and abiotic environment.

1. Introduction

Woody debris is an important and abundant component of forest ecosystems where it fulfils crucial ecological functions, e.g. as a habitat for myriad organisms and energy flow and nutrient cycling (Harmon et al., 1986). Decomposition is one of the main loss pathways of woody debris, having a profound effect on the global carbon cycle (Cornwell et al., 2009). The presence of detritivorous macro-fauna has been shown to accelerate the decomposition rate of plant leaf litter by 1.6–66% depending on litter type and climate (González and Seastedt, 2001; Vasconcelos and Laurance, 2005; Riutta et al., 2012). In a reciprocal incubation experiment, Anderson (1973a, 1973b) found that leaf litter breakdown and leaching of chemical components to soil were influenced by tree species, soil animals and environment. Macro-fauna are also important for the decomposition of woody debris (Stokland et al.,

* Corresponding author. Tel.: +31 0 20 5986970.
E-mail address: j.zuo@vu.nl (J. Zuo).

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2012; Ulyshen and Wagner, 2013), but this role has been less studied in quantitative terms than for leaf litter.

Diplopoda (millipedes) and Isopoda (woodlice) are among the most abundant macro-decomposers in temperate forests, and have been found to play a significant role in decomposition and nitrogen release (Wall et al., 2008; David and Handa, 2010; Vos et al., 2011). As saprophages, they participate in decomposition by consumption, fragmentation and transformation of dead organic material and by moving it to biologically more favourable microclimate conditions (Sutton et al., 1980; Rushton and Hassall, 1987; David and Handa, 2010), thereby stimulating microbial colonization, growth and activity and, hence, litter decomposition. By producing faeces, the substrate quality for microbes will be changed (usually improved), and macro-detritivores thereby influence microbial functioning (Teuben and Roelofsma, 1990). Macro-detritivores, especially Isopoda, may also feed on microbes including decomposing fungi, like other soil fauna groups such as Collembola and Acari, thereby also affecting wood debris turnover (Bradford et al., 2002; Crowther et al., 2011). In temperate woodlands macro-fauna have been shown to be most important for the breakdown of more recalcitrant litter types (Riutta et al., 2012), but they prefer easily decomposable litter, and so are thought to feed on recalcitrant litter only in later stages of decomposition (Paoletti and Hassall, 1999; Vos et al., 2011).

In forests the diversity of macro-detritivores is influenced by several factors (Fig. 1). One is tree species, which determines microclimatic conditions and also the quantity and quality of dead organic substrate, i.e. leaf litter and dead wood, for macro-detritivores (Stasiov et al., 2012). While much is known about the effect of leaf litter quantity and quality on macro-detritivore communities (Zimmer et al., 2005; Gessner et al., 2010; de Oliveira et al., 2010), less is known about how differences in dead wood traits affect macro-detritivores. It is known that an increase in the amount of dead wood on the forest floor enhances macro-detritivore diversity and abundance (Jonsson et al., 2005; Stokland et al., 2012). Woody debris can be both a resource and a hiding place, which might be tree species specific. However, whether and how tree species differ in these effects on macro-detritivores is poorly known.

Physical and chemical traits of wood, such as wood density and nutrient content, have been shown to influence the composition of saprophagous insect assemblages (Stokland et al., 2012). These traits affect the accessibility of wood to saprophagous species. As traits differ between tree species, they may account for tree species-specific effects on macro-detritivore communities. During the first stage of decomposition bark traits are probably important as they determine the quality of the wood as shelter site and resource for macro-detritivores (Franceschi et al., 2005; Stokland et al., 2012). Wood properties that are important in explaining variation in associated community composition of invertebrates do not only cohere with tree species, but also with the stage of decay of wood and the environment in which decomposition takes place (Harmon et al., 1986; Stokland et al., 2012). Whilst previous studies on dead wood traits focussed mostly on their role in decomposition (Weedon et al., 2009; Van Geffen et al., 2010; Freschet et al., 2012), some studies indicated that the decay stage seems to influence macro-detritivore community composition (Grove, 2002; Jonsell et al., 2007; Ulyshen and Hanula, 2010). As wood decay progresses, the tree species identity seems to become less important for the substrate selection of macro-detritivores, presumably because of convergence of wood properties, and their community composition on different host trees becomes more similar (Grove, 2002; Jonsell et al., 2007).

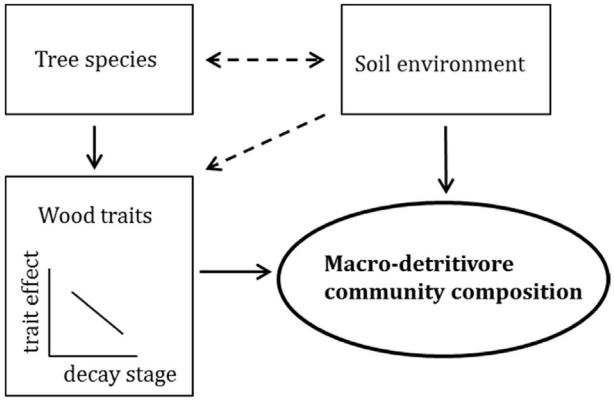

Fig. 1. Conceptual scheme showing the relationship between tree species, wood traits, decay stage, soil environment and macro-detritivore community composition. The soil environment has a direct effect on community composition (via abiotic conditions; solid line), but also an indirect effect as it may determine forest tree species composition (dashed line) and wood trait values (dashed line). The trait box represents the hypothesis that community composition depends on wood traits. The trait values will change with wood decay and the trait variance will decrease with decay stage, leading to a convergence of community composition over time.

Soil macro-fauna diversity is heterogeneously distributed and this spatial variation in species composition is partly caused by the spatial heterogeneity of environmental conditions (Ettema and Wardle, 2002; Berg, 2012). Among the environmental factors that affect the distribution of macro-detritivores, the predominant ones are thought to be soil type, which strongly affects soil moisture regime, soil chemistry (especially pH and Ca content) and overall substrate availability. These factors may influence the micro-environment in dead wood as well as the macro-faunal species pool at a site. Thus, we also expect the soil surface environment to be important in determining macro-fauna communities in dead wood (Fig. 1). Based on these previous findings, it can be expected that the abundance and community composition of Diplopoda and Isopoda will differ between tree species, decay stage and forest soil environment, with possible interactions between these factors.

In this study we aim to experimentally unravel these interactions by comparing the macro-detritivore community composition in dead wood of two contrasting tree species, one deciduous species (*Betula pendula*) and one coniferous species (*Picea abies*), both in a range of decay stages and in two contrasting forest environments: a dry, acid sandy soil versus a moist, clay soil with a pH close to neutrality. Specifically, we hypothesize that:

(1) Different tree species, through variation in dead wood and bark traits, will host different Diplopoda and Isopoda communities.
(2) Diplopoda and Isopoda abundance and species composition in dead wood will change with the progression of its decomposition, as indicated by a decline in wood density (Harmon et al., 1986; Freschet et al., 2012). Their abundance will increase as more decayed, softer wood becomes accessible to the animals, with a higher moisture content and more available resources (nutrients, carbon and microbes). But as wood decay progresses, different tree species will become more similar in community composition, because structural and chemical components that inhibit access to wood will breakdown during decomposition and microbes that are an important additional food source will increase in abundance.
(3) The environment in which dead wood decays will interact with the factors decay stage (see hypothesis 2) and tree species (see hypothesis 1) as trees and logs of different species may influence site conditions, such as temperature,