

Wood decomposition as influenced by invertebrates

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ABSTRACT

The diversity and habitat requirements of invertebrates associated with dead wood have been the subjects of hundreds of studies in recent years but we still know very little about the ecological or economic importance of these organisms. The purpose of this review is to examine whether, how and to what extent invertebrates affect wood decomposition in terrestrial ecosystems. Three broad conclusions can be reached from the available literature. First, wood decomposition is largely driven by microbial activity but invertebrates also play a significant role in both temperate and tropical environments. Primary mechanisms include enzymatic digestion (involving both endogenous enzymes and those produced by endo- and ectosymbionts), substrate alteration (tunnelling and fragmentation), biotic interactions and nitrogen fertilization (i.e. promoting nitrogen fixation by endosymbiotic and free-living bacteria). Second, the effects of individual invertebrate taxa or functional groups can be accelerative or inhibitory but the cumulative effect of the entire community is generally to accelerate wood decomposition, at least during the early stages of the process (most studies are limited to the first 2–3 years). Although methodological differences and design limitations preclude meta-analysis, studies aimed at quantifying the contributions of invertebrates to wood decomposition commonly attribute 10–20% of wood loss to these organisms. Finally, some taxa appear to be particularly influential with respect to promoting wood decomposition. These include large wood-boring beetles (Coleoptera) and termites (Termitoidae), especially fungus-farming macrotermitines. The presence or absence of these species may be more consequential than species richness and the influence of invertebrates is likely to vary biogeographically.

Key words: arthropods, biodiversity, ecosystem services, insects, Isoptera, saproxylic.

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I. INTRODUCTION

Some [insects] prey upon the soundest timber; while others make no attempt upon it till it begins to decay:--but all contribute, in one way or other, to the same end; one taking up the office, where another resigns it; till that which from its bulk and solidity appeared calculated to last as long as the earth that gave it birth, by the successive efforts of various kinds of insects is reduced in no very long time to its original dust. So powerful are the effects produced by instruments which we too often overlook or despise.

William Kirby, 1800

Although Kirby (1800) wrote these words before the importance of fungi, bacteria and other microorganisms to wood decomposition was known, a substantial body of research conducted over the past century largely supports his contention that invertebrates strongly promote wood decay, at least at the beginning of the process. A large proportion of forest invertebrate species are either dependent on dead wood (e.g. ~20–30% of all forest insects are ‘saproxyllic’) or utilize it opportunistically (Speight, 1989; Stokland, Siitonen & Jonsson, 2012). Major functional groups include phloem and wood feeders, fungus feeders, detritus feeders and predators (Stokland *et al.*, 2012), all of which may have either accelerative or inhibitory effects on decomposition rates. While the suggestion has been made by many researchers that invertebrates, especially termites (epifamily Termitoidae) and wood-boring beetles (various families of Coleoptera), contribute significantly to wood decomposition, their importance in this regard remains largely overlooked. The purpose of this review is to assess what is currently known about the influence of invertebrates on wood decomposition in terrestrial ecosystems. Properly recognizing the ecosystem services provided by saproxyllic invertebrates and other taxa associated with dead wood is particularly important with respect to their threatened status in many parts of the world (Stokland *et al.*, 2012; Ulyshen, 2013).

II. THE DECOMPOSITION PROCESS

Although various physical and chemical defences protect the wood of healthy plants from fungal or invertebrate attack, wood presents a challenge to these organisms even after it dies. Owing to its large size, the presence of decay-resistant compounds and the recalcitrant nature of its main structural compounds (i.e. cellulose, hemicellulose and lignin), dead wood decomposes slowly over the span of decades and can accumulate greatly in forests, often accounting for as much

as 10–25% of above-ground biomass (Muller & Liu, 1991; Delaney *et al.*, 1998; Mobley, Richter & Hein, 2013). In addition to representing an important terrestrial carbon store, dead wood provides a critical resource for a large fraction of biodiversity (Stokland *et al.*, 2012), acts as a short-term sink and long-term source of nutrients, and fuels forest fires. There is therefore great interest in understanding the factors behind wood decomposition that ultimately influence the size of the dead wood pool. Wood decomposition is the transformative process by which cellulose, hemicellulose and lignin are catabolized into smaller units and ultimately mineralized, i.e. returned to the environment in inorganic forms (Swift, Heal & Anderson, 1979). The three main pathways by which this happens are respiration, combustion and physical degradation (Cornwell *et al.*, 2009). Except where fires are common or severe, respiration is by far the most important pathway in most ecosystems (Chambers, Schimel & Nobre, 2001), driven primarily by fungi and other microbes (fungi are hereafter grouped with microbes for convenience even though many decay fungi produce macroscopic structures) capable of producing the enzymes necessary to break down wood (Stokland *et al.*, 2012). Despite the ubiquity of these organisms, however, the strength of the lignocellulose complex seriously constrains decomposition rates. For example, lignin fills spaces between cellulose microfibrils and hemicellulose and acts to protect these compounds from enzymatic attack (Jeffries, 1990).

Other factors limit the activities of microbial decomposers as well, including physical conditions, substrate quality and accessibility. Like all organisms, microbes require a range of physical conditions to survive and function, and are inhibited by extremes in humidity, temperature and oxygen limitation. Such conditions vary at both regional and local scales and with within-wood location. With respect to substrate quality, wood tends to be more nutrient-limiting than other plant tissues like leaves, flowers, seeds, etc. (Käärik, 1974; Woodwell, Whittaker & Houghton, 1975). The nitrogen content of wood, for instance, is only 0.03–0.1% by dry mass compared with 1–5% for most herbaceous tissues (Käärik, 1974, and references therein). In addition, many woody plants produce heartwood, the decomposition of which is inhibited by higher concentrations of extractives (i.e. various waxes, fats, fatty acids and alcohols, steroids, resins, etc.), reduced permeability and water content, and lower nutrient availability relative to sapwood (Panshin & de Zeeuw, 1970; Rayner & Boddy, 1988; Meerts, 2002; Cornwell *et al.*, 2009). Finally, resource accessibility is another limitation faced by microbial decomposers in dead wood. The longitudinal arrangement of the conducting elements in wood inhibits the radial movement of rot fungi, for instance.

