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Quantifying arthropod contributions to wood decay

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Summary

1. Wood decomposition is driven primarily by microbial activity but proceeds at greatly varying rates depending on regional or local differences in physical conditions and other determinants. Although many arthropod taxa (e.g. termites, wood-boring beetles) are known to consume or excavate dead wood, their contributions to the decay process remain largely unmeasured.

2. Quantifying arthropod contributions to wood decay is fraught with challenges, but no guidelines are available to assist researchers in designing and carrying out studies of this kind. We therefore sought to provide a critical review of previous studies on this important topic and discuss methodological considerations that may benefit future researchers.

3. The biggest challenge inherent to such research involves excluding arthropods from dead wood (i.e. the reference treatment) without otherwise affecting the decay process. Because mesh bags are likely to alter physical conditions relative to unenclosed substrates and insecticides are likely to inhibit microbial growth, additional experimentation is needed to isolate the arthropod effect. Alternatively, partial exclusion or temporary exposure methods may produce less confounded results.

4. In determining the initial volume of a wood sample (e.g. to estimate the initial mass using specific gravity data), there is a trade-off between the accuracy of this measurement and the realism of the study. A method involving image analysis is described for obtaining accurate initial volume estimates for naturally occurring woody substrates. When measuring changes in specific gravity during the decay process, initial sample volumes must be used in these calculations as opposed to the water displacement technique which fails to measure wood removed by arthropod activity.

5. Termites carry large amounts of soil into dead wood, and this behaviour complicates efforts to measure their contributions to wood decay. A novel method for isolating termite soil by burning the wood is described, and some preliminary results are presented.

6. These and other recommendations described herein should aid efforts to quantify the contributions of arthropods to wood decay. Such research is of great interest given the broad importance of dead wood to forest ecosystems–including its role in carbon storage–and the diversity and conservation concern of the species involved.

Key-words: Coleoptera, ecosystem services, insects, invertebrates, Isoptera, saproxylic

Introduction

The decomposition of plant debris is an important ecological process by which nutrients stored in dead tissues are returned to the soil. Decay is driven primarily by microbial activity which, in turn, is influenced by a wide range of environmental factors including climate, soil conditions, substrate quality, etc. (Rayner & Boddy 1988). Arthropods are also thought to play a role in decay (Ausmus 1977; Swift & Boddy 1984), but their importance in this regard remains poorly understood. Even their contributions to leaf litter decay are unclear despite over 50 years of intensive research. According to a review by Kampichler & Bruckner (2009), this uncertainty stems from the difficulty of excluding arthropods without affecting other factors (e.g. moisture and temperature) likely to also influence decay rates. Relatively few studies have sought to measure the contributions of arthropods to wood decay, but their findings are similarly clouded by a variety of assumptions and design limitations (Table 1). It became apparent to us while working on our own research that little guidance or discussion is available in the existing literature to assist researchers in designing and carrying out studies of this kind. To address this need, we herein review previous studies on the relationships between arthropods and wood decay and discuss methodological approaches that may benefit future research on this important topic.

Constituting around 10–20% of the plant biomass in forests, dead wood represents an important store of carbon (Cornwell *et al.* 2009; and references therein) as well as an essential resource for a substantial fraction of forest biodiversity (Stokland, Siitonen & Jonsson 2012). A diverse assemblage of arthropods and other invertebrates rely on dead wood or benefit from it to some extent. This includes a number of taxa that actively consume or excavate wood. The degree to which these species–along with their endo- or ecto-symbiotic microbial

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Table 1. Chronology of studies on the contributions of saproxylic arthropods to wood decay (studies aimed at measuring soil, grass or leaf litter decomposition are not included). Dashes for 'wood source' indicate this information is either not applicable or not clear

