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Ecosystems

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# Fauna Community Convergence During Decomposition of Deadwood Across Tree Species and Forests

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## ABSTRACT

Natural forests contain a large amount of deadwood, which is a key contributor to biodiversity, especially by providing dynamic habitats and resources for a huge variety of invertebrates. However, for managing forest biodiversity we need to better understand what drives the dynamics of invertebrate communities in deadwood. We hypothesized that the invertebrate communities in logs will converge from initial to middle decomposition stage among tree species and forest stands as the differentiating role of bark diminishes and xylem traits converge during decay. We investigated invertebrate communities in decomposing logs of ten tree species over 4 years in the “tree cemetery” LOGLIFE experiment in two contrasting

forests in the Netherlands. The predominant faunal groups studied were Annelida (earthworms), Isopoda (woodlice), Chilopoda (centipedes), Diplopoda (millipedes), Diptera (flies, midges) and Coleoptera (beetles). We demonstrated that (1) tree species, decay stages and incubation forests all had effects on the invertebrate communities; (2) community compositions of fauna in logs first were very dissimilar and then became more similar among tree species through the decay years; and (3) this converging pattern of faunal community dynamics also manifested itself, both across and within given tree species, between two contrasting forests over decomposition time. Thus, invertebrate communities generally converged during deadwood decay, which adds fundamental insights into the role of interacting drivers of community succession. These findings also highlight that, both within and among forests, more functionally different tree species and logs in different decay stages, will support relatively high biodiversity of invertebrate communities; these patterns may inform forest management strategies aimed at maximizing biodiversity.

**Key words:** Deadwood; Decomposition; Invertebrate; Macro-detritivore; Tree species; Trunk.

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## HIGHLIGHTS

- Decaying logs of diverse tree species together support rich invertebrate fauna.
- Fauna communities are very dissimilar in initial decay logs among tree species and forests.
- They converge in composition among tree species and forests over four years.

## INTRODUCTION

A good understanding of community succession is one of the foundations in ecology, necessary for predicting changes in biodiversity and ecosystem functions across time and space (Fukami and others 2010; Chang and Turner 2019). Whether stochastic or deterministic processes influence community assembly over succession is controversial (Samuels and Drake 1997; Chase 2003; Dini-Andreote and others 2015). The distinction between the two processes will help our ability to predict biodiversity changes in response to environmental changes. The view about stochasticity in succession is that community structure is historically contingent, with key roles for stochastic dispersal and colonization which cause community structure to diverge (Chase 2003; Kreyling and others 2011). However, divergence in community composition occurs because of several mechanisms, environmental heterogeneity arguably being the most important factor (Tews and others 2004; Caruso and others 2012; Stein and others 2014). The deterministic view holds that succession is largely determined by abiotic environmental filters early in succession (Douma and others 2012) while biotic interactions (for example, competition and facilitation) become more important as succession progresses (Connell and Slatyer 1977; Callaway and Walker 1997; Chang and HilleRisLambers 2016). In contrast to the stochastic perspective, under the deterministic perspective successional changes are directional and dissimilarities in abiotic and biotic selective pressures among patches decrease over time, making community compositions converge in terms of identities, absolute and relative abundances of constituent species (Grover and Lawton 1994; Samuels and Drake 1997; Anderson 2007; Bittleston and others 2016). Convergence has mostly been tested in plant communities (Houseman and others 2008; Fukami and others 2005; Li and others 2016), but also in, for instance, microbial communities (Castle and others 2016), intertidal oyster reefs (Walters and Coen 2006), marine

algae (Steneck 1986), fish communities of artificial reefs (Paxton and others 2018), and invertebrate communities (Watts and others 2008; Widenfalk and others 2015).

Although the forest soil detrital system is highly species rich, little is known about its concurrent invertebrate community dynamics, despite the importance of invertebrates in detrital system dynamics. Even less is known about the colonization and community assembly by invertebrates associated with succession in deadwood. A special characteristic of (semi-)natural forests is that they tend to contain a large amount of dead trees, which are a key contributor to forest biodiversity and fulfil important ecosystem functions (Harmon and others 1986; Cornelissen and others 2012). The decomposition of deadwood substantially influences biogeochemical cycling (Cornwell and others 2009) and deadwood is an essential source of biodiversity (Harmon and others 1986; Jönsson and Jonsson 2007; Stokland and others 2012; Andringa and others 2019) by providing myriad microhabitats for breeding, feeding and sheltering of organisms (Rotheray and others 2001; Michel and others 2011; Stokland and others 2012; Seibold and others 2015). Logs get colonized by a vast array of invertebrate species once downed, but the extensive literature on deadwood invertebrates (Grove 2002; Castro and Wise 2010; Déchéne and Buddle 2010; Ulyshen and others 2011) has still left important questions unanswered about the drivers of community assembly of fauna that inhabit dead trees. Experimental studies that quantified how, and how much, different factors determine the deadwood-related invertebrate community effects are rare, although successional patterns of some invertebrate groups in deadwood of certain tree species have been studied. For example, saproxylic beetle communities differ among decay classes in loblolly pine (Ulyshen and Hanula 2010) and white spruce (Lee and others 2014); beetle communities are determined by species and stage of decay of wood in a tropical deciduous forest (Muñoz-López and others 2016); Diptera (midge and fly) communities change in dead beech wood decomposition (Hövmeyer and Schauer mann 2003); and Zuo and others (2014) found that tree species, woody debris decay stage and environment all influence and interact on deadwood-dwelling invertebrate communities. Although within a given area, both abiotic and biotic factors have been reported to drive community succession in general, as reported above, we argue here that invertebrate succession in deadwood is fundamentally different in that it is driven principally by biotic afterlife drivers

throughout, particularly because environmental filtering acts importantly via variation in bark traits.