The enzymatic breakdown of woody tissues largely drives decomposition with respect to key processes like mineralization and humification. These processes, in turn, are strongly promoted by the mechanical degradation or fragmentation of wood into smaller pieces. This can be brought about by numerous forces including wind damage, breakage upon impact with the forest floor, vertebrate damage or the boring activities of invertebrates. Fragmentation hastens wood decomposition by increasing the area of wood exposed to microbial activity as well as to the environment, thus enhancing accessibility and improving aeration and other microclimatic conditions. Conversely, chemical breakdown promotes fragmentation by undermining the structural integrity of wood.

Wood becomes increasingly infiltrated and degraded by fungi and other microbes as decomposition proceeds, eventually culminating in the incorporation of humus into the soil. There is a succession of wood-feeding arthropod taxa throughout the decomposition process beginning with primary wood feeders capable of digesting sound wood. These include various well-studied groups of Coleoptera (Anobiidae, Bostrichidae, Brentidae, Buprestidae, Cerambycidae, Lymexylidae, Zopheridae), Diptera (Pantophthalmidae, Tipulidae of the genus *Ctenophora*), Lepidoptera (Cossidae, Hepialidae, Sesiidae), Hymenoptera (Siricidae, Xiphydriidae) and Blattodea [all families of termites (currently classified as the epifamily Termitoidea) and cockroaches belonging to the genus *Cryptocercus*]. Other notable wood-destroying taxa do not feed on wood but excavate galleries for the purpose of cultivating fungi (ambrosia beetles) or nesting [various ants (e.g. *Camponotus* spp.), wood-nesting bees (Megachilidae, xylocopine apids), etc.].

These early colonists are gradually replaced by less economically important secondary wood feeders (e.g. some termites, various beetles, etc.) that feed only on decomposing wood and may derive a substantial proportion of their nutrition from microbial biomass. Members of the primarily tropical beetle family Passalidae, for instance, live in subsocial family groups (Costa, 2006) and cause considerable damage to decomposing logs on the forest floor (Preiss & Catts, 1968; Morón, 1985; Castillo & Morón, 1992; Castillo & Reyes-Castillo, 2003, 2009). The substrate consumed by tertiary wood or soil feeders (e.g. some termites, earthworms, scarab beetles) near the end of the decomposition process is particulate and soil-like in nature, largely humified and dominated by microbial activity.

III. THE INVERTEBRATE INFLUENCE

At least 30 studies have explicitly sought to quantify the contributions of invertebrates to wood loss (Table 1). Although methodological differences and design limitations preclude meta-analysis (Harrison, 2011; Ulyshen & Wagner, 2013), these studies consistently support the notion that invertebrates can strongly influence wood decomposition. Additional support comes from a much larger body of literature

focused on the biology and ecology of wood-dwelling invertebrates. Although conspicuous wood-feeders like beetles and termites have been the focus of most research in this area, other invertebrate functional groups (e.g. fungus feeders, detritus feeders and predators) have the potential to influence the decomposition process as well. The various mechanisms by which invertebrates are likely to influence the process can be assigned to four broad and interrelated categories. As outlined below, these are enzymatic digestion, substrate alteration, biotic interactions and nitrogen fertilization.

(1) Enzymatic digestion

The effect of wood-feeding invertebrates on wood decomposition (e.g. mass loss) is a function of volume consumed (or processed by fungus-farming termites) and assimilation efficiency. When present, termites typically consume or process larger volumes of wood than other invertebrate taxa. In the southeastern USA, for instance, Ulyshen, Wagner & Mulrooney (2014) found that subterranean termites (*Reticulitermes* spp.) consumed about six times more wood volume than all other insects combined over a 2-year period. The amount of wood consumed by many beetles is not insignificant, however. For example, Preiss & Catts (1968) estimated that the passalid beetle *Odontotaenius disjunctus* (Illiger) produces five times its live mass in dry frass per week. Termites also tend to exhibit higher assimilation efficiencies than other invertebrates, almost always exceeding 50% and often approaching 100% for cellulose (Wood, 1976; Breznak & Brune, 1994). Termites even rival wood-rotting fungi in terms of wood utilization. As translated and summarized by Lee & Wood (1971a), for instance, Seifert (1962) showed that termites could achieve as much or more wood degradation in one passage through the gut as could the dry-rot fungus *Coniophora cerebella* Pers after 270 days. Lavelle *et al.* (1993) concluded the mineralization of wood is largely complete once it has been consumed by termites. By contrast, beetles typically exhibit much lower rates of assimilation efficiency (see table 15.4 in Haack & Slansky, 1987). Baker, Laidlaw & Smith (1970), for instance, determined that larvae of the beetle *Anobium punctatum* (De Geer) feeding on Scots pine (*Pinus sylvestris* L.) wood utilized about 40% of the ingested cellulose but digested only small amounts of lignin and hemicelluloses. Similarly, Kukor & Martin (1986) reported cellulose assimilation rates for *Monochamus marmorator* Kirby in Richardson of ~27% when fed fungus-infected wood and much lower rates (~4%) when fed a fungus-free diet. The researchers proposed that fungal enzymes ingested by *M. marmorator* and other wood-feeding insects greatly increase the assimilation efficiencies exhibited by these organisms. Any undigested wood is returned to the environment as frass which can then be colonized by microbes and may make additional passages through invertebrate guts.

