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Faunal community consequence of interspecific bark trait dissimilarity in early-stage decomposing logs

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Summary

1. Dead tree trunks have significant ecosystem functions related to biodiversity and biogeochemical cycles. When lying on the soil surface, they are colonized by an array of invertebrate fauna, but what determines their community composition is still unclear.

2. We apply community assembly theory to colonization of tree logs by invertebrates. During early decomposition, the attached bark is critically important as an environment filter for community assembly through habitat provision. Specifically, we hypothesized that the more dissimilar bark traits were between tree species, the more their faunal community compositions would differ.

3. We tested this hypothesis by investigating the effects of bark traits on the invertebrate communities in the early-decomposing logs of 11 common, temperate tree species placed in the 'common garden' experiment LOGLIFE. Bark traits included bark looseness, fissure index, outer bark thickness, ratio of inner to outer bark thickness, punch resistance, water storage capacity and bark pH. The predominant faunal groups studied were Annelida, Isopoda, Chilopoda, Diplopoda, Diptera and Coleoptera.

4. Our results showed (i) strong interspecific differences in bark traits, (ii) that bark traits related to environmental buffering had profound effects on the abundance of specific invertebrate groups, and (iii) the higher the overall bark trait dissimilarity between tree species, the more dissimilar these tree species were in faunal community composition, and the higher was the joint invertebrate family richness.

5. A suite of bark traits together has fundamental afterlife effects on invertebrate community assembly, strongly filtering the colonizing invertebrates in early-decomposing logs, driving variation in their community composition and diversity. Our findings indicate that bark trait dissimilarity among tree species in forest stands is likely a better indicator of early-phase dead trunk fauna diversity than tree species diversity *per se*.

Key-words: afterlife effect, assembly rules, biodiversity, cortisphere, dead wood, functional trait, invertebrate community, macro-detritivore, tree trunk

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Introduction

Dead tree trunks are a key contributor to forest biodiversity and important ecosystem functions (Harmon *et al.* 1986; Wijdeven, Moraal & Veerkamp 2010; Cornelissen *et al.* 2012). So far, most research in this field has focused on wood. The decomposition of tree logs substantially influence biogeochemical cycling (Cornwell *et al.* 2009a). Also, tree logs are an essential source of biodiversity (Harmon *et al.* 1986; Jönsson & Jonsson 2007; Stokland, Siitonen & Jonsson 2012) and provide a high diversity of microhabitats for breeding, feeding and sheltering of organisms (Rotheray *et al.* 2001; Michel, Winter & Linde 2011; Stokland, Siitonen & Jonsson 2012). In contrast to knowledge about causes and consequences of dead wood decomposition, little is known about variation in traits of decomposing bark and its effect on biogeochemistry and diversity.

A dead trunk is colonized by a vast array of species when it falls to the ground, but the extensive literature on dead wood invertebrates (Grove 2002; Castro & Wise 2010; Déchêne & Buddle 2010; Ulyshen, Pucci & Hanula 2011) has still left questions unanswered about how, and how much, different factors determine the community composition of log-related fauna. This is partly because most field sampling studies cannot disentangle the (interactive) effects of forest environment and log microenvironment, wood and bark traits of tree species, their decomposition stage, time of the year and the available pool of invertebrate species. Experimental studies that quantified these effects are rare (e.g. Abrahamsson *et al.* 2009), but Zuo *et al.* (2014) found that tree species, decay stage and environment all had influences and interactions on branch-dwelling invertebrate communities. The colonization and assembly of dead trunk invertebrates at a site may be understood from assembly theory (Díaz, Cabido & Casanoves 1998; Weiher, Clarke & Keddy 1998), which poses that the observed community at a site is determined by an environmental filter and a limiting similarity (competition) filter respectively. Newly fallen tree trunks constitute a site for colonizing fauna, thus the environmental filter that restricts the range of viable strategies (Cornwell & Ackerly 2009b) should be particularly strong at the early decomposition stage. The secondary phloem inside the outer bark is particularly important by providing resources and habitat to invertebrates. However, in living trees, structural and chemical defence traits, mainly in the outer bark, play a crucial role in protecting these nutrient-rich tissues against herbivores (Wainhouse, Cross & Howell 1990; Paine *et al.* 2010) and may have afterlife effects (Cornwell *et al.* 2009a) that may inhibit invertebrate access. Therefore, in the early (initial 1–2 years) decomposition stage, when the bark (cortisphere; Pfanz & Aschan 2001) is still attached to the wood, bark traits may be a crucial environmental filter for associated fauna assembly (Wu, Yu & Zhou 2008; Barbour *et al.* 2009; Zuo *et al.*

2014). At later decomposition stage, wood traits will become more important, partly because much of the bark will have fallen off and/or bark traits of different species become more similar due to degradation. Bark traits can also affect the species composition indirectly, by changing predator–prey interactions.

Bark structural and morphological traits vary greatly among tree species (Poorter *et al.* 2014; Rosell *et al.* 2014). However, besides anecdotal knowledge, there is little quantitative evidence on the ecological consequences of interspecific variation in bark traits for invertebrate community assembly in dead trunk. Here, we try to single out the bark trait effect of invertebrate communities *per se* by asking: how important is interspecific variation in bark traits for the invertebrate community assembly in logs at the early decomposition stage in a given forest environment? Specifically, we hypothesize that (i) bark traits of different tree species are a major driver of the abundance of key invertebrate taxa inhabiting early-decomposing dead trunks; (ii) at the community level, the more dissimilar bark traits are between tree species, the more the invertebrate faunal community composition will differ and the more invertebrate faunal richness can be supported by those tree species. This is because, if tree species differ more in bark traits, they should also differ in the environmental conditions (i.e. microclimate, shelter, food) that invertebrates are adapted to.