Reference	Country	Ecosystem	Taxon/taxa	Wood source	Exclusion treatment	Conclusions	Comments
Maldague (1964)	Congo	Forest	Termites	–	None	Annual consumption equivalent to about half-annual litter fall	Based on estimated population size and oxygen consumption. After correcting errors in this calculation, Lee & Wood (1971b) revised figure to 10% or less
Hopkins (1966)	Nigeria	Savanna, forest	Termites	Wooden blocks	None	Wood decay largely dependent on termites (wood decayed much more rapidly at sites where termites were active)	
Lee & Wood (1971a)	Australia	Dry woodland	Termites (*Nasutitermes exitiosus*)	–	None	Annual consumption equivalent to ~ 17% annual input of dead wood	Based on laboratory consumption test data
Ocloo (1973)	Ghana	Not clear	Termites	Wooden stakes	None	In 65 days, consumed ~ 3% and 16% of heartwood and sapwood volume, respectively	
Haverty & Nutting (1975)	USA	Desert	Termites (*Heterotermes aureus*)	–	None	Annual consumption equivalent to ~ 17.5% annual input of dead wood	Modelling study using data from multiple sources
Usher (1975)	Ghana	Open woodland	Termites	Wooden blocks	None	Annual consumption equivalent to ~ 20% annual litter fall, 8–10% annual primary production	Conclusions are based on feeding rates, and food availability estimates published previously
Wood (1976)	Nigeria	Open woodland	Termites	–	None	Consumption equivalent to ~42–84% of annual litter fall	Calculation based on consumption rates as measured in the laboratory, many assumptions made
Abe (1978, 1980)	Malaysia	Forest	Termites	Trunk and limb sections	None	Most wood decay can be attributed to termites	
Buxton (1981)	Kenya	Dry scrubland	Termites	Naturally occurring fallen wood	None	'Almost all' dead wood is removed by termites (slowly) with macrotermitines being the most important	
Collins (1981)	Nigeria	Open woodland	Termites	Log and twig samples	Suspending off ground	Annual consumption equivalent to ~ 60% of annual wood fall with macrotermitines being the most important	
Gentry & Whitford (1982)	USA	Forest	Termites	Wooden blocks	Chlordane	Termites removed 3–20% wood mass (varying widely) within 9 months	Mass loss was only measured from attacked blocks
Collins (1983)	Malaysia	Forest	Termites	–	None	Consumption equivalent to ~15–16% and ~1–3% of litter production in forests with and without macrotermitines, respectively	Calculation based on various sources of information, many assumptions made
Salick, Herrera & Jordan (1983)	Venezuela	Nutrient-poor floodplain forests	Termites	–	None	Consume <5% of annual litter and treefall	Consumption estimates based on population size and the literature values. Martius (1994) suggested this estimate is much too low
Martius (1989)	Brazil	Floodplain forest	Termites (*Nasutitermes macrocephalus* and *N. corniger*)	–	None	Consumption by *N. macrocephalus* and *N. corniger* equivalent to 1.4% and 4.0% of annual wood fall, respectively. Entire termite fauna likely to consume at least 20% of annual wood fall	Information taken from Martius (1994)
Zhong & Schowalter (1989)	USA	Forest	Ambrosia beetles	Logs	None	Excavated ~ 0.2% of sapwood volume during first year	Change in wood density/mass not measured
Edmonds & Eglitis (1989)	USA	Forest	Bark beetles and wood-boring beetles	Logs	Window screening	Wood exposed to beetles decayed more rapidly, due primarily to wood borer activity	Logs initially were not in contact with the soil, effect of the screen used to exclude beetles on decay not determined
Schowalter (1992)	USA	Forest	Insects	Felled trees	None	Removed ~ 1% of sapwood volume during first 2 years	
Takamura & Kirton (1999)	Malaysia	Forest	Termites	Logs	Steel pan with screened bottom	Excluding termites did not affect decay rate (based on carbon content) over 3 yrs	

Table 1. (continued)