As mentioned previously, the digestion of lignocellulose requires special enzymes and multiple enzymes are often required for complete catabolism of these complex compounds (Swift, 1977a). The complete degradation of cellulose, for instance, requires a 'cellulase complex' that

Table 1. Chronology of studies aimed at quantifying the contributions of invertebrates to volumetric or gravimetric wood loss*

Reference	Country	Focal taxon/taxa	Main findings
Leach <i>et al.</i> (1937)	USA	Beetles (wood-borers and bark beetles)	Logs unprotected from insects were more decayed and there was a strong correlation between <i>Monochamus</i> spp. activity and heartwood decay
Maldague (1964)	Congo	Termites	Annual consumption equivalent to about half annual litter fall. Lee & Wood (1971 <i>b</i>) revised this figure to 10% or less.
Hopkins (1966)	Nigeria	Termites	Wood decay largely dependent on termites (wood decayed much more rapidly at sites where termites were active)
Preiss & Catts (1968)	USA	Beetles (passalids)	After 4 weeks, an oak log provided to seven passalid beetles was completely riddled with tunnels
Lee & Wood (1971 <i>a</i>)	Australia	Termites (<i>Nasutitermes exitiosus</i>)	Annual consumption equivalent to ~17% annual input of dead wood
Ocloo (1973)	Ghana	Termites (<i>Pseudacanthotermes militaris</i>)	In 65 days, consumed ~3 and ~16% of heartwood and sapwood volume, respectively
Haverty & Nutting (1975)	USA	Termites (<i>Heterotermes aureus</i>)	Based on models using multiple sources of data, annual consumption was estimated to be equivalent to ~17.5% annual input of dead wood
Usher (1975)	Ghana	Termites	Annual consumption equivalent to ~20% annual litter fall, 8–10% annual primary production
Wood (1976)	Nigeria	Termites	Consumption equivalent to ~42–84% of annual litter fall (many assumptions were made in making this estimation)
Abe (1978, 1980)	Malaysia	Termites	Most wood decay can be attributed to termites
Ikeda (1979)	Japan	Beetles (cerambycids)	The cerambycid <i>Phymatodes maaki</i> consumed about 18% of wood volume available in woody vines
Buxton (1981)	Kenya	Termites	'Almost all' dead wood is removed by termites (slowly) with macrotermitines being the most important
Collins (1981)	Nigeria	Termites	Annual consumption equivalent to ~60% of annual wood fall with macrotermitines being the most important
Gentry & Whitford (1982)	USA	Termites (<i>Reticulitermes</i> spp.)	Termites removed 3–20% wood mass (varying widely) within 9 months
Collins (1983)	Malaysia	Termites	Termites consume up to 15–16% of annual litter production
Salick, Herrera & Jordan (1983)	Venezuela	Termites	Termites consume <5% of annual litter and tree fall. Martius (1994) considered this estimate to be too low
Martius (1989)	Brazil	Termites	Termites likely consume at least 20% of the annual wood fall (summarized from Martius, 1994)
Zhong & Schowalter (1989)	USA	Beetles (scolytine ambrosia beetles)	Excavated ~0.2% of sapwood volume during first year
Edmonds & Eglitis (1989)	USA	Beetles (wood-borers and bark beetles)	Wood exposed to beetles decayed more rapidly, due primarily to wood-borer activity
Schowalter (1992)	USA	Insects	Removed ~1% of sapwood volume during first 2 years
Takamura & Kirton (1999)	Malaysia	Termites	Excluding termites did not affect decay rate (based on carbon content) over 3 years
Takamura (2001)	Malaysia	Termites	Termites increase decay rate (based on carbon content) for one of the two wood species tested
Müller <i>et al.</i> (2002)	Finland	Beetles (bark beetles)	Logs protected from insects decomposed significantly more slowly

Table 1. Continued

Reference	Country	Focal taxon/taxa	Main findings
Schuurman (2005)	Botswana	Termites	Macrotermite abundance determines almost all variation in decay rates
Warren & Bradford (2012)	USA	Termites (<i>Reticulitermes</i> spp.)	Wood mass loss 11.5% higher when termites present
Angers <i>et al.</i> (2012)	Canada	Beetles (wood-borers and bark beetles)	Wood density decreased significantly with increasing wood-boring beetle activity
Ulyshen <i>et al.</i> (2014)	USA	Termites (<i>Reticulitermes</i> spp.) and beetles	Termites consumed 15–20% of wood volume after 2 years (much more than beetles) but did not affect mass loss
Ulyshen (2014)	USA	Termites (<i>Reticulitermes</i> spp.)	Approximately 20.5 and 13.7% of wood specific gravity loss after 31 months was attributable to the activity of insects (primarily termites) in seasonally flooded and unflooded forests, respectively
Bradford <i>et al.</i> (2014)	USA	Termites (<i>Reticulitermes</i> spp.)	Termites significantly contributed to mass loss from experimental wooden blocks

*Because it was not possible (even with help from a translator, see Section V) to confirm the results of Mamaev (1961) as summarized in the figure provided by Ghilarov (1967) and later reproduced by Dajoz (2000), this paper is not included here. Indeed, unless further clarification can be provided on the source of the data used to create that figure, the results presented therein should be interpreted cautiously.

includes three major classes of enzymes: the endoglucanases, exoglucanases and β -glucosidases (Watanabe & Tokuda, 2010). Fully exposing cellulose to enzymatic attack requires the degradation of hemicellulose and lignin and these processes involve additional enzymes (Lo, Tokuda & Watanabe, 2011). Most work on invertebrate-mediated enzymatic digestion of plant material has focused on cellulose digestion (Martin, 1983, 1991) whereas lignin degradation by invertebrates remains somewhat controversial (Geib *et al.*, 2008; Scharf & Tartar, 2008; Tartar *et al.*, 2009; Brune & Ohkuma, 2011; Scharf *et al.*, 2011; Sethi *et al.*, 2012; Griffiths *et al.*, 2013). Because a thorough review of this literature is beyond the scope of this article, my goal here is to demonstrate that invertebrates promote the enzymatic degradation of wood by producing their own endogenous digestive enzymes and through endo- and ectosymbiotic relationships with fungi, protists and other microbial organisms. Although discussed separately below, enzymes from both sources act together to affect lignocellulose degradation (Tartar *et al.*, 2009).

(a) Endogenous enzymes

The ability of some wood-feeding invertebrates to produce their own cellulases was unknown until relatively recently. Researchers began to suspect this was the case when termites were found capable of digesting cellulose even in the absence of gut protists (Yokoe, 1964) but this was not fully accepted until endoglucanase genes were discovered in the genomes of termites (Watanabe *et al.*, 1998) and a wide range of other invertebrate taxa (Watanabe & Tokuda, 2001, 2010). Endoglucanase genes belonging to the glycosyl hydrolase family 9 were apparently inherited from an early ancestor of bilaterian animals but have since been lost from all vertebrate and many invertebrate lineages (Lo *et al.*, 2011). Genes encoding β -glucosidases have also been identified in

termites, beetles and other insects (Lo *et al.*, 2011). Although the diversity of cellulase genes encoded in invertebrate genomes is low compared with many cellulolytic microbes and does not permit complete degradation of cellulose, they are thought to play an important role in providing energy for many wood-feeding termites and other invertebrate taxa (Lo *et al.*, 2011).