To test our hypotheses, we will first quantify the variation in selected bark traits among tree species, as consequences of the trade-offs and coordination among functions of the tree species (Rosell *et al.* 2014). Secondly, we will show how faunal groups are influenced by these bark traits. For instance, we predict bark looseness (access to resources and shelter for invertebrates), surface texture [fissure index; affects the buffering of climate variability under the bark (MacFarlane & Luo 2009)] and the ratio of inner bark (resource-rich secondary phloem that transports and stores photosynthates) to outer bark (protective layer, see below) (Stokland, Siitonen & Jonsson 2012; Poorter *et al.* 2014) to be positively correlated with invertebrate abundance. We also predict that the thickness and resistance to puncturing (i.e. toughness) of the outer bark (resource-poor layer protecting the cambium and phloem; Wainhouse, Cross & Howell 1990; Paine *et al.* 2010) are negatively correlated with invertebrate abundance. Bark water storage capacity and pH may also influence associated invertebrate communities directly or indirectly (e.g. by influencing fluxes of chemical compounds through water storage capacity, Levia & Herwitz 2005). To test our hypotheses and specific predictions, we incubated logs of 11 common, temperate tree species (10 angiosperms, one gymnosperm), in a common forest site in the LOGLIFE experiment (Cornelissen *et al.* 2012) for 15 months. We compared these tree species quantitatively for the above bark traits and for their effects on macro-invertebrate abundances and community compositions.

Materials and methods

STUDY AREA, TREE SPECIES AND LOGS

In January 2013, trees of 11 species, with a trunk diameter of ± 25 cm at mid-height, were extracted from monospecific forestry plantations in Hollandse Hout (52·46°N, 5·42°E), province of Flevoland, in the central part of the Netherlands. These species (with abbreviations, taxonomic family) were: *Acer pseudoplatanus* L.(ACE; Sapindaceae); *Alnus glutinosa* (L.) Gaertn. (AGL, Betulaceae); *Carpinus betulus* L. (CBE, Betulaceae); *Castanea sativa* Mill. (CSA, Fagaceae); *Fraxinus excelsior* L. (FEX, Oleaceae); *Pinus nigra* J.F.Arnold (PNI, Pinaceae); *Prunus avium* (L.) L. (PRA, Rosaceae); *Robinia pseudoacacia* L. (RPS, Fabaceae); *Salix alba* L. (SAL, Salicaceae); *Tilia cordata* Mill. (TIL, Malvaceae); *Ulmus × hollandica* Mill. (ULM, Ulmaceae). In total, 11 species × 5 individual trees per species were cut. Each tree was sawn into five 1-m long logs of 25 ± 2 cm in diameter, and each log was placed in one of the five LOGLIFE plots in a poplar (*Populus × canadensis*) plantation (for details of the full experimental design of LOGLIFE see Cornelissen *et al.* 2012). The soils in the Hollandse Hout, including the incubation site, have formed in marine clay and are calcareous, moist, fertile and pH 7-8 (details in Cornelissen *et al.* 2012). In February 2014, in each plot one randomly selected log of each tree species was sawn into two halves. One half was sampled for other analyses. The remaining half was carefully laid back in its original position. In April 2014, these remaining 50 cm logs were sampled, animals on the outside of the logs were removed, and the logs were sealed into plastic bags in order to retain all invertebrate fauna and carefully transported to the laboratory at Vrije Universiteit Amsterdam. There bark traits were measured and invertebrates were extracted from these logs. All logs were stored in a cold room at 3 °C until processing. The bags were opened briefly once every 2 weeks to let fresh air in and logs were selected randomly and processed one by one within 2 months, by which time the animals in the logs were generally still alive.

BARK TRAITS

Seven bark traits that might act as crucial environmental filters for fauna communities were selected (see Introduction); we measured these bark traits for each harvested log (11 species × 5 replicates). Bark looseness, measured on the entire log, was defined as the % of bark surface area that could easily be dislodged by hand; to minimize sampling bias the same person assessed loose bark for all samples. Bark fissure index (BFI), which quantifies the complexity of the texture, was computed following MacFarlane & Luo 2009: $BFI = \sum_{i=1}^{n} yi$, where n = the number of fissures along the transect and y_i is the depth of the ith fissure. BFI uses the number and depth of bark fissures along the circumference at the middle part of the log. All log samples had the same diameter of 25 ± 2 cm, thus species with rough bark had a large index, while a species with smooth bark would have an index close to zero. The depths of ten random, but subsequent, fissures were measured using electronic callipers (to the nearest 0·01 mm). The total distance between the 10 fissures was measured in order to extrapolate to the entire circumference of the log. When a log had fewer than 10 fissures across, all fissures were measured. The ratio of inner to outer bark (RIOB) was calculated from the thickness of the inner and outer bark respectively; these tissues were mostly easily distinguished by difference in internal structure or colour. Four random subsamples along the circumference of the middle section of each log were measured. The middle section generally contained bark both at top and bottom (relative to soil surface), and had not been affected by sawing. The thickness of the inner and outer bark was measured by software (cellSens Entry 1·7) on pictures taken with a digital camera (Olympus SC30) through a microscope (magnification nine times). For thick bark, pictures were directly taken with a digital camera and the thickness was measured by electronic callipers (to the nearest μm). The bark of *Robinia pseudoacacia* was damaged and thickness of the inner bark could not be measured; for inner bark thickness of *R. pseudoacacia*, we took the average of four measurements on the inner bark on disks cut from the same tree collected adjacent to the original logs before incubation in the LOGLIFE project (Cornelissen *et al.* 2012). Punch resistance tests measure the maximum force required for a needle to penetrate bark. Measurements were made on bark pieces of 4 × 2 cm, both air dried (dried for 2 months) and water saturated (fully submerged for 72 h in ziplockbags containing water). Bark toughness may be different at the top and at the bottom of the log through variation in decomposition rate; for this reason, four subsamples were taken from both the top and the bottom. Thus, eight subsamples were taken from each log at 5 cm from the middle section along the circumference, and 5 cm from the top or the bottom. To measure punch resistance, a Mecmesin Ultra Test with AFG-1000N force gauge (Slinfold, West Sussex, UK) was used, with a stainless steel needle of 1 mm diameter. The acceleration was standardized to 150 mm per second for all samples. Maximum force was expressed per cross-section area of bark (specific force to punch, MN m^{-2}). Bark water storage capacity was measured before each punch resistance measurement as:

$$\frac{water - saturated\ weight - air - dried\ weight}{air - dried\ weight} \times 100\%$$

Bark pH of subsamples was measured following Cornelissen *et al.* (2011). From an air-dried bark sample along the circumference of the middle section of each log, fine bark powder was produced using a hand file and mixed with 1·2 mL demineralized water in a 2·5 mL Eppendorf tube (volume ratio 1:8). After 1 h of shaking at 250 rpm, the tubes were centrifuged for 5 min at 12000 *g* and the supernatant measured using a narrow (5 mm diameter) SenTix Mic electrode connected to an Inolab Level 2 pH meter (both: WTW, Weilheim, Germany).

We checked whether variation in bark traits could be attributed partly to the height of the bark along the original standing tree trunk, by comparing trait values among logs taken from different positions (see Fig. S1, Supporting information for details). There was no significant effect of original height of a log on the trunk for any of the bark traits (Fig. S1).

SAMPLING ANIMALS

For each log, after collecting the bark trait subsamples, all remaining bark was removed from the trunk, making sure no animals could escape. Macrofauna (body size broadly larger than 0·3 cm) on and in the bark were collected with forceps and pooters after the bark had been peeled off and fragmented to small pieces, and transferred to vials with 70% ethanol. We counted and identified invertebrates using identification keys. Diplopoda (millipedes) and Isopoda (woodlice) are saprophagous and key regulators of decomposition, therefore these clades were identified to species level. The four other selected fauna groups were identified to family level: Annelida (earthworms), Chilopoda (centipedes), Diptera (flies and midges) and Coleoptera (beetles) (see Table S1 for invertebrate list and abundance). Other invertebrate taxa were either too small-bodied for reliable and comprehensive collecting by hand, rare or were thought not to be directly associated with decomposing wood and were therefore not taken into the analysis: i.e. Acari, Arachnida, Collembola, Gastropoda, Hymenoptera, Opiliones, Symphyla.

STATISTICAL ANALYSIS

To test for differences in single bark traits among tree species, the nonparametric Kruskal–Wallis Test was used. For the traits that were measured from subsamples from one log (e.g. punch resistance), we averaged traits first per log, and used the logs as replicates (11 species × 5 replicates). If the trees differed in trait values, then a nonparametric Dunn *post hoc* test for pairwise multiple comparisons of independent samples was applied to assess which species differed from each other, applying a Bonferroni-type adjustment of *P*-values using the *post hoc* Kruskal Dunn test function in R (Pohlert 2014). To test for differences in punch resistance between top and bottom position of bark on trunks, we used repeated measure ANOVA, with position (top or bottom) as within-subject factor and tree species as between-subject factor.

A Pearson's correlation was used to test the relationships between bark traits and the abundance of each fauna group across tree species, checking for normality using the Shapiro–Wilk test. Non-normal distribution data (abundance of Annelida, Coleoptera, Diptera and total abundance of all clades) were $\log_{10}(x + 1)$ transformed.

To compare bark traits and invertebrate community, we first used a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001), and analysis of similarity (ANOSIM) (Clarke 1993) to demonstrate that there were statistically significant differences in invertebrate community composition among tree species. Secondly, similarity percentage analysis (SIMPER) (Clarke 1993) was used to assess the contribution of each major clade to the observed dissimilarities between all possible pairs of tree species. Thirdly, non-metric multidimensional scaling (NMDS) was used to obtain a graphic presentation of the similarity of the invertebrate communities using the mean of five replicates for each tree species. Then, we performed a BIOENV analysis, for linking the invertebrate community patterns to bark trait variables. The invertebrate community similarity matrix was fixed, while subsets of the bark traits were used in the calculation of the trait distance matrix. A Spearman rank correlation coefficient was then calculated between the two matrices and the best subset of bark traits was identified (Clarke & Ainsworth 1993).