Reference	Country	Ecosystem	Taxon/taxa	Wood source	Exclusion treatment	Conclusions	Comments
							Arthropods capable of flying or climbing were not excluded; wood removed by termites not considered
Takamura (2001)	Malaysia	Forest	Termites	Logs	Steel pan with screened bottom	Termites increase decay rate (based on carbon content) for one of the two wood species tested	Arthropods capable of flying or climbing were not excluded; wood removed by termites not considered
Müller *et al*. (2002)	Finland	Forest	Beetles	Logs	Nylon mesh	Caged logs decayed more slowly than uncaged logs, especially in managed forests where beetles were more abundant (a 5.6% difference in weight loss after 28–30 months)	Caged logs were open at the bottom, allowing arthropods to colonize logs through the soil
Schuurman (2005)	Botswana	Woodland and grassland	Termites	Logs	None	Macrotermitine abundance determines almost all variation in decay rates	
Warren & Bradford (2012)	USA	Forest	Termites	Wooden blocks	Absent equals excluded	Wood mass loss 11.5% higher when termites present	
Angers, Drapeau & Bergeron (2012)	Canada	Forest	Bark beetles and wood-boring beetles	Standing dead trees	None	Wood density decreased significantly with increasing wood-boring beetle activity	

partners–contribute to the decay process remains largely unknown. Termites and wood-boring beetles are widely believed to be the most important wood-consuming arthropod taxa (Cornwell *et al*. 2009). Of the 23 previous studies addressing this topic, 18 have focused on termites (Table 1). Eight of these took place in Africa where termites were consistently found to remove a substantial amount of the annual wood fall. Similar conclusions were reached in studies carried out in Southeast Asia, Australia, South America and North America (Table 1). Studies on other wood-feeding insect taxa indicate that large wood-boring beetles also have a positive influence on wood decay (Table 1). Most of these studies involved estimation based on population sizes and consumption rates (often determined in the laboratory) instead of direct field measurements or controlled experimentation. Those involving field measurements often did not involve an arthropod-exclusion treatment for reference or were limited by designs that confounded arthropod effects with differences in physical conditions or substrate quality.

Obtaining more and better estimates for the contributions of arthropods to wood decay across many regions and forests types would greatly enhance our ability to model carbon and nutrient budgets (Schuurman 2005; Cornwell *et al*. 2009) and would provide useful information regarding the conservation value of arthropods associated with dead wood (Ulyshen in press). Although many current climate models assume the turnover of dead wood can be entirely predicted based on physical parameters, for example, decay rates often vary at both regional and local scales beyond what can be explained by differences in physical conditions alone. An excellent example of this was recently provided by Schuurman (2005) who studied the impacts of termites on wood decomposition at two locations in the Okavango Delta region of Botswana. At each location, the researcher distributed rolls of toilet paper and short sections of dead branches to determine termite community composition and wood decay rates, respectively. Even though all dead branches experienced similar climatic and soil conditions, belonged to the same tree species and were similar in size, decay rates varied up to six-fold. Almost all of this variation was attributed to whether or not a particular termite taxon (i.e. the subfamily Macrotermitinae) was present. Clearly, our understanding of wood decay and our ability to predict the rate at which it proceeds will be limited without properly recognizing the importance of arthropods to this process.

Design considerations

WOOD SOURCE

A number of researchers have used machined blocks of wood in field-based decay studies (Table 1). Blocks of wood provide a more uniform substrate and can be more easily measured (e.g. volume, dry weight) at the beginning of a study than natural sources of wood (see section on measurements below). The decay process in machined blocks of wood will differ greatly from what happens in natural sources of dead wood, however, especially with respect to arthropod activity. Under most natural conditions, a dying or recently dead piece of wood has a phloem layer rich in sugars and nutrients and covered by a protective layer of bark. Phloem-feeding beetles are among the first insects to colonize dead wood and are thought to contribute to decay by facilitating colonization by wood-decaying fungi through tunnelling (Swift & Boddy 1984) and by vectoring fungi on or within their bodies (Dowding 1984; Swift & Boddy 1984). These species would never utilize artificial blocks of wood. Indeed, the only insects likely to use such wood are termites. Blocks of wood can be used to compare termite consumption rates among different habitats, but it is probably a mistake to use these data to extrapolate more broadly. For example, some researchers have used consumption rates measured on blocks of wood to estimate how much of the annual input of dead wood is consumed by termites (Usher 1975). Such estimates should be interpreted with caution.