(b) Endosymbioses

Although much has been learned about the diversity of gut microbes and their importance to the digestion of cellulose (Martin, 1983; Ohkuma, 2003), lignin (Geib *et al.*, 2008) and other compounds, the taxonomy and ecology of these communities remain poorly understood. Only a brief summary of this research is provided here; recent and detailed reviews of the literature are available elsewhere (Ohkuma, 2003; Brune & Ohkuma, 2011; Ohkuma & Brune, 2011; Brune, 2014). Although initially mistaken as parasites (Leidy, 1881), the protists found in the guts of non-termitid termites and *Cryptocercus* cockroaches were among the first endosymbionts of wood-feeding invertebrates to be discovered by biologists. The first experimental evidence that protists play an important role in the digestion of wood was provided by Cleveland (1923) who showed that non-termitid termites quickly die of starvation in the absence of their symbionts. Multiple flagellate species are associated with most non-termitid termite species and these typically perform different functions with respect to the digestion of lignocellulose (Brune & Ohkuma, 2011). Interestingly, these organisms have their own prokaryotic associates (intracellular endosymbionts, surface-attached ectosymbionts or both) that perform a variety of functions including lignocellulose digestion and nitrogen fixation (Brune & Ohkuma, 2011; Ohkuma & Brune, 2011; Desai & Brune, 2012; Brune, 2014).

Free-living bacteria are also common in both non-termitid and termitid termites (i.e. the 'lower' and 'higher' termites, respectively), the typical gut contains several hundred bacterial phylotypes, most of which remain undescribed and have never been cultivated (Ohkuma & Brune, 2011). Tokuda & Watanabe (2007) treated *Nasutitermes takasagoensis* (Shiraki) with antibiotics and saw a significant reduction in cellulase activity in the hindgut, suggesting that some bacteria may play an important role in wood digestion. Similarly, Warnecke *et al.* (2007) conducted a metagenomic and functional analysis of the microbial community inhabiting the hindgut of *Nasutitermes* sp. and documented the presence of various bacterial genes for cellulose and xylan hydrolysis.

It is clear from research on beetles that diverse communities of wood-digesting gut microbes are not limited to termites (Zhang, Suh & Blackwell, 2003; Nardi *et al.*, 2006; Urbina, Schuster & Blackwell, 2013). For example, Suh *et al.* (2003) isolated yeasts from the guts of passalid beetles collected from North and Central America capable of fermenting and assimilating xylose or of hydrolysing xylan, major components of hemicellulose. Several years later, the same team of researchers surveyed the yeast fauna among many more wood-dwelling beetle species and isolated over 650 taxa (Suh *et al.*, 2005). Almost a third of these yeasts were undescribed, underscoring how much remains to be discovered regarding the gut microbes of wood-feeding insects. The females of many stag beetle (Lucanidae) species have a mycangium near the ends of their abdomens containing xylose-fermenting yeasts (Tanahashi *et al.*, 2010). This structure is missing from males as well as from closely related beetle families. The researchers suggest that female lucanids may inoculate their oviposition sites with the yeast to benefit their larvae, especially those feeding on white-rot. Grünwald, Pilhofer & Höll (2010) found 12 previously unknown yeast strains inhabiting the guts of four cerambycid beetle species along with a wide variety of bacteria. Reid *et al.* (2011) estimated that the gut of another cerambycid species, *Prionoplus reticularis* White, harbours at least 1800 bacterial phylotypes including at least one probable symbiont.

(c) *Ectosymbioses (fungiculture)*

Two major groups of invertebrates promote the deterioration of dead wood through ectosymbiotic [often considered agricultural (Farrell *et al.*, 2001; Mueller *et al.*, 2005)] relationships with wood-digesting fungi. The first group consists of ~3400 species of 'ambrosia beetles', belonging to the curculionid subfamilies Scolytinae (which also includes bark beetles) and Platypodinae (Francke-Grosmann, 1967). Ambrosia beetles carry ascomycetous (e.g. species of the genera *Ambrosiella*, *Fusarium*, *Raffaella*) fungal symbionts in specialized glandular structures called mycangia and these organisms are cultivated on the walls of galleries excavated in the wood for this purpose (Francke-Grosmann, 1967; Farrell *et al.*, 2001; De Fine Licht & Biedermann, 2012). The beetles feed and develop almost exclusively on the fungal gardens which often consist of an assemblage of fungi and bacteria in addition to the primary fungal symbiont (Mueller *et al.*,

2005). The larvae of certain species consume and partially digest fungus-infested wood as well, however (De Fine Licht & Biedermann, 2012). Although much remains unknown about the enzymatic utilization of wood by ambrosia fungi or their hosts, De Fine Licht & Biedermann (2012) recently showed that the fungus associated with *Xyleborinus saxesenii* (Ratzeburg) is primarily involved in the degradation of hemicellulose and simple sugars whereas cellulase activity was minimal. Although represented by fewer species and less-well studied, ship-timber beetles (Lymexylidae) are also known to live ectosymbiotically with ascomycetous fungi (*Endomyces* spp.). The fungal symbiont, which is only found growing in association with the larval tunnels, is transmitted by egg-laying females in mycangia located near the end of the ovipositor (Francke-Grosmann, 1967). As seen in some ambrosia beetle species, lymexylid larvae feed on wood in addition to their symbiotic fungi (Francke-Grosmann, 1967; De Fine Licht & Biedermann, 2012). To my knowledge, no effort has been made to explore the nature of enzymatic wood degradation by lymexylid fungal symbionts.