Bark trait dissimilarity, faunal community dissimilarity and joint family richness for each pair of two tree species were calculated across 11 tree species. Interspecific bark trait dissimilarity was calculated using the Euclidean distance (ED) (Appendix S1). It was calculated (following Walker, Kinzig & Langridge 1999; Heemsbergen *et al.* 2004) as a standardized and integrative distance between two species in a seven-dimensional bark trait space (Fig. 1). Punch resistance of water-saturated bark was excluded from analysis because it was strongly correlated with air-dry punch force ($r = 0.83$, $P = 0.001$; Fig. S2). Since the traits were
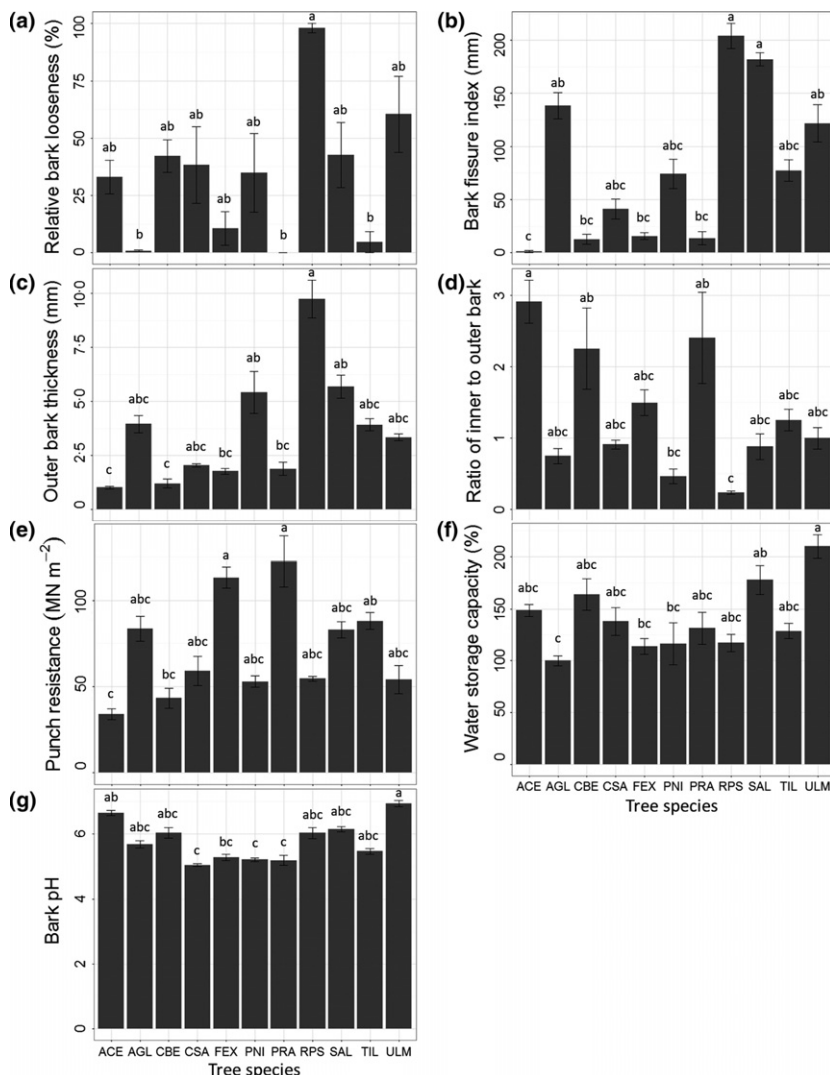

Fig. 1. Bark traits (Mean ± SE of 5 logs) of 11 temperate tree species. Traits differed significantly among tree species: (a) relative bark looseness ($H = 38.2$, $P < 0.001$), (b) bark fissure index ($H = 49.9$, $P < 0.001$), (c) outer bark thickness ($H = 48.7$, $P < 0.001$), (d) ratio of inner to outer bark ($H = 38.0$, $P < 0.001$), (e) air-dry bark punch resistance ($H = 42.8$, $P < 0.001$), (f) water storage capacity ($H = 33.8$, $P < 0.001$), (g) bark pH ($H = 46.9$, $P < 0.001$), d.f. = 10 for all. Tree species are arranged in alphabetical order. See Materials and methods for full names relating to species codes. Different letters indicate significant pairwise differences between tree species.

measured in different units, values were normalized between 0 and 1 values for each bark trait of all logs.

Faunal community composition dissimilarity between pairs of tree species was calculated using the Bray–Curtis dissimilarity index (BC) (Appendix S1). Different patterns were expected to occur at different taxonomic scales (Berg & Bengtsson 2007); therefore dissimilarity in community composition was calculated at three levels of taxonomic resolution: all six major clades, all 41 families of macro-invertebrates and 13 species within Isopoda and Diplopoda (see Table S1).

Family richness was calculated by counting the number of different families occurring in each pair of tree species across 11 tree species; overall family richness and macro-detritivore species richness were calculated separately.

We calculated the bark trait dissimilarity matrix and faunal community dissimilarity matrix using the vegdist function, PER-MANOVA using the adonis function, ANOSIM using the anosim function, SIMPER using simper function and BIOENV analysis using bioenv function from the vegan package in R (Oksanen *et al.* 2013). Mantel tests were used to compare two matrices (Legendre & Legendre 1998) using Spearman correlation. The relationships between bark trait dissimilarity and faunal community dissimilarity, and between bark trait dissimilarity and family richness were used as a direct test of our main hypotheses.

Statistical analyses were performed in R language version 3.0.3 (R Core Team, 2014).

Results

TREE BARK TRAITS

All measured bark traits differed significantly among tree species (Fig. 1). Outer bark thickness was positively related to relative looseness (Pearson correlation, $r = 0.61$, $P = 0.047$) and fissure index ($r = 0.88$, $P < 0.001$), and negatively to RIOB ($r = -0.78$, $P = 0.005$). Relative looseness was negatively related to bark punch resistance ($r = -0.63$, $P < 0.037$); BFI negatively to RIOB ($r = -0.77$, $P < 0.005$); bark water storage capacity positively to bark pH ($r = 0.71$, $P < 0.015$). Other pairwise correlations between bark traits were not significant.