Logs provide a dynamic habitat caused by gradual substrate disintegration and decomposition by microbial and invertebrate decomposers. The changes in habitat quality, determined by the changing log properties during decomposition (Graham 1925; Swift 1977; Lachat and others 2013), in turn can cause community succession of the associated organisms. Within species, deadwood decay time and decay stage are important drivers shaping the invertebrate communities during decomposition (González and others 2003; Berg and others 1998; Zuo and others 2014; Fujii and Takeda 2017; Kamczyc and others 2019). Across tree species, bark traits that provide protection to living trees have afterlife effects on the decomposer community (Hagge and others 2019). Initially, bark trait differences among tree species will lead to high dissimilarity of invertebrate communities (Zuo and others 2016a). The quality and strength of this bark filter will change as decay progresses, and microbes (especially fungi) and invertebrates will interact more strongly with each other (Smith and others 2011; Zuo and others 2016b; Novais and others 2017), making community assembly in logs more complex. The resource availability in the relatively nutritious inner bark should diminish over time, which may result in fewer available niches and probably increased competition among bark-inhabiting species. Moreover, bark traits may affect fauna composition indirectly by changing the composition of prey species to predators. As decay progresses and bark may have disintegrated or fallen off, wood is increasingly colonized by invertebrates; therefore, the importance of wood traits for invertebrate community composition may increase. Convergence of wood traits may lead to community convergence between tree species as log decay progresses (Zuo and others 2014).

The objective of this study was to document the succession of invertebrate communities in deadwood of different tree species at several time intervals from tree death (for example, due to logging). Starting with different “species pools” of invertebrates in environmentally contrasting forests, the community composition of invertebrates in logs should first be dissimilar among tree species within forests and then become more similar both among tree species and between forests as the differentiating role of bark traits (see Zuo and others 2016a) diminishes and wood traits converge during decay (Figure 1). Thus, we hypothesize that: (1) the invertebrate communities should first be dissimilar because the afterlife effect of bark traits

constitutes a major environmental filter, and then become more similar as most bark has fallen off or decayed whereas wood traits converge during decay. (2) The invertebrate communities in logs should first be dissimilar between contrasting forests as they start with different “species pools” of invertebrates, and then become more similar as the log traits converge during decay. To test these hypotheses, we investigated invertebrate communities colonizing the logs of ten temperate tree species in two contrasting forest environments in the same region over four years of decay through early- and mid-successional stages. Understanding the successional mechanisms of deadwood invertebrate communities will advance our conceptual understanding of community assembly and inform management decisions to promote forest invertebrate diversity.

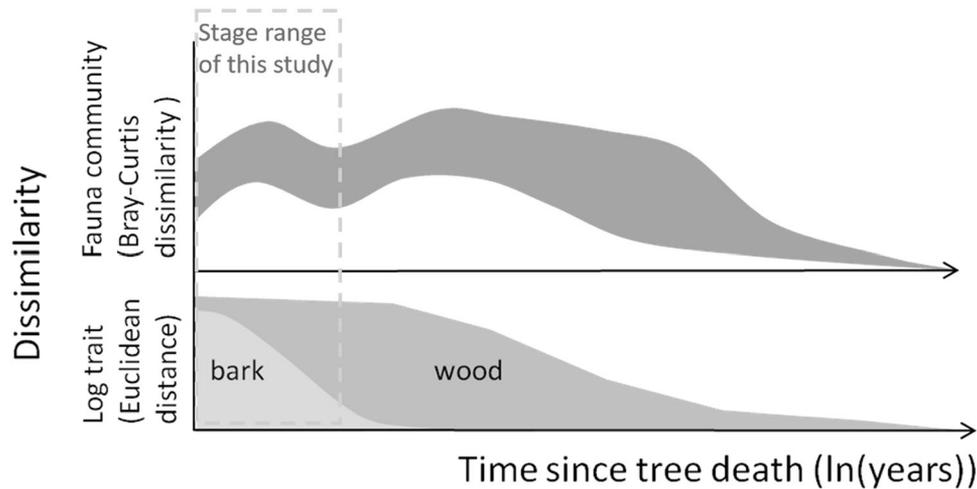
## MATERIALS AND METHODS

### Study Area

This study was part of the LOGLIFE experiment (details in Cornelissen and others 2012). The two environmentally contrasting sites in the central Netherlands represent two predominant temperate forest types and soils in NW Europe: (1) a forest plantation in Flevoland on fertile soil (hereafter site F) (52.46 N, 5.42 E) and (2) the forest estate Schovenhorst in the Veluwe region on infertile soil (hereafter site S) (52.25 N, 5.63 E). Site F was reclaimed from the former Zuiderzee (a bay of the North Sea) in the 1960s, that is, drained to become new land. This relatively young soil consists of marine clay and is calcareous, moist and fertile, with a  $\text{pH}_{\text{H}_2\text{O}}$  close to neutrality. This site mainly consists of monospecific plantations of different tree species used for commercial forestry. In contrast, site S has a sandy and podzolic soil that is well drained. The soil is acidic and has a lower fertility.