EXCLUSION TREATMENT

Comparing wood loss between a treatment in which arthropods have been excluded and another where colonization by arthropods is permitted may seem, at first glance, to be a simple way of determining the extent to which these organisms accelerate the decay process. Efforts to exclude arthropods often give rise to serious complications, however, as learned after more than 50 years of research on leaf litter decay. Although mesh bags have been widely used in these studies to exclude arthropods, few efforts have been made to determine how the bags themselves may affect decay by altering physical conditions relative to unenclosed substrates (Kampichler & Bruckner 2009; and references therein). That mesh bags can substantially alter physical conditions has been shown in several studies, however. For instance, Lousier & Parkinson (1976) found the moisture levels in fine-mesh litter bags to be higher than in coarse-mesh bags in Canada. Such concerns led Kampichler & Bruckner (2009) to conclude that '…we cannot supply even a tentative estimation of the real role of microarthropods in terrestrial decomposition'. The authors suggest addressing this complication by including additional treatments or experiments aimed at correcting for these unintended effects. Researchers interested in measuring the contributions of arthropods to wood decomposition would be wise to heed this important lesson from the leaf litter literature.

Excluding arthropods can itself be a challenge (Müller *et al.* 2002). Indeed, given the exceedingly small sizes of many mites and collembolans, it is probably impossible to exclude all arthropods from wood without completely sealing it off from the outside world. Furthermore, as pointed out by Pawson & Sky (2009), even large-bodied insects have the potential to colonize enclosed wood by ovipositing through the mesh from the outside. To prevent this from happening, the researchers built mesh-covered cages around logs that were also placed in mesh bags. Although this approach effectively prevents oviposition through the mesh, it will not prevent colonization by microarthropods and is even more likely to alter physical conditions relative to unenclosed logs. The researchers addressed this latter point by covering the logs to be exposed to arthropod attack with the same mesh material. Large cuts were made in the mesh to allow colonization. In addition, these logs were placed under a cage similar to that constructed for the exclusion treatment but with only the top surface covered by mesh. These methods are still likely to result in differences in environmental conditions between treatments, however, and may also underestimate the contributions of arthropods by limiting their access to the logs.

Considering the complications inherent to the mesh bag approach, partial exclusion techniques may be preferable in some situations. This may be especially true for research on termites and arthropod taxa that colonize wood by moving across or through the soil. Excellent examples of this method come from research carried out in Malaysia by Takamura & Kirton (1999) and Takamura (2001). The researchers cut holes along the sides and in the bottom of stainless steel trays. The holes were left open in the reference treatment and were covered with stainless steel mesh in the exclusion treatment. Because the tops of all trays were left open, there should not have been differences in temperature or humidity between treatments (although the stainless steel mesh used in the exclusion treatment may have reduced soil-wood contact). The disadvantage of such open-topped design is that arthropods capable of flying would not be excluded from the wood. Indeed, Takamura & Kirton (1999) mentioned that numerous small holes, most likely created by scolytine or platypodine weevils, were observed in both treatments. Although this method does not exclude all major wood-feeding arthropod groups, it does effectively isolate the contributions of termites and other soil-dwelling arthropods to the decay process. In Nigeria, Collins (1981) excluded arthropods by suspending logs off the ground. Despite being an effective way of preventing termite colonization, logs in contact with the soil are likely to decay more quickly due to differences in moisture alone. To what extent this resulted in an overestimation of termite effect in that study cannot be determined.

Temporary exposure methods may also have utility under certain circumstances. In Finland, for example, Müller *et al.* (2002) put nylon mesh cages around groups of experimental logs. The cages were removed from one group of logs at each location for a 3-week period each spring to temporarily permit insect colonization. While this approach largely solves the problem of differences in physical conditions between treatments (i.e. except for the 3-week exposure period), it is also likely to underestimate the contributions of arthropods to the decay process. Such methods may be most useful in studies interested in isolating the contributions of bark beetles or other early arriving species to the decay process.