The second major example of ectosymbiosis between invertebrates and wood-decaying fungi involves 'fungus-farming' termites belonging to the subfamily Macrotermitinae. Distributed throughout tropical Africa and Asia, about 330 species of macrotermitines cultivate symbiotic *Termitomyces* spp. fungi (Basidiomycota) within their nests (Wood & Thomas, 1989; Mueller *et al.*, 2005). Akin to the symbioses between leaf-cutting ants and their fungi (Aanen *et al.*, 2002; Nobre, Rouland-Lefèvre & Aanen, 2011), *Termitomyces* spp. grow on wood and other plant material provided by the termites. How the termites benefit from the relationship varies among genera (Rouland, Lenoir & Lepage, 1991; Hyodo *et al.*, 2003; Ohkuma, 2003; Nobre *et al.*, 2011). For example, Hyodo *et al.* (2003) showed that the main role of the fungi for *Macrotermes* spp. is to degrade lignin whereas the fungi itself serves as the food source for members of other genera. As mentioned previously, macrotermitines are thought to contribute more to wood decomposition than other termite taxa (Buxton, 1981; Collins, 1981, 1983; Schuurman, 2005). Their ectosymbiosis with *Termitomyces* spp. allows them to process wood more quickly than species reliant on gut microbes (Schuurman, 2005). In addition, a greater proportion of the wood processed by the macrotermitine–*Termitomyces* partnership is assimilated, especially lignin (Brune & Ohkuma, 2011).

(2) Substrate alteration

(a) *Tunnelling*

The holes and tunnels created by wood-consuming and excavating invertebrates vary greatly in size and location depending on the taxa involved. Phloem-feeders are among the first insects to colonize a fresh piece of dead wood, targeting the soft and nutritious layers beneath the outer bark. Accessing the phloem typically involves boring through the outer layer of protective bark, resulting in open holes through which other organisms may gain entry. While some

phloem-feeders, such as many bark beetles, remain confined to the cambial region, many cerambycids, buprestids and other taxa begin tunnelling through the wood later in development, thus becoming xylophagous (Graham, 1925). The depth and extent of these tunnels vary greatly depending on the species. Some are shallow and are confined to the sapwood whereas others pass through the heartwood and can reach the centres of logs. There are three ways by which tunnelling is likely to affect wood decomposition: by facilitating colonization by microbes and other organisms, by improving aeration and by promoting fragmentation.

By permitting entry to airborne spores and by providing avenues of least resistance for hyphal penetration (Rayner & Boddy, 1988), researchers have long suggested that tunnels created by bark and wood-boring insects may accelerate the decay process. Richards (1926, p. 278), for instance, stated that ‘the holes formed [by insects attacking pine stumps] allow fungi to enter and their mycelia soon become abundant under the bark and in the wood’. Schowalter *et al.* (1992, p. 380) echoed this view years later by stating that ‘penetration of the bark barrier by xylophagous insects is critical for colonization by decomposer fungi’. Although there is little evidence that invertebrates accelerate wood decay significantly by creating holes through bark, the tunnels created by wood-boring species appear to accelerate the establishment of rot fungi. Perhaps the earliest and best support for this comes from an exclusion study carried out by Leach, Orr & Christensen (1937) who showed that the boring activities of *Monochamus* spp. (Cerambycidae) in red pine (*Pinus resinosa* Aiton) substantially accelerated heartwood decay [especially by the fungus *Phlebiopsis gigantea* (Fr.) Jülich]. This was especially evident in logs with sealed ends where decay spread very slowly into the heartwood except where access was provided by *Monochamus* spp. tunnels (the fungi spread easily throughout the sapwood regardless of insect activity, however). Because the researchers were unable to isolate *P. gigantea* from *Monochamus* spp. eggs, larvae, larval frass or adults, it was concluded that the tunnels themselves were what facilitated establishment by the fungus. In the same study, by contrast, Leach *et al.* (1937) found no evidence that fungi were aided by the tunnels created by large buprestid beetle larvae. This difference was attributed to the fact that *Monochamus* spp. larvae expel frass from their tunnels whereas buprestid larvae do not (i.e. open *versus* closed tunnels, respectively). The importance of *Monochamus* spp. in facilitating the establishment of wood rot fungi relative to other tunnelling beetles was later shown by Edmonds & Eglitis (1989) in Washington State, USA. Douglas-fir bark beetles had comparatively little effect on decomposition. Similarly, in Canada, Angers, Drapeau & Bergeron (2012) associated lower wood densities with cerambycid activity whereas bark beetle activity appeared to have no such influence. Müller *et al.* (2002) reported a positive relationship between wood mass loss and bark beetle activity in Europe, however. The greater influence of cerambycids on wood decay can probably be attributed to their galleries being larger and longer than those of bark beetles and open tunnels are probably more important in this regard than

frass-filled tunnels. As pointed out by Dowding (1984), it should be mentioned that invertebrate tunnels are probably of minimal importance to the establishment and spread of wood rot fungi in highly fragmented or cross-cut debris where the vascular tissue is exposed to fungal colonization.

Tunnels may facilitate colonization by other invertebrates as well and this is likely to accelerate humification and nutrient export in the latter stages of decomposition (Swift, 1977a). In a study of invertebrates associated with dead wood at different stages of decay in the southeastern USA, Ausmus (1977) observed that many secondary invertebrate colonists (earthworms and other annelids, Collembola, Symphyla, nematodes, centipedes and mites) entered wood after tunnelling by termites and other primary colonists. In Malaysia, Abe (1980) noticed termites entering wood through holes made by beetles.

The second way by which tunnels may promote decomposition is by improving gas exchange (Carpenter *et al.*, 1988). Wood-rotting fungi generally respond negatively to increasing concentrations of carbon dioxide and positively to increasing oxygen concentrations (Jensen, 1967) and this appears to be especially true with respect to lignin degradation (ten Have & Teunissen, 2001). The degree to which tunnels have an aerating effect is likely to depend on various factors. Whether a tunnel is open or frass-filled will have obvious implications for gas exchange, for instance. In addition, tunnels could conceivably reduce aeration if they were to increase the moisture-holding capacity of wood (Harmon *et al.*, 1986), although they are generally thought to have the opposite effect (Swift & Boddy, 1984). Finally, the effect of tunnels on aeration may depend on the level of invertebrate activity occurring within the tunnels. Paim & Beckel (1963) found the presence of large cerambycid larvae to have no effect on gas concentrations relative to uninhabited tunnels, however.