Robinia pseudoacacia had almost 100% loose bark, the highest BFI (204 ± 12 mm, mean $\pm$ SE) and the thickest outer bark (9.7 ± 0.9 mm). *Alnus glutinosa*, *P. avium* and *T. cordata* had almost no loose bark. *Alnus glutinosa*, *S. alba* and *Ulmus × hollandica* had rough bark with BFI higher than 100 mm; *A. pseudoplatanus*, *C. betulus*, *F. excelsior* and *P. avium* had relatively smooth bark with BFI between 0 and 10 mm. *Acer pseudoplatanus* outer bark was the thinnest (1.0 ± 0.1 mm). Species with thick outer bark, e.g. *R. pseudoacacia*, had in general a small RIOB and *vice versa*, e.g. *A. pseudoplatanus*. *Ulmus × hollandica* had the highest water storage capacity and bark pH value. Bark punch resistances were greater for air-dry bark than for water-saturated bark, the difference being significant for all tree species except *R. pseudoacacia* (Fig. S2). There was no difference between bark taken from the top part or bottom of logs (Repeated measure ANOVA, $F_{1,44} = 0.95$, $P = 0.34$; Fig. S2). *Prunus avium* and *F. excelsior* had a high punch resistance (>100 MN m^{-2}), while *A. pseudoplatanus* had the lowest punch resistance.

RELATIONSHIPS BETWEEN BARK TRAITS AND FAUNA COMMUNITY

Invertebrate communities differed across tree species, as indicated by faunal clades having different abundances among tree species (Fig. S3). *Robinia pseudoacacia* had the most individuals per log (481 ± 92), followed by *P. nigra* (151 ± 25) and *C. betulus* (143 ± 39), *P. avium* and *T. cordata* had the fewest (22 ± 7, 22 ± 4 respectively) (Fig. S3). Moreover, some groups were relatively more abundant in certain tree species, e.g. Diptera in logs of *A. pseudoplatanus, C. betulus* and *R. pseudoacacia;* Isopoda in logs of *A. glutinosa* and *P. nigra*.

The abundance of each major clade was positively related to relative bark looseness, outer bark thickness and BFI, and negatively to RIOB and punch resistance (Table 1, Fig. S4). Among the positive effects, relative bark looseness was significantly related to abundance of Annelida (Pearson $r = 0.75$, $P = 0.008$), Diptera ($r = 0.78$, $P = 0.004$) and Coleoptera ($r = 0.82$, $P = 0.002$), outer bark thickness was significant for all fauna groups except

Table 1. Pearson's correlation coefficients (*r*, with *P*-values in parentheses) between the abundance of invertebrate clades and single bark traits across tree species ($N = 11$)

Phylum **Subphylum** class order	Annelida	Arthropoda Crustacea Malacostraca Isopoda	Arthropoda Myriapoda Chilopoda	Arthropoda Myriapoda Diplopoda	Arthropoda Hexapoda Insecta Diptera	Arthropoda Hexapoda Insecta Coleoptera	Total abundance
Relative looseness	**0·75 (0·008)**	0·23 (0·498)	0·41 (0·207)	0·57 (0·069)	**0·78 (0·004)**	**0·82 (0·002)**	**0·85 (<0·001)**
Outer bark thickness	**0·73 (0·011)**	**0·64 (0·035)**	**0·67 (0·023)**	**0·81 (0·002)**	0·23 (0·498)	0·57 (0·065)	0·59 (0·056)
Ratio of inner to outer bark	**−0·64 (0·035)**	**−0·66 (0·027)**	−0·52 (0·101)	−0·55 (0·082)	0·10 (0·775)	−0·42 (0·195)	−0·31 (0·353)
Bark fissure index	**0·67 (0·024)**	0·56 (0·071)	0·57 (0·070)	**0·76 (0·007)**	0·08 (0·806)	0·42 (0·204)	0·45 (0·162)
Punch resistance	−0·49 (0·123)	−0·15 (0·650)	−0·17 (0·613)	−0·20 (0·551)	−0·54 (0·085)	−0·48 (0·137)	**−0·61 (0·044)**
Water storage capacity	0·14 (0·681)	−0·28 (0·401)	−0·03 (0·937)	0·11 (0·737)	0·35 (0·298)	0·13 (0·701)	0·14 (0·686)
Bark pH	0·23 (0·491)	−0·10 (0·770)	−0·06 (0·858)	0·22 (0·509)	0·52 (0·103)	0·30 (0·364)	0·47 (0·141)

Significant relationships at a $P < 0.05$ level are indicated in bold.

Diptera. BFI was significant for Annelida ($r = 0.67$, $P = 0.024$) and Diplopoda ($r = 0.76$, $P = 0.007$). The negative effects of RIOB were significant for Annelida ($r = -0.64$, $P = 0.035$) and Isopoda ($r = -0.66$, $P = 0.027$). Total abundance had a positive relationship with relative bark looseness ($r = 0.85$, $P < 0.001$), and a negative relationship with RIOB ($r = -0.61$, $P = 0.044$).

There were statistically significant differences of invertebrate community composition among tree species both at major clade level (PERMANOVA, $F = 5.4$, $P = 0.001$; ANOSIM, $R = 0.52$, $P = 0.001$), and at family level (PERMANOVA, $F = 3.9$, $P = 0.001$; ANOSIM, $R = 0.54$, $P = 0.001$). Diptera, Coleoptera and Annelida combined explained nearly 80% of the observed dissimilarity in community composition between pairs of trees, of which Annelida and Coleoptera consistently contributed to dissimilarity as they had the highest mean contribution to standard deviation ratio (Table S2).