### Reciprocal Incubation of Logs

Six tree species were sampled in each forest, with two species overlapping between both forests, adding up to ten species (six broad-leaved and four coniferous species (Table S1)) that were used in this common garden decomposition experiment. Tree species (with abbreviation) *Quercus robur* L. (QRO) and *Picea abies* (L.) Karst. (PAB) were sampled from both sites to compare the indirect (afterlife) effects of growing conditions via intraspecific variability in deadwood traits. The other four tree species collected at site F were *Betula pendula* Roth (BET), *Fraxinus excelsior* L. (FEX), *Populus x canadensis*



**Figure 1.** Hypothetical dissimilarity trend of invertebrate community composition (upper panel) in the same batch of logs of tree species (lower panel) through the log decomposition trajectory. During early decay, the fauna community dissimilarity (upper dark grey area) is high due to a strong effect of bark trait filtering (bottom grey area), while wood has not been colonized yet. The dissimilarity in fauna community composition will first increase due to colonization of the bark and then decrease with a diminishing bark cover and with an increase in bark trait similarity between species due to decomposition. As decay proceeds, wood colonization by specialist wood-boring arthropods will commence. Wood traits will strongly filter the community composition leading to an increase in community dissimilarity, because of a colonization event. A long phase of continuous species turnover takes place, in which the competitive exclusion filter might gain strength. The broad range in community dissimilarity is because tree species will not only vary in wood traits at given decay stage, but will also differ in decay stage owing to differences in decomposition rate, which adds to trait dissimilarity even if trees have the same initial traits. Towards very advanced wood decay stages, wood traits will converge and the dissimilarity in invertebrate composition will decrease accordingly.

(POP) and *Fagus sylvatica* L. (FSY). The other four tree species extracted at site S were *Larix kaempferi* (Lamb.) Carr. (LKA), *Pseudotsuga menziesii* (Mirb.) Franco (PME), *Abies grandis* (AGR) and *Populus tremula* L. (PTR). All these species are important and representative for NW European forests or forestry plantations.

Between mid-January and mid-February 2012, ten healthy trees of each species with a trunk diameter of approximately 25 cm at mid-height were cut. In total 120 trees were extracted from the two forest sites. Each individual tree trunk was chain-sawed into five similar sections (hereafter logs), each of 1 m length and  $25 \pm 3$  cm diameter, and without major side branches, often leaving out the bottom and top part of the trunk. The logs were transported to incubation plots in each of the two extraction forest areas, minimizing any damage to the bark. Five individual trees (replicates), each divided into the five logs (subsamples), were placed in each of five incubation plots in site F and the other five trees in each of five incubation plots in site S, that is, each tree individual was placed in a separate plot (statistical block) (Cornelissen and others 2012). The replicate plots each measured 12 by 12 m with minimum distances of 20 m. Logs

and big branches naturally present in the incubation plots were removed before log placement. At site S, each incubation plot had a 1.2 m high fence around it to keep out wild boar that is abundant in this Veluwe area. Thus, in total 600 logs (6 tree species  $\times$  2 extraction forests  $\times$  2 incubation forest sites  $\times$  5 retrieval times  $\times$  5 replicates) were placed in their respective incubation plots. Within each replicate plot, the tree species were randomized spatially. The five logs of each individual tree were positioned approximately 30 cm apart. Distances between logs of different species were at least 40 cm.

The incubation plots were in each of the larger extraction forests described above. The plots at site F are in a *Populus x canadensis* Moench stand with a discontinuous canopy, and a sumptuous herb layer dominated by the nitrophilic herbs *Urtica dioica* L. and *Galium aparine* L.. The plots at site S are in a *Larix kaempferi* (Lambert) Carriere stand with also a relatively open canopy and relatively high irradiance in the understory. It has a low and dense ground layer of predominantly the acidophilic grass *Deschampsia flexuosa* (L.) Trin. intermingled with mosses and patches of the dwarf shrub *Vaccinium myrtillus* L. and tree seedlings. Microclimate varied

between the two sites, normalized soil moisture content was on average higher in site F, air temperature did not differ much between two sites and the relative humidity was on average higher in site F (de Beaumont 2015).