Finally, the tunnelling activities of wood-boring arthropods can promote fragmentation by undermining the structural integrity of wood. This is especially true for standing dead trees. Based on their study of insect succession in hickory (*Carya* spp.), for instance, Blackman & Stage (1924, p. 9) noted that ‘the burrows of insects in the wood of a tree not only very much hasten the process of decay but also often greatly weaken it mechanically and cause the tree to fall much sooner than it would otherwise’. The authors specifically noticed that concentrations of burrows created by the ambrosia beetle *Xyleborus celsus* Eichh. determined the line along which the sapwood broke. Speeding the fall of dead trees and branches is an important contribution because wood in contact with the forest floor decomposes much more quickly than standing or suspended wood (Swift *et al.*, 1976; Swift & Boddy, 1984). Fragmentation also improves gas exchange which, as discussed above, is known to favour fungal activity.

(b) Fragmentation

(i) *Wood.* Aside from weakening woody stems, thereby accelerating breakage and tree fall (see Section III.2a), there

are two additional pathways by which invertebrates are likely to promote wood fragmentation. First, wood-dwelling invertebrates provide a food source for foraging woodpeckers and other vertebrates. These organisms commonly remove large chunks and smaller chips of wood during their search for wood-dwelling insects. Second, wood-boring invertebrates also produce a variety of fine particulate matter or boring dust during the excavation of tunnels and galleries. A wide range of wood fragment sizes can therefore be attributed in part, either directly or indirectly, to invertebrate activity. How decomposition rates vary across the range of fragment sizes is not clear but several studies suggest a non-linear relationship with differential responses among decomposers. Coarse fragmentation is likely to accelerate decomposition by exposing more surfaces to microbial attack and to the environment. This is readily apparent in fragmented logs on the forest floor where wood is often obviously more decomposed near the points of breakage than near the centres of the fragments. Experimental support for this comes from Boddy (1983) who found that the rate of wood decomposition under laboratory conditions could be increased by more than 40% (as measured by carbon dioxide production) by cutting branches in half, due to improved oxygen availability in the shorter sections of wood. Although fine fragmentation, such as the production of boring dust by invertebrates, has been assumed to accelerate microbial decomposition further (Harmon *et al.*, 1986), recent research suggests this may not be the case. In laboratory mesocosm experiments, van der Wal *et al.* (2007) found wooden blocks to decompose faster than sawdust. Fungi were less active in the sawdust whereas bacteria exhibited the opposite pattern. These findings suggest that decreasing fragment size only promotes fungal decomposition up to a point beyond which there is an inhibitory effect. Invertebrate frass represents a special category of woody particulate matter. As discussed below, there is some evidence that microbial activity is increased on frass.

Wood-feeding invertebrates are also sensitive to the size of their resource. In Washington State, for instance, Edmonds & Eglitis (1989) reported higher decay rates in larger-diameter logs, possibly because these were attacked more readily by the wood-boring beetle *Monochamus scutellatus* Say. Similarly, Abe (1980) found termites to attack sections of tree trunks and large branches much more readily than small branches in a Malaysian forest. Not all wood-feeding invertebrate taxa prefer larger resources, however; some termite taxa preferentially attack smaller pieces of wood as assessed using vibrational signals (Evans *et al.*, 2005). Wood fragmentation and fragment size therefore have important consequences with respect to wood-feeding insect activity and decomposition rates.

Although woody particulate matter may decay more slowly compared with larger fragments in the external environment, the fine fragments created and consumed by wood-feeding invertebrates represent a special case worth mentioning here. Some of the highest rates of wood degradation occur in the guts of these organisms. The

hindgut of termites is dilated which reduces the transit time for ingested particles and increases their exposure to intestinal microbes and associated enzymes (Brune & Ohkuma, 2011). Moreover, the ingested fragments are small enough to be phagocytosed by symbiotic protists in the guts of non-termitid termites. Similarly, Bayon (1981) showed the hindgut of larval *Oryctes nasicornis* (L.), a species of scarab beetle, to be swollen and filled with bacteria, thus functioning as a fermentation chamber for wood fragments.

(ii) *Bark*. Although poorly studied, the contributions of invertebrates to the fragmentation of bark may also have important consequences for wood decomposition. Early-arriving phloem-feeding species, for instance, bore holes through bark, help separate the bark from the wood and provide food for foraging vertebrates. All of this is likely to accelerate bark loss, especially from standing dead trees. Evidence for such a relationship comes from Weslien *et al.* (2011) who found a negative correlation between the number of emergence holes by the cerambycid *Monochamus sutor* (L.) and the percentage of bark remaining on tall stumps after 10 years in Sweden. Whether bark loss accelerates or slows wood decomposition depends on how wood moisture changes relative to the requirements of the decomposer community. Because bark retains moisture, its loss may retard decomposition in many situations. Standing dead trees, for instance, lose bark more quickly than fallen trees and this may be one reason why they dry out more quickly and decompose more slowly. Although no experimental studies have been conducted to explore the importance of bark to wood decomposition, Blackman & Stage (1924) observed that removing the bark from a dead hickory tree (*Carya* sp.) greatly delayed decomposition and tree fall.

(3) Biotic interactions

(a) Microorganisms

As discussed below, there are two main ways by which invertebrates are likely to interact with microbes in dead wood; by affecting microbial activity and by altering microbial community characteristics. Although poorly studied, both mechanisms are likely to alter decomposition rates and may even outweigh the direct effects of invertebrates on wood decomposition (Hättenschwiler, Tiunov & Scheu, 2005).

(i) *Microbial activity*. Invertebrates have the potential both to promote and retard microbial activity. As already discussed in previous sections, positive influences on fungal activity include facilitating the establishment of rot fungi by creating tunnels into the heartwood and promoting wood fragmentation. The tendency of many termites to carry soil into wood (Greaves, 1962; Abe, 1980; Grove, 2007; Ulyshen *et al.*, 2014) may also promote wood decomposition by microbes. Support for this idea comes from a study carried out in Malaysia in which Abe (1980) noticed that heartwood in contact with soil carried in by termites was softer and more decayed than the surrounding wood. Bacterial communities also appear to be influenced by invertebrate activity. These

organisms are thought to benefit from the particulate matter (e.g. frass, boring dust, etc.) created by wood-feeding insects, for instance (Ausmus, 1977; Kitchell *et al.*, 1979; van der Wal *et al.*, 2007). The implications of this for nitrogen fixation within decomposing wood are discussed in Section III.4.