Invertebrate community at major clade level (Fig. 2a), invertebrate community at family level (Fig. 2b), the subset of best four bark traits combination (Fig. 2c) and all bark traits (Fig. 2d) were plotted using NMDS. Outer bark thickness, punch resistance, RIOB and relative looseness, in combination, best predicted the major clade level faunal community patterns ($\rho_s = 0.51$, Table S3) with high predictive power of family level invertebrate community pattern too ($\rho_s = 0.60$), followed by BFI. The subset of outer bark thickness and punch resistance best predicted the family level invertebrate community patterns ($\rho_s = 0.61$).

LINKING BARK TRAIT DISSIMILARITY AND INVERTEBRATE COMMUNITY DISSIMILARITY BETWEEN TREE SPECIES

There were significant positive relationships between bark trait dissimilarity (Euclidean distance) and Bray–Curtis dissimilarity across all the pairs of 11 tree species, both for major invertebrate clades (Mantel $r = 0.32$, $P = 0.034$; Fig. 3a) and for families (Mantel $r = 0.38$, $P = 0.023$; Fig. 3b). There was a significant positive relationship between bark trait dissimilarity and overall family richness across all the pairs of 11 tree species (Mantel $r = 0.42$, $P = 0.032$; Fig. 3c). The relationships for macro-detritivore (Isopoda and Diplopoda) community dissimilarity (Mantel $r = 0.31$, $P = 0.041$) and species richness (Mantel $r = 0.31$, $P = 0.095$) were positive.

Discussion

We showed that bark traits of logs after 1 year of decomposition varied greatly among 11 tree species in the same forest stand. These bark traits affected both invertebrate abundance and community composition in logs. We found strong support for our main hypothesis, i.e. the more dissimilar bark traits of logs were between tree species, the more the invertebrate community composition differed and the greater was their joint invertebrate family richness. We discuss below, in the context of the current literature, how important bark traits are for the faunal community assembly in early stage decomposing trunks.
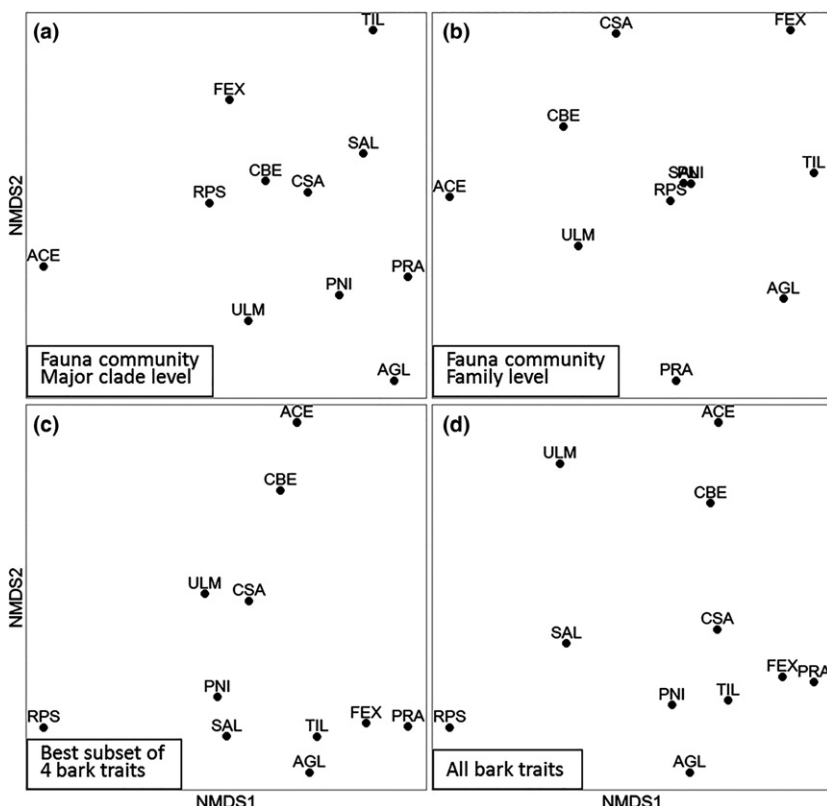

Fig. 2. Non-metric multidimensional scaling (NMDS) ordinations of the 11 tree species, based on (a) fauna community composition at major clade level; (b) fauna community composition at family level; (c) subset of the four bark traits (Relative looseness, Outer bark thickness, Ratio or inner to outer bark, Punch resistance); (d) all bark traits. (c) and (d) using normalized bark trait values (see Materials and methods). The associated "matching coefficients" ρ_s between four bark trait and all bark traits to fauna community similarity patterns at major clade level are (c − a): 0.51, (d − a): 0.33; between four bark trait and all bark traits to fauna community similarity patterns at family level are: (c − b): 0.60, (d − b): 0.41. Stress values for the two-dimensional ordinations are (a): 0.09, (b): 0.11, (c): 0.03, (d): 0.05.