## Log Retrieval and Animal Extraction

In February of the years 2013, 2014 and 2016, one random log out of five in each replicate incubation plot was sawn into two halves of 50 cm length. One half was removed and sampled for wood density and fungal infection. The remaining half of 50 cm length was carefully laid back in its original position. Around 20 April of each of these years, that is, after presumably leaving sufficient time for the invertebrate community to recover from any sawing disturbance, and to become active with the increasing temperatures in spring, these logs were sealed individually into plastic bags and carefully transported to the laboratory at Vrije Universiteit Amsterdam for animal extractions. Animals on the outside of the logs that were considered not to be in intimate contact with them were removed beforehand. All logs were stored at 4 °C and aired weekly until processing. The logs were randomly selected and processed within two months, by which time the animals in the logs were generally still alive. At the 2013 retrieval, based on observations of bark properties and invertebrates in the field, we concluded that virtually no or very few animals could have been present in logs of most tree species except *Picea* and *Populus*, thus only one log of the other tree species was retrieved for analysis. Animals only colonized bark in the first year, so the wood was not sampled then. At the 2014 and 2016 retrieval, one log per replicate tree was collected per retrieval (6 tree species × 2 extraction forests × 2 incubation forest sites × 5 replicate plots × 2 retrieval times). In 2014, animals were collected mostly from bark with a small portion from wood. In 2016, animals that had been collected from mosses attached to the logs, bark and wood were summed up for each log. In total, 289 logs were included in the analysis. Information about the number of logs and related issues is shown in Table S2.

During sampling, each log was put in a large tray with tall enough edges for the animals not to crawl out. To collect the invertebrates, all attached bark was removed from the log. All invertebrates (larvae and adults) in and under the bark of every log were collected with forceps and pooters while the bark was being peeled off, fragmented and subsequently systematically searched. Animals were transferred

to vials with 70% ethanol for identification and counting, which were done using identification keys. Diplopoda (millipedes) and Isopoda (woodlice) are saprophagous and key regulators of decomposition; therefore, these clades were identified to species level. Additionally, Coleoptera (adult beetles and their larvae) were identified to species level because (1) they are partly also important to decomposition; (2) they tend to have particularly high diversity in deadwood and tend to include many sensitive taxa with high conservation value according to a large body of literature (for example, Grove 2002; Seibold and others 2016; Hardersen and Zapponi 2018; Ulyshen 2018). The dataset used for this analysis also included beetle species that could not be identified to species level but could be consistently recognized as separate morpho-species. However, many beetle larvae were found and as larvae could often only be identified to family level the species-level analyses are likely to be less accurate than those for the Diplopoda and Isopoda. The three other selected taxa were identified to family level: Annelida (earthworms), Chilopoda (centipedes) and Diptera (flies and midges). The few individuals that could be identified as belonging to one of these clades but not to family level we recorded as unknown. With the exception of Chilopoda, which are predators of other invertebrates, these taxa can feed directly on inner bark, its residues or on microbes that grow in logs, that is, they are directly or indirectly involved in decomposition.

## Statistics

To test the effect of collection forest on the fauna community, we compared the logs of *P. abies* and *Q. robur*, which had been extracted from both sites, by using permutational multivariate analysis of variance (PERMANOVA) on Bray–Curtis dissimilarity. Because the tree collection forest site affected the faunal community composition much less than incubation forest site and retrieval year (Table S3), we grouped the logs that had been extracted from the two different forest sites for *P. abies* and for *Q. robur*.

To test the effects of tree species, retrieval year and incubation forest site on fauna communities in logs, permutational multivariate analysis of variance (PERMANOVA) on Bray–Curtis dissimilarity was used. To test how the fauna community composition differed among tree species, and between the two forests sites during decay, a non-metric multidimensional scaling (NMDS) was used where

the Bray–Curtis method was chosen for the distance calculations.

To test the trends of dissimilarity pattern of the logs among tree species during decay, Bray–Curtis dissimilarity index (Appendix S1) was calculated for each possible pair of logs between two tree species in each year. The values for each combination would result in a list of dissimilarity indices for all the combinations of two tree species in each year. The overall dissimilarity indices for each retrieval year separately were calculated, after which Friedman test was used to test the effect of retrieval year, and then the pairwise Wilcoxon rank sum test was used to compare the difference among years with Bonferroni adjustment method of P-values. To test if the tendency was the same within each of the two sites and at the larger regional scale, the calculation and comparison were done not only for site F and S separately, but also for the two sites combined. The mean values of tree species from five blocks were used.

Different patterns were expected to occur at different taxonomic scales (Berg and Bengtsson 2007); therefore, all the above analyses about community composition were done at three levels of taxonomic resolution: (1) at the level of the six major clades (Annelida, Chilopoda, Coleoptera, Diplopoda, Diptera, Isopoda), (2) at that of the families of macroinvertebrates and (3) species within Isopoda and Diplopoda (macro-detritivore species) and within Coleoptera (see above). For dissimilarity analyses of invertebrates at detritivore species level (Isopoda and Diplopoda), when two logs contained only zero values, the index could not make a reliable comparison. For this reason, one individual of the isopod species *Trichoniscus pusillus* was added to those logs for calculations. This small species generally had a high abundance so adding one individual did not really affect the results but resulted in a valid test without errors.

Statistical analyses were performed in R language version 3.5.0 (R Core Team 2018). The faunal community dissimilarity matrix was calculated using the `vegdist` function, from the `vegan` package in R (Oksanen and others 2013).