As mentioned previously, wood is only partially decomposed after a single passage through an invertebrate and some taxa are less efficient assimilators than others (e.g. beetle larvae assimilate consumed wood less efficiently than termites). In what Mason & Odum (1969) referred to as an external rumen, fresh frass is colonized and further digested by microbes before reingestion by invertebrates of the same or different species (Szlávecz & Pobożny, 1995). Some invertebrates have been shown to feed preferentially on decayed frass (i.e. several weeks old) compared with fresh frass (Hassall & Rushton, 1985). After assimilating the substrates made available by the previous round of microbial activity, the cycle repeats with the production of fresh frass. Mason & Odum (1969) found the passalid beetle *Odontotaenius disjunctus* (Illiger), a wood-feeder associated with moderately decayed logs, to be highly dependent on such frass cycling. Indeed, individuals deprived of frass were found to lose weight rapidly and die prematurely. Wood-feeding invertebrates with higher assimilation efficiencies, by contrast, such as the cockroach *Cryptocercus punctulatus* Scudder, supposedly benefit less from the reingestion of their frass (Burnett, Mason & Rhodes, 1969). For instance, the caloric value of *O. disjunctus* frass was shown to increase by about 10% after a period of 7 days but no such increase was observed for *C. punctulatus* frass (Burnett *et al.*, 1969). Frass and other forms of particulate woody matter, sometimes collectively referred to as wood mould (Kühnelt, 1976) or tree humus (Speight, 1989), accumulate as decomposition proceeds. Many invertebrates associated with decomposing wood consume this material (Kühnelt, 1976; Szlávecz & Pobożny, 1995), including various tree-hole specialists (e.g. scarabaeids) and key non-saprophytic soil taxa such as earthworms (Speight, 1989). Microbes appear to be especially active on the fresh frass produced by invertebrates (Ghilarov, 1970), perhaps due to the intense mixing which occurs during gut passage (Lavelle *et al.*, 1997) and to the higher nutritional quality and partially degraded nature of this material (Jönsson, Méndez & Ranius, 2004; Micó *et al.*, 2011). Swift & Boddy (1984) reported some unpublished data suggesting that microbes decompose *Tipula* spp. frass about four times faster than branch wood, for instance. Similarly, soil microbes are 3–13 times more abundant in earthworm castings than in the surrounding soil (Ghilarov, 1970). The positive feedback between coprophagous invertebrates and microbes presumably promotes the degradation of lignocellulose as well as humification and the stability of soil organic matter (Swift & Boddy, 1984). Although such relationships remain largely unstudied, some support for this notion was provided by Striganova (1968) who reported substantial increases in the concentration of humic substances (humic and fulvic acids) in the excrement of earthworms feeding on wood relative to the original food material. No such differences were observed for isopods feeding on the same

material, however. It should be noted that not all frass produced by wood-feeding invertebrates is recycled within woody debris. For example, termites often transport ingested wood back to their nests, away from their feeding areas.

Microbial activity can also be inhibited by invertebrates in important ways. For example, Warren & Bradford (2012) found the presence of ants to reduce the rate at which wood decomposed in the southeastern USA. In addition to the ants preying upon termites and possibly other wood-feeding insects, these results were attributed in part to the antimicrobial compounds ants secrete from their metapleural glands. Although these secretions have been shown in previous work to inhibit the growth of fungal mycelia in the soil, this is one of the only studies to demonstrate the effect specifically within dead wood. The secretions and behaviours of termites are also known to have antimicrobial effects (Rosengaus, Guldin & Traniello, 1998; Rosengaus, Lefebvre & Traniello, 2000; Hamilton, Lay & Bulmer, 2011; Bulmer *et al.*, 2012) but it is not clear how these affect wood decomposition.

A recent review of laboratory microcosm experiments by A'Bear, Jones & Boddy (2014) demonstrates that, depending on the species involved, invertebrates can exert a strong influence on wood decomposition by grazing on the mycelia of decay fungi. Their meta-analysis indicates that, on average, direct mycelial grazing by invertebrates reduces fungal growth and increases wood decomposition. Up to a point, decay fungi are thought to compensate for mycelial damage caused by grazing by increasing enzyme activity and this, in turn, results in more rapid wood decomposition (A'Bear *et al.*, 2014). There is a level of mycelial damage beyond which grazing has a neutral or negative effect on wood decomposition, however. The effects of invertebrate grazing on fungal growth and wood decomposition were shown to vary greatly depending on the fungal and invertebrate species examined. Whereas grazing by micro- (nematodes) and meso-invertebrates (collembolans, enchytraeids and oribatid mites) did not significantly affect wood decomposition, grazing by macro-invertebrates (including a species of millipede and an isopod) sped up decomposition. Moreover, the effects of individual invertebrate species on fungal growth and wood decomposition varied among fungal species, as determined by differences in palatability and food preferences. The implications of these findings for wood decomposition outside the laboratory, where numerous species of decay fungi coexist and compete for resources, remain poorly understood.

(ii) *Microbial community characteristics.* Differences in microbial richness, community composition and colonization order are known to affect wood decomposition. A number of studies, for instance, have shown a positive relationship between fungal taxonomic richness and decomposition rates, presumably due to functional complementarity among the species involved (Gessner *et al.*, 2010; Nielsen *et al.*, 2011; van der Wal *et al.*, 2013). Other studies have reported a negative relationship, by contrast, perhaps due to competition for space among the interacting species (Fukami *et al.*, 2010). The composition of these communities may be

of greater consequence than species richness *per se*, however, especially with respect to the representation of key functional groups such as cord-forming basidiomycetes (Moorhead & Sinsabaugh, 2006; Crowther *et al.*, 2013). There has recently been much interest in 'priority effects' with respect to community structure and ecological function. By experimentally manipulating the arrival order of fungal colonists in wood, for instance, Fukami *et al.* (2010) caused threefold differences in fungal species richness and decay rates. Subsequent work by Dickie *et al.* (2012) showed that assembly history effects do not attenuate at higher levels of ecological organization, i.e. priority effects can strongly affect key ecosystem processes such as wood decomposition. Invertebrates, therefore, have the potential to affect wood decomposition strongly by altering microbial community characteristics. This may involve substrate modification, direct interactions with microbes or some combination of both.