BARK TRAIT VARIATION AND ITS EFFECTS ON ASSOCIATED INVERTEBRATES

A suite of bark traits together had fundamental effects on invertebrate community assembly. The subsets of bark traits that correlated strongly with invertebrate community mostly included habitat-related rather than resource-related traits. Bark looseness was very important for the log-associated invertebrate community in early decay stage, as it was included in almost every predictive bark
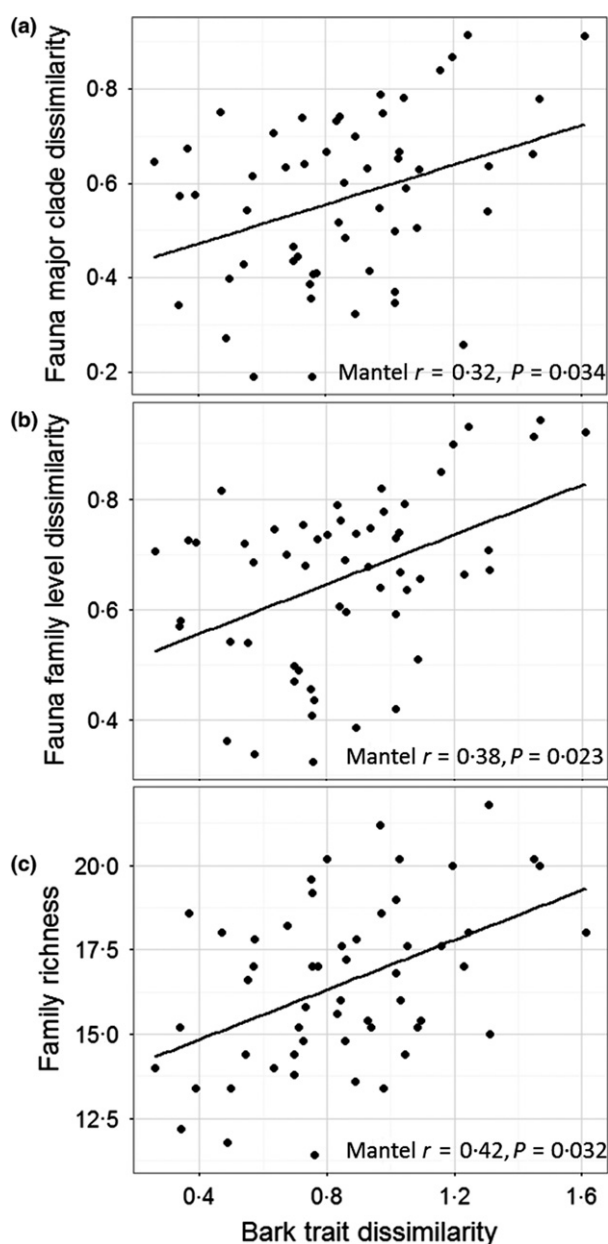

Fig. 3. Relationship between dissimilarity in bark traits (Euclidean distance) of all tree species pairs and dissimilarity in faunal community composition of those tree species pairs at (a) major clades level; (b) family level of those clades; (c) family richness supported by each pair. Each point represents the mean value of a specific pair of tree species based on five logs per species.

trait subset (Table S3). Outer bark thickness and bark fissure index seem to buffer microclimate variations as bark creates its own environment and offers shelter (MacFarlane & Luo 2009) for the invertebrates. Rough bark surface can influence the faunal colonization by increasing an invertebrate's ability to grip the bark (Ferrenberg & Mitton 2014). The literature generally predicted a thick rhytidome to offer protection to the tree and reported a negative effect on the abundance of, especially, xylophagous animals (Wainhouse, Cross & Howell 1990; Paine *et al.* 2010). Surprisingly, we found that thicker outer bark was positively related to the abundance of the major invertebrate clades studied. This may be because these invertebrates are rather sensitive to drought (O'Neill 1969; Dias *et al.* 2013) and a thick outer back might offer protection against desiccation. It may also buffer against strong fluctuations in moisture and temperature under the bark, resulting in a more stable abiotic environment for associated invertebrates (Rosell *et al.* 2014). Also, more outer bark means more volume for the animals to move around in. Protection by outer bark should be based on both structure (thickness) and tissue quality (density). As an alternative explanation, Poorter *et al.* (2014) and Rosell *et al.* (2014) also showed a negative relationship between bark thickness and bark density; i.e. a thicker outer bark is not necessarily better at protecting wood against entrance of animals or protecting invertebrates living under the bark against predators and parasites that live outside tree trunks in the early-decomposing stage. Bark punch resistance did not explain abundance of most clades, but was included in the subset of bark traits that was a good predictor of the invertebrate community composition, suggesting that bark tissue density is important for faunal community composition at the early decay stage. Bark water storage capacity is affected by bark texture and impacts the moisture regime of the cortisphere, thereby potentially affecting both microbial and invertebrate communities. However, we did not find strong effects of bark water storage in this study, possibly because other structural traits that affect bark water storage had stronger direct influence. Perhaps if the logs had been standing, water storage capacity could have altered the stemflow (Levia & Germer 2015), which can play an important role in the ecology of the cortisphere. Bark pH is an important determinant of the ecological communities inhabiting the cortisphere, directly or indirectly by reflecting the chemical composition of the bark and its suitability as a microhabitat to associated organisms (Köhler *et al.* 2015). Microclimate in the cortisphere was probably essential for the associated fauna, and greatly determined especially by the habitat-related traits. Actual measurement of the microclimate is needed in further research to improve our understanding of the cortisphere biodiversity. Also, it would be good to test for any indirect effects of bark traits of different species by leaching of chemical compounds, thereby potentially attracting or deterring different invertebrates and causing variation in

the species pool in the direct vicinity of logs of different tree species.

The divergent preferences of different faunal major clades and families for bark properties are supported by our analysis (Table 1, Fig. 3). Diptera, Coleoptera and Annelida together contributed strongly to the overall faunal community dissimilarity. This may be because Diptera and Coleoptera had a high species richness, which allows for tree species specialization. For example, bark beetles, a dominant group in recently fallen logs, show a high level of trees-species specialization (Freude, Harde & Lohse 1981). Annelida are sensitive to drought and pH because of their permeable skin, and their abundance was related to most of the habitat-related bark traits. Bark looseness explained the abundance of Diptera and Coleoptera. More loose bark may provide more space between wood and bark for beetle and fly larvae (Teskey 1976). Abundances of Diplopoda and Isopoda were explained by outer bark thickness, bark fissure index (BFI) and ratio of inner to outer bark (RIOB). As macro-detritivores, they prefer to feed on decomposed substrate, i.e. bark or wood litter in different stages of log decomposition (Paoletti & Hassall 1999; Vos *et al.* 2011). Therefore, their abundances were explained by these microhabitat-related traits, of which RIOB is also a resource-related trait (fraction of resource-rich inner bark). Chilopoda abundance was related to outer bark thickness among tree species, possibly through its microclimatic buffering effect (see above). The effect of bark traits on Chilopoda can also be explained by the fact that they are polyphagous predators, therefore affected by bark traits indirectly through the abundance of prey species; this may also explain the lesser contribution of Chilopoda to the overall community dissimilarity. Together these observations demonstrate that there were profound combined effects of bark traits on the abundance of decomposer fauna and their predators.