## RESULTS

### Invertebrate Colonization

In total, we sampled more than 3900 Annelida, 3100 Chilopoda, 14,200 Coleoptera, 2400 Diplopoda, 5700 Diptera and 5700 Isopoda individuals. The abundances for each major clade in each sample year are shown in Table S2. The total

abundance and abundances of each major clade that were sampled from the logs of each tree species are shown in Figure S1 and Figure S2. Tree species, decay years and incubation forests all had significant effects on the invertebrate community composition (Table 1).

### Fauna Community Among Tree Species During Log Decay

The total abundance of invertebrate individuals in the logs differed significantly among tree species (Figure S1). There was particularly high fauna abundance in logs of *Picea abies* and *Populus tremula* after one year of decay in both forests. The abundance of fauna changed significantly during the four years of decomposition within each major taxon. The total abundance of Coleoptera was much higher after one year of decay, because of the high abundance of bark beetles (known to be early colonisers of deadwood). The abundances of Chilopoda, Diplopoda and Isopoda were much higher after four years of decay (Table S2).

The invertebrate community compositions in the logs differed significantly through decay years for all three taxonomic levels (Table 1). The fauna community composition initially differed across tree species but community composition converged over four years of decay (Figure 2). The Bray–Curtis dissimilarity values decreased significantly from year 1 to year 4 across tree species both within the F and within the S site (Table 2).

### Fauna Diversity Between Forest Sites During Decay

The invertebrate community compositions in the logs differed among the two forests (Table 1, Figure 2). For the same tree species (with equal origin) that had been incubated in the two forests, the fauna communities in the logs were very different after one year both for the abundance (Figure S1) and community composition (Figure 2, Figure S4). However, the community compositions in the logs that had decayed in the two contrasting forests became similar (as indicated by the overall absolute distances between data points) as decomposition progressed in year 2 and especially in year 4 (Figure 2, Figure S4). The Bray–Curtis dissimilarity values also decreased significantly from year 1 to year 4 across tree species across the two sites (Table 2). For each tree species, there was a similar trend of community convergence over four years of decay with the community distance decreasing in year 4 (Figure S3).

**Table 1.** Main Results from Permutational Multivariate Analysis of Variance (PERMANOVA) on Bray-Curtis Distances for Invertebrate Community Composition in Logs of Different Tree Species, Retrieval Years and Incubation Forest sites

	Df	SS	MS	F	Pr (> F)
<i>(a) Major clades level</i>					
Tree species (TS)	9	10.65	1.18	7.67	0.001***
Retrieval year (RY)	1	6.61	6.61	42.83	0.001***
Incubation forest site (IS)	1	3.85	3.85	24.96	0.001***
TS × RY	9	6.72	0.75	4.84	0.001***
TS × IS	9	2.84	0.32	2.04	0.001***
RY × IS	1	0.49	0.49	3.15	0.007**
TS × RY × IS	9	2.61	0.29	1.88	0.001***
Residuals	249	38.41	0.15		
Total	288	72.17			
<i>(b) Family level</i>					
Tree species (TS)	9	9.37	1.04	4.69	0.001***
Retrieval year (RY)	1	6.17	6.17	27.80	0.001***
Incubation forest site (IS)	1	11.93	11.93	53.73	0.001***
TS × RY	9	6.86	0.76	3.43	0.001***
TS × IS	9	4.70	0.52	2.35	0.001***
RY × IS	1	2.86	2.86	12.86	0.001***
TS × RY × IS	9	3.62	0.40	1.81	0.001***
Residuals	249	55.29	0.22		
Total	288	100.81			
<i>(c) Detritivore species level</i>					
Tree species (TS)	9	5.36	0.60	2.38	0.001***
Retrieval year (RY)	1	6.79	6.79	27.13	0.001***
Incubation forest site (IS)	1	18.03	18.02	72.05	0.001***
TS × RY	9	4.55	0.51	2.02	0.001***
TS × IS	9	4.93	0.55	2.19	0.001***
RY × IS	1	3.43	3.43	13.73	0.001***
TS × RY × IS	9	3.57	0.40	1.59	0.001***
Residuals	249	62.29	0.25		
Total	288	108.95			

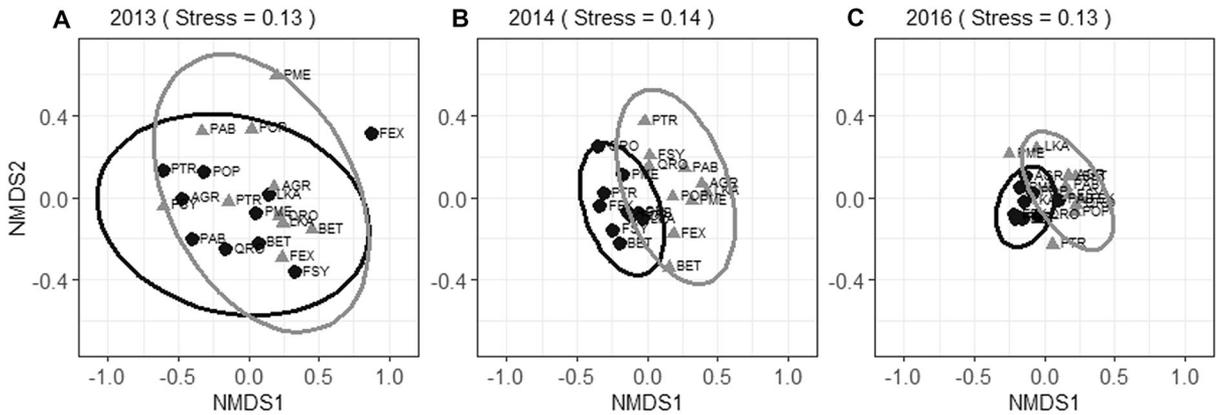
Analyses were done for (a) major clade level, (b) family level, (c) detritivore species level.