Chemical barriers may also provide an effective means of excluding termites and other soil arthropods from dead wood. In Ghana, Usher (1975) dug a large pit (1 m wide, 4 m long and 20 cm deep), treated it and the surrounding soil with dieldrin (no longer considered to be a safe compound), and then filled the pit with untreated soil. This provided an area in which wood decay could be studied in the absence of termites. In the south-eastern United States, Gentry & Whitford (1982) excluded termites from wooden blocks by soaking the soil with chlordane (another compound that is no longer in use). A number of studies have used naphthalene to exclude arthropods from leaf litter (Kampichler & Bruckner 2009; and references therein), and this compound may have some utility in studies on wood decay. Fungi may also be inhibited by this compound, however, and termites may exhibit a greater tolerance for it than many other arthropod taxa (Chen *et al.* 1998). Similarly, Pant & Tripathi (2010) found wood treated with chlorpyrifos (a broad-spectrum insecticide still in use) to be highly resistant to fungal decay even at low concentrations. Przewloka *et al.* (2007) promisingly found fipronil (another commonly used insecticide) to exhibit no fungicidal activity, but more research is needed to confirm this.

Some researchers have avoided exclusion methods using blocks of wood with machined surfaces that can be easily examined for arthropod feeding. In the south-eastern United States, for instance, Warren & Bradford (2012) compared wood mass loss between blocks attacked by termites, and those that had not been attacked by the end of the study. They determined that blocks attacked by termites had 11·5% less mass compared with blocks that had not been attacked. Although this approach avoids many problems associated with exclusion methods, it creates a new set of issues that cannot be ignored. Because termites are discriminant feeders, for instance, blocks that have not been attacked by the end of a study may differ in important physical or chemical properties from attacked blocks. Wood density, resin content, nitrogen concentration and other properties are well known to affect the activities of both microbial and arthropod decay agents. Microbial activity may therefore also be reduced in blocks lacking termites, potentially leading to overestimates of termite effect. Finally, it is not realistic to expect some blocks to remain unattacked in longer-term studies.

Measurements

MEASURING WOOD LOSS

One approach to determining the contributions of arthropods to wood decay involves carefully measuring the volume of wood they remove during their tunnelling and feeding activities. This was performed by Zhong & Schowalter (1989) who determined that ambrosia beetles excavated about 0·2% of sapwood volume during the first year after tree death in Oregon. The problem with this approach is that it overlooks some of the more subtle contributions of arthropods to the decay process. For instance, if arthropods really do play an important role in inoculating wood with fungi, the wood next to tunnels may be more thoroughly degraded by microbial activity than it would be in the absence of arthropods. Such an effect would not be visually evident. This would result in underestimating the effects of arthropods on decay. In addition, such an approach is only feasible for short-term studies. After long periods, it will likely become difficult or impossible to distinguish between arthropod tunnels and other sources of damage.

The effect of arthropods on wood decay can be more fully measured in terms of dry mass loss. Accurately measuring the dry mass of a piece of wood requires temperatures exceeding 101°C (i.e. to drive off bound water) for 24–72 h depending on sample size (Williamson & Wiemann 2010). Determining mass loss requires knowledge of the initial dry mass which should not be measured from the wood to be used in the experiment as this would affect insect colonization. Representative subsamples are sometimes used for this purpose (e.g. Buxton 1981). If a piece of wood is too large to weigh at the beginning of a study or if a sample is to be collected and analysed at some later point in time, its initial mass can be estimated based on its initial specific gravity (i.e. as measured from samples) assuming the original volume can be determined. Considering how best to determine this reveals a trade-off between measurement accuracy and the realism of the study design. For example, in a realistic design in which wood samples will be collected from the centres of long logs, it will be very difficult to determine the original volume of wood with a high degree of accuracy. Initially, measuring the diameter of the log where samples will later be taken provides only a very rough estimate as few logs are perfectly round, and the thickness of the bark layer cannot be known without considerable disturbance (note: because it will fall away and fragment during the decay process, bark should not be included in these measurements).