Outer bark thickness was significantly correlated with relative bark looseness, RIOB and the BFI. Thicker bark is easier to come loose from the xylem and pronounced fissures can only occur in thick bark, while the ratio was largely determined by variation in the thickness of outer bark. Besides, bark thickness is also tightly linked with other functions, e.g. fire resistance (Vines 1968; Poorter *et al.* 2014), protection, water storage and photosynthesis (Rosell *et al.* 2014). The partial correlations and apparent trade-offs between the traits studied made it difficult to disentangle the specific effects of any individual bark trait on invertebrates, although outer bark thickness was an important factor strongly explaining abundances of five clades of invertebrates. A key finding from this work is that habitat-related bark traits seem particularly important for predicting invertebrate community composition in early-stage decomposing logs.

Special fauna groups acted differently from the whole faunal community. The relationships between bark trait dissimilarity and invertebrate community dissimilarity were stronger at major faunal clade and family level. At the level of macro-detritivore species, the relationship was weaker for the community dissimilarity, confirming the view that level of aggregation affects the predictability of variation in soil fauna communities (Berg & Bengtsson 2007). Fauna family richness increased with the dissimilarity of bark traits, indicating that instead of tree species diversity *per se,* more dissimilar bark traits among tree species would support more fauna families.

STRENGTH OF THE ENVIRONMENTAL FILTER

Filtering processes govern community assembly by either allowing or excluding available species to enter a local community (Diamond 1975; Weiher & Keddy 1995; McGill *et al.* 2006). Newly fallen dead trunks will have to be colonized by the invertebrate fauna present in the surrounding area. Resource in phloem is sufficiently available at this stage but is difficult to reach owing to the presence of outer bark, limiting the role of resource competition. Bark traits, at this early stage of decay, thus act as a strong environmental filter for invertebrate community assembly, thereby directly and indirectly changing the local soil faunal community composition. Variation in bark traits can thus greatly promote forest invertebrate biodiversity, which strongly depends on small-scale forest structures (Harmon *et al.* 1986; Addison, Trofymow & Marshall 2003). Although we harvested logs and collected fauna at the time that was the most representative of the actual faunal community sampled, both bark traits and the invertebrate community might vary between the fresh trunk and different decomposition states. Thus, more measurements over time would improve our understanding of the invertebrate community assembly process associated with tree trunks.

CONCLUSION AND OUTLOOK

This study has shown the fundamental effects of combined bark traits among tree species on the forest soil fauna community composition, which is an important component of forest biodiversity. Bark traits differ strongly across temperate tree species and, alone or in combination, are key drivers of invertebrate community assembly in logs during early-stage decomposition. Different faunal clades show similar trends in response to interspecific variation in bark traits such as outer bark thickness, but the relative importance of these bark traits differs among clades. As we hypothesized, the more dissimilar bark traits are between tree species, the more their faunal community composition will differ, and the more fauna family richness will be supported. These results indicate that functional trait diversity among tree species in forest stands is likely a better indicator of early-phase dead trunk fauna diversity than tree species diversity *per se.* Some soil invertebrates are themselves also important as decomposers (Ulyshen 2016), thus bark trait afterlife effect on the community composition and diversity of soil

fauna will feed back to dead tree decomposition rate and biogeochemical cycling.

While our findings confirm that faunal community composition dissimilarity is positively related to inter-specific bark trait dissimilarity at the early stage of decay, further study should extend the trajectory towards more advanced decay stages. We expect that, with the progression of decay, invertebrates will interact more strongly with each other negatively (e.g. competition, predation), while it is unknown whether and how facilitative effects seen during early decomposition (Zuo *et al.* 2016a) play a role later on; these factors will make community assembly in dead wood less predictable. At later decomposition stage, variation in wood traits will become more important than bark traits, partly because much of the bark will have fallen off, but especially because wood-specialized decomposers, such as wood-boring beetles, will colonize the wood. How wood trait dissimilarity and associated invertebrate community dissimilarity will change over this next phase of wood decay will be important to complete our understanding of the role of tree log traits for forest invertebrate diversity.

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Data accessibility

Data for this paper are accessible at the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n6k49 (Zuo *et al.* 2016b).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Fig. S1. Testing the possible effect of vertical height along the tree for each bark trait.

Fig. S2. Comparing air-dried and water-saturated bark punch resistance of 11 tree species.

Fig. S3. Mean fauna abundance ($n = 5$ logs) of each major clade for 11 tree species.

Fig. S4. Relationships of each fauna clade abundance and single bark trait among 11 tree species.

Table S1. List of taxa per clade observed in the samples.

Table S2. Contribution of each faunal major clade to dissimilarity in community composition between all possible pairwise comparisons of the 11 tree species.

Table S3. Combinations of bark traits that were consistent with the faunal community patterns.

Appendix S1. Formulas for Euclidean distance and Bray–Curtis dissimilarity index.