The overall dissimilarity pattern among tree species first showed an increase up to year 1, because we assumed it was 0 at the beginning as there was virtually no fauna. After logs had been colonized in the first year, there was a more or less steady decrease in dissimilarity (that is, convergence) after two and four years of decay (Table 2). The trend was similar for both forest sites (that is, within F site or within S site) at three levels of taxonomic resolution (that is, major clade, family level and species level, Figure 2, Table 2). When the two forests were combined (that is, across the two sites), the overall pattern of dissimilarity showed the same pattern of first increase and then decrease (Table 2) if we assumed it was 0 at the beginning.

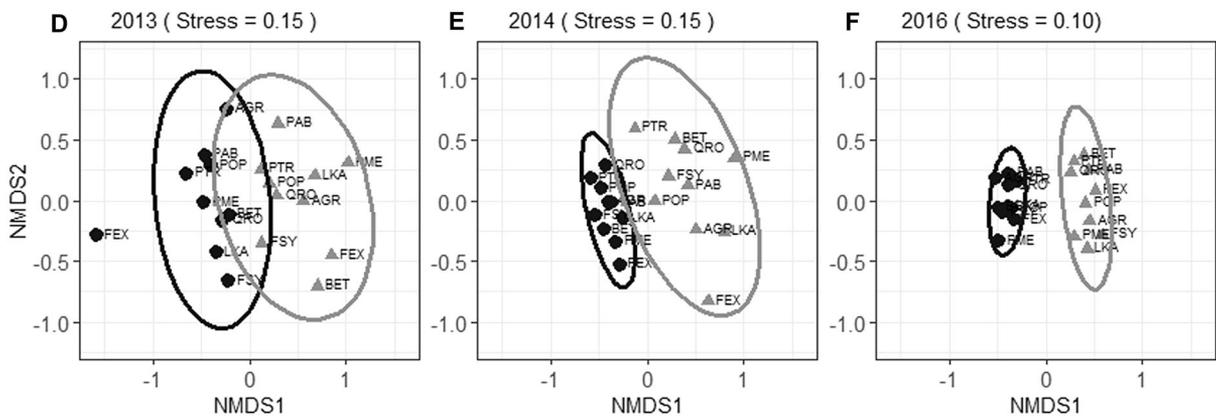
## DISCUSSION

We asked in this study how macroinvertebrate community composition in decomposing logs changes over a period of four years across tree species as well as within and across forest types. It adds a new dimension to current concepts of succession, as biotic afterlife factors drive invertebrate succession in deadwood both in environmental filtering and in species interactions. Our LOGLIFE “tree cemetery” experiment revealed that invertebrate community composition initially diverged and then progressively converged as bark and wood decomposition progressed. Similar patterns of divergence followed by convergence were observed at three levels of taxonomic resolution (that is, major clades level, family level and species level of macroinvertebrates) and at different hierarchical spatial scales (that is, among tree species within site

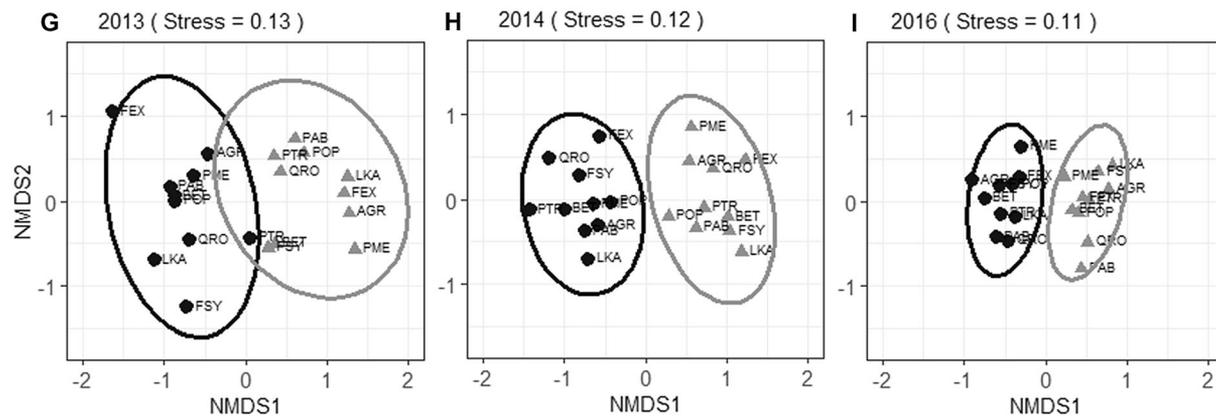
Major clade level



Family level



Detritivore species level



**Figure 2.** Non-metric MDS plots of fauna communities in logs during the decomposition years (indicated above the panels) at F site (black) and S site (grey). **A–C** at major clade level, **D–F** at family level, **G–I** at detritivore species level. The mean values per tree species in each site are based on 5 replicate logs. Points are the tree species with abbreviations, the full names are shown in Table S1.