One might instead estimate initial volumes at the time of sampling. This might include, for instance, measuring the average thickness of a 'wet' piece of wood with callipers and measuring the surface area of one or both faces by weighing cut-out tracings made on paper of known density. A drawback to this approach is that wood swells or contracts somewhat depending on water content. To control for this possibility, Angers, Drapeau & Bergeron (2012) used dry volume in determining the density of wood. Using dried wood is less accurate with respect to estimating the original volume, however, and the extent to which wood shrinks during the drying process may be affected by the amount of arthropod activity. Importantly, attempts to estimate the original volume of a piece of wood based on its dimensions at the time of sampling is only a possibility at early stages of decay before the wood begins to collapse and change shape.

A more accurate strategy is to initially photograph the cut ends of each log (including a ruler for scale) to be used in an experiment. Image analysis software (e.g. Image-Pro) can then be used to accurately determine initial wood surface area as measured beneath the bark and phloem, using the ruler for calibration (see image in Supplemental Fig. S1). Wood samples can later be collected near the photographed ends where dimensions would have been similar. The thickness of the wood can be collected at the time of sampling as this measure changes little during the decay process (Hann 1969). Although this method requires that sampling take place near the cut ends of logs, it permits one to estimate the original log volume with a high degree of accuracy–even if the logs are highly decayed at the time of sampling.

Properly accounting for wood hollowed out by insect activity is essential to research of this kind. Some studies have failed to do so, however. In the otherwise well-designed studies carried out by Takamura & Kirton (1999) and Takamura (2001), the tunnels and other hollow areas created by insect activity were not accounted for when comparing decay rates. The researchers bored holes into the wood with an electric drill and analysed the resulting wood chips for nutrient concentrations and carbon content. They equated the loss rate of carbon with wood mass loss 'since carbon is the main component of wood' without accounting for wood consumed by termites in the control treatment. The researchers noted that the loss rates determined in their study were much lower than those reported in the same area by Abe (1980) and suggested that this difference was due to differences in wood density between studies. The difference is much more likely due to differences in methodology, however, as Abe determined the mass loss of wood which more properly accounts for wood consumed by termites.

Finally, it is essential that researchers interested in measuring the change in specific gravity over time use initial volumes in their calculations. For sound wood, volume measurements often involve submerging wood samples in a water bath placed on a scale. Because this 'water displacement' technique fails to account for portions hollowed out by insects (Mackensen & Bauhus 1999), however, it is not suitable for research aimed at measuring the contributions of insects to wood decay.

Fig. 1. Set-up for burning wood to isolate soil carried in by termites. A resulting soil sample is shown in the inset.

ACCOUNTING FOR TERMITE SOIL

The tendency of termites to carry substantial amounts of soil into wood has been observed among termites worldwide (Greaves 1962; Ocloo 1973; Abe 1980; Grove 2007), complicating efforts to measure wood consumption. Perhaps the first to recognize this experimental challenge was Ocloo (1973) who sought to measure the volume of wood consumed by termites in Ghana. The researcher concluded that only when termites attacked the surface of the wood–and the soil could be cleaned away with relative ease–was it possible to accurately measure termite damage by volume. Faced with a similar problem in Malaysia, Abe (1980) removed as much soil as possible by washing the wood after soaking it in water for 24 h. Because it was not possible to remove all soil from larger branches and trunk sections, estimates were based on small subsamples. Completely burning the wood away to leave only the soil behind is perhaps the most accurate way to determine the true final dry wood weight (i.e. by subtracting soil weight from dry wood weight before burning). One of us (TLW) developed a method for accomplishing this. As pictured in Fig. 1, this involves placing a dried wood sample on a steel pan placed atop a propane burner. An electric fan can be used to provide aeration and is useful in blowing away ash and light pieces of char. Preliminary results from a study of wood infested by *Reticulitermes* spp. in the south-eastern United States clearly demonstrate the importance of correcting for soil carried into wood by termites. On average, soil accounted for 3·5%, 9·0% and 19·4% of dry wood weight in 3, 4 and 5 year-old logs, respectively, and exceeded 59% in some logs (T.L. Wagner, unpublished data). Although we do not yet have data on exactly how accurate this method is in isolating soil from wood, we are encouraged by the resulting samples which contain only negligible amounts of charred wood. Furthermore, based on our observations, only minimal amounts of soil appear to be lost during the burning process. One disadvantage of this approach, of course, is that the wood sample is destroyed in the process.

ACCOUNTING FOR FUNGAL BIOMASS

A significant proportion of dead wood consists of fungal mycelia (Swift 1973) and failing to account for this biomass results in underestimation of wood loss. Although long recognized, this limitation is usually accepted in studies on wood decay given the difficulties inherent in determining the proportion of dry weight attributable to fungi. It is possible to estimate dry mycelial biomass by measuring a product (e.g. glucosamine) of chitin hydrolysis (i.e. chitin is found in fungal cell walls but is absent from plant tissues) assuming the ratio of that product to dry mass in pure mycelia is known (Swift 1973; Gurusiddaiah, Blanchette & Shaw 1978; Jones & Worrall 1995). As this ratio varies greatly among fungal taxa as well as among substrates and with age (Jones & Worrall 1995; and references therein), however, it is extremely difficult to accurately determine fungal biomass in field settings where fungal communities can be diverse and unevenly distributed. Arthropods are known to influence fungal communities to some extent (Müller *et al.* 2002; Weslien *et al.* 2011), but their impacts on fungal biomass remain largely unknown. Thus, research aimed at better understanding the contributions of arthropods to wood decay would benefit greatly from an improved ability to determine fungal biomass in dead wood.

MEANINGFUL ESTIMATION

It is particularly important for efforts aimed at quantifying the contributions of arthropods to wood decay to include wood that is not obviously colonized or attacked by wood-feeding insects in the calculations. In the south-eastern United States, for example, Gentry & Whitford (1982) only measured the quantity of wood removed from blocks in which 'sufficient channelization [by termites] had occurred'. Without knowing how much wood was removed from the other blocks, it is impossible to know what percentage of the wood loss observed for all blocks can be attributed to termite activity. The claim that 'termites removed between 3% and 12% of the original mass of over one-fourth of the pine blocks during the growing season' is not, therefore, particularly meaningful.

Conclusions

Research on the contributions of arthropods to wood decay under natural conditions is fraught with challenges, and no single experimental protocol is perfect. Some methods are better than others, however. Several general conclusions based on the considerations discussed previously are listed below:

1 The most valuable studies will use naturally occurring, intact woody substrates that are minimally manipulated (i.e. as opposed to machined blocks).

2 Many exclusion methods, such as mesh bags or chemicals, are likely to affect wood decay beyond their effects on the arthropod fauna. Although likely to underestimate arthropod contributions to decomposition, partial exclusion or temporary exposure methods may yield more informative (i.e. less confounded) results.

3 In determining the initial volume or mass of a wood sample, there is a trade-off between measurement accuracy and the realism of the study design. Considerable estimation errors are sometimes unavoidable.

4 Where termites are present, an effort must be made to determine how much soil has been carried into the wood by these organisms. We believe burning to be an accurate way to accomplish this.

5 Improved methods for measuring microbial biomass in dead wood are of particular interest.

6 To be meaningful, efforts to quantify the contributions of arthropods to wood decay must include all wood in the calculation, whether colonized by arthropods or not.

Looking forward, the development of methodology for excluding termites and perhaps other arthropods from small plots of undisturbed soil would be of great interest as this would allow researchers to study wood decay under more natural circumstances. Contact between the soil and dead wood would be more direct compared with many other approaches, for instance. The three-dimensional nature of woody debris could also be more properly preserved using this approach, allowing for some portions to be in contact with the ground while other portions are elevated or suspended in the air. The greatest advantage of this approach would be the ability to measure other services provided by wood-dwelling arthropods. These include improving soil fertility through nutrient mineralization and enhanced soil aeration, plant productivity, etc. (Lavelle *et al.* 1997; Jouquet *et al.* 2011). There is clearly much to be gained from research on this subject, and we hope this paper will aid researchers in planning and carrying out such efforts.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. The photographed end of a log showing how computer software can be used to accurately measure the original cross-sectional area for volume calculations (bark excluded).