and between contrasting forest sites). For practical reasons, some faunal groups could not be identified to species level and were therefore not analysed at this level here. However, based on the findings for

Diplopoda, Isopoda and the preliminary findings for Coleoptera, our results suggest a general community assembly trajectory of increasing convergence in coarse woody debris over time also at

**Table 2.** The Bray–Curtis Dissimilarity Values (mean  $\pm$  SE) of Funa Community in Logs Among Tree Species for (a) Major Clade Level, (b) Family Level, (c) Detritivore Species Level

	BC dissimilarity			Friedman test	
	2013	2014	2016	chi-sq	P
<i>(a) Major clades level</i>					
Within F site	0.73 $\pm$ 0.03a	0.49 $\pm$ 0.02b	0.35 $\pm$ 0.03c	28.9	< 0.001***
Within S site	0.76 $\pm$ 0.03a	0.62 $\pm$ 0.03b	0.37 $\pm$ 0.02c	48.9	< 0.001***
Across two sites	0.73 $\pm$ 0.01a	0.60 $\pm$ 0.01b	0.40 $\pm$ 0.01c	148.8	< 0.001***
<i>(b) Family level</i>					
Within F site	0.83 $\pm$ 0.02a	0.58 $\pm$ 0.02b	0.42 $\pm$ 0.02c	55.6	< 0.001***
Within S site	0.83 $\pm$ 0.02a	0.71 $\pm$ 0.02b	0.44 $\pm$ 0.02c	56.8	< 0.001***
Across two sites	0.86 $\pm$ 0.01a	0.72 $\pm$ 0.01b	0.61 $\pm$ 0.01c	186.0	< 0.001***
<i>(c) Detritivore species level</i>					
Within F site	0.66 $\pm$ 0.03a	0.54 $\pm$ 0.02b	0.51 $\pm$ 0.03b	15.5	< 0.001***
Within S site	0.68 $\pm$ 0.03a	0.57 $\pm$ 0.03b	0.46 $\pm$ 0.03b	18.3	< 0.001***
Across two sites	0.77 $\pm$ 0.01a	0.72 $\pm$ 0.01ab	0.68 $\pm$ 0.02b	21.5	< 0.001***

Analyses were done within the Flevoland (F) site only, within the Schovenhorst (S) site only, and across these two incubation forest sites. The BC dissimilarity values show the trends of fauna community dissimilarities among tree species during decomposition. Friedman test results show the differences of dissimilarities among the retrieval years for each site (within F site and within S site) and across two sites (chi-sq, Friedman Chi-squared. \*\*\* $P < 0.001$ ). Different letters indicate significant difference ( $P < 0.05$ ) of pairwise Wilcoxon rank sum tests.

species level. We discuss these key findings, about the community dynamics of invertebrates associated with deadwood succession in forests, in more detail below.

### Dynamics of Fauna Diversity Associated with Logs

Our first hypothesis was that the invertebrate communities in deadwood would converge among tree species from the initial to the middle stage of decomposition. Interspecific differences in bark traits and the log conditions (for example, moisture regime, resource quantity and quality) would influence the accessibility and suitability of deadwood to macroinvertebrates, hence, macroinvertebrate community assembly. We indeed found that shortly after the tree stem had been cut and laid down as logs, a great diversity in fauna community composition developed in the different species in the first year, and then the composition tended to converge over time (both among species and between forest sites) (Figure 2). First, divergence in community composition at the start might be caused by interspecific difference in the fresh log features and traits, initial decay providing a variety of different microhabitats, microclimates in and below bark types, and resources, including nutrients and sugars in fresh or degrading phloem and cambium. Tree species vary greatly in a range of functional traits (Freschet and others 2012; Dossa and others 2018; Zuo and others 2018), which have important afterlife effects on the decomposition of

their woody debris as well as on the community composition of the associated organisms. Initial species divergence is likely caused by the inter-specific dissimilarity in bark traits, such as bark thickness and secondary chemistry (for example, wide-ranging differences in composition and amounts of terpenes and terpenoids, phenolic compounds, suberins), which may deter or attract specific invertebrate taxa (Zuo and others 2016a). For instance, in the early stage of bark colonization wood-boring arthropods, especially bark beetles (Scolytinae), are very species-specific in their host preference (Rudinsky 1962; Zuo and others 2016b) and this is likely related to the bark secondary chemistry. This deterministic initial filtering by bark traits may be extended to intraspecific variation in bark traits, which might partly explain the substantial intraspecific variation we found in initial community assembly. However, at this level also stochasticity related to priority effects (“first come, first colonize”; see Introduction) may play a role; in-depth research involving assessment of bark trait variation both between and within tree species would be needed to distinguish between these two processes.

As the logs gradually decompose, the observed gradual convergence of macroinvertebrate community composition over time occurs for a variety of reasons. First, bark degrades and becomes loose (or even falls off) and can no longer provide habitat and resources for bark beetles and other invertebrates. Second, more similar micro-environments

may develop in the space between bark and the xylem of different tree species due to degradation of the bark and, thereby, lead to convergence of bark traits with decay. Third, an invertebrate community gradually develops inside the decaying xylem, and structural and chemical xylem traits may converge over time (Zuo and others 2014) as complex large-chain secondary compounds gradually are broken down into smaller, more similar molecules as decomposition progresses. All these and perhaps further factors may explain the convergence of the fauna communities among logs among tree species as the logs decompose over 4 years of incubation.

Similar patterns have been found for some invertebrate groups in deadwood of certain tree species. For example, for saproxylic beetles the species richness peaked within the first year as a diverse assemblage in logs of loblolly pine (Ulyshen and Hanula 2010). Although abundance and diversity pattern may vary, for example, Hammond and others (2001) found beetle abundance in *Populus* wood was higher in the first year and the diversity was higher in the second year, suggesting that early species may “precondition” the wood for some succeeding species, as was also found after bark beetle colonization (Zuo and others 2016b). In our study, even though not all beetles could be named to actual species and instead morpho-species were identified, we included the preliminary species-level analysis anyway because of the special status of beetles in forest diversity and conservation (see above and Grove 2002; Seibold and others 2016; Hardersen and Zapponi 2018). Also for beetles we found a similar trend of convergence in composition over decay time. Together, these findings add to the general knowledge that logs provide a dynamic habitat, which change the biotic and abiotic characteristics of this microhabitat drastically (Lachat and others 2013). These changes lead to strong dynamics in the community composition of associated organisms (Fukami and Nakajima 2011), including invertebrate fauna (Seibold and Thorn 2018).

### Fauna Community in Logs Across Forests

Our second hypothesis was that the communities would converge in composition between contrasting forest sites during the log decomposition. We observed a difference in species composition in logs of the same tree species that were incubated in the two contrasting forest environments. The invertebrates that colonize the logs come from the local forest “species pool”. For winged beetles and

dipterans (for example, wood-associated flies and midges) the spatial dimensions of this species pool are likely to be larger than a single forest site, while for the more dispersal-limited wingless invertebrates (that is, woodlice, millipedes, centipedes, earthworms) species are restricted in their movement to their site (Berg and others 2010). We expect the two local invertebrate species pools of the two study sites to be dissimilar (as confirmed for wingless taxa by our unpublished results from a pitfall study in the two sites) because of the significant variation in soil properties, that is, sand vs clay, and, related to this in soil moisture regimes, as well as in local and adjacent tree species composition, all of which are known to determine soil fauna community composition (Fromm and others 1993; Giller 1996; Dias and others 2013; Korbolewsky and others 2016). Besides, tree species composition, age and tree density can also affect the invertebrate assembly in logs by affecting the forest environment. For example, canopy cover above logs and associated stand temperature regime can act as habitat filters for saproxylic beetle species assemblages (Gossner and others 2016). Hence, logs of the same tree species, when exposed to different species pools will select for a dissimilar subset of species in a dry and less fertile forest compared to a moist, fertile site. Only a subset of generalist species will be present in both sites. The ranges of dissimilarity in community composition over tree species were generally wider for the drier, less fertile site S than for the moister, fertile site F (Figure 2). However, the convergence patterns in community composition over time were remarkably similar for all three taxonomic fauna levels among species in both sites. This may indicate that the invertebrates associated with logs have similar dynamics at regional scale. Together, these results indicate that the fauna communities associated with deadwood will differ between environmentally contrasting forests, but that they all converge in composition as the logs get progressively decomposed.

### Conclusion and Outlook

This study has shown important general trajectories of invertebrate community assembly on coarse woody debris, with key role for deterministic afterlife effects of deadwood properties on invertebrate community composition. These results indicate that community convergence is a strong contributor to biodiversity dynamics in detrital systems. Some of these forest surface-dwelling invertebrates are also important decomposers

(Ulyshen 2016), and also have effect on other organisms, for example, the saprotrophic fungal community (Jacobsen and others 2018). The dynamics of invertebrates could potentially have large consequences for decomposition rate and biogeochemical cycling both directly and indirectly (Ulyshen and others 2016). It is possible that the low (that is, family level) taxonomic resolution in several clades in this study has masked differences between communities in certain families for which differences at species level have remained undetected; in-depth analysis within these families at species level would be interesting for further research.

Although our findings confirm fauna community convergence in detrital system between the early and middle stage of decay, whether this convergence also extends into the latter stages of tree decomposition is also a priority area for further study (Figure 1). We expect that, with the progression of decay, wood traits will continue to become more important. With the progression of wood decay, invertebrate communities may eventually become more and more similar due to a decrease in wood trait dissimilarity. How fauna community dynamics will change over the next phase of wood decay will be important to complete our understanding of the role of woody debris for forest invertebrate diversity and ecosystem functioning. These dynamics should be high on the future research agenda because of the importance of deadwood for forest biodiversity, the global carbon budget and climate.

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