With respect to substrate modification, the importance of deep and open tunnels to the establishment of rot fungi in heartwood has already been discussed (Leach *et al.*, 1937). If the activities of tunnelling invertebrates hasten the establishment of specific fungal taxa, there may be lasting priority effects with respect to fungal community structure and decomposition rates (Fukami *et al.*, 2010). The comminution of wood by invertebrates is another form of substrate modification likely to be important to microbial communities. Among the first to suggest this was Ausmus (1977) who concluded that the creation of particulate matter by tunnelling arthropods shifts the competitive advantage from fungal to bacterial species. Swift & Boddy (1984) reached a similar conclusion from a comparison of microbial communities before and after small branches were invaded by invertebrates. Whereas the communities prior to invasion were dominated by basidiomycetes, non-basidiomycetes (e.g. Mucorales, *Trichoderma* spp., *Penicillium* spp., etc.) dominated post-invasion. Bacterial numbers were also higher in branches invaded by invertebrates. The researchers suggested that these species may be better adapted to live on insect frass, boring dust and other particulate wood resources than are mycelial fungi (Swift & Boddy, 1984). More recent work by van der Wal *et al.* (2007) supports the notion that comminuted wood favours bacterial growth over fungal growth.

Direct interactions with microbes can take many forms. The transport or vectoring of non-symbiotic microbes is a major mechanism by which invertebrates may influence the assembly history of microbial communities. Bark and wood-boring beetles commonly carry spores of decay fungi upon their bodies as they disperse from one woody resource to another, for instance (Harrington, Furniss & Shaw, 1981; Pettey & Shaw, 1986; Persson *et al.*, 2009), and many of these can be found growing within their galleries (Persson, Ihrmark & Stenlid, 2011). Although the blue-stain fungi vectored by bark beetles generally digest the contents of dead woody cells and play no part in the enzymatic degradation of wood (Käärik, 1974), they may nevertheless influence the decomposition process by inhibiting other fungi. As summarized by Käärik (1974), for example, von Pechman

et al. (1967) showed that *Stereum* spp. fungi decomposed wood previously colonized by blue-stain and mould fungi less rapidly than sound wood. Although wood-rotting fungi do not require invertebrates to colonize dead wood, often relying on the wind dispersal of spores instead, invertebrates are more dependable colonization vehicles and may appreciably hasten fungal colonization and alter the colonization history of the microbial community. For example, Weslien *et al.* (2011) reported a positive association between the bark beetle *Hylurgops palliatus* (Gyll.) and the fungus *Fomitopsis pinicola* (Sw.) in Sweden. Because the flight time of *H. palliatus* coincides with *F. pinicola* sporulation, there is a strong possibility that the beetles vectored spores of the fungus. No such associations were detected between *F. pinicola* and scolytine beetle species with different flight periods in that study, by contrast, and the fungus appeared to be inhibited by the cerambycid *Monochamus sutor*. Similarly complex interactions were reported from Finland by Müller *et al.* (2002) who found a negative correlation between fungal taxonomic richness (i.e. the number of operational chemotaxonomical units) and the amount of *H. palliatus* damage. Some individual fungal taxa appeared to be facilitated by bark beetle activity in that study whereas others were inhibited. Such findings suggest the composition of the invertebrate community has important implications for microbial community characteristics and possibly also for decomposition rates.

Another important direct interaction involves the targeted consumption of fungi by invertebrates. Many invertebrate species graze on fungal mycelia (Ingham, 1992), for instance, and this can alter interspecific interactions among fungal species. While this has been shown to a limited extent for microarthropods such as collembolans in leaf litter (Newell, 1984*a,b*), stronger effects have been observed from studies of macroarthropods such as isopods and millipedes. For example, Crowther, Boddy & Jones (2011) recently showed that isopods in soil and wood could prevent the competitive exclusion of two fungal species by preferentially feeding on a third cord-forming species. Subsequent work using woodland-soil mesocosms found that intense grazing of basidiomycete cords by isopods significantly increased fungal diversity, altered fungal community composition, reduced the fungal:bacterial ratio and increased Collembola abundance (Crowther *et al.*, 2013). According to the researchers, this represents the first conclusive evidence for top-down control of fungal communities. Interestingly, the increase in fungal diversity resulting from isopod activity corresponded with reduced cellulolytic activity. This was caused by a shift away from communities dominated by basidiomycetes, the species most responsible for the decomposition of lignocellulose. Because cord-forming basidiomycetes dominate fungal communities in many temperate and boreal forest soils (Boddy, 1999) and many invertebrates appear to focus their feeding activities on these organisms (Crowther, Boddy & Jones, 2012), the alteration of fungal communities and reduction of decay rates by fungus-grazing invertebrates may be widespread.

(b) Invertebrates

As for the interactions with microbes summarized above, interactions among invertebrates may influence decomposition rates by altering the activities or community characteristics of these organisms. No previous studies have explored the relationship between invertebrate diversity and wood decomposition rates but, as for microbial communities, the composition of these communities may be more important than species richness *per se* (Hättenschwiler *et al.*, 2005). The presence and activities of keystone taxa such as large wood-boring beetle larvae and termites have been shown to be especially influential. This was demonstrated most clearly by Schuurman (2005) who could explain almost all the variation he observed in wood decomposition rates in Botswana by whether or not macrotermitines were present.

(i) Invertebrate activity. A large proportion of saproxylic and non-saproxylic invertebrates in decomposing wood are predators or parasitoids (Stokland *et al.*, 2012) and these organisms have the potential to influence decomposition rates by controlling the numbers of wood-boring beetles, termites and other key taxa. Although I am not aware of any studies addressing this question with regard to wood decomposition, studies on litter decomposition support the notion that predators can alter decomposition rates by affecting invertebrate populations. The magnitude and direction of this influence appears to depend on the sizes and diets of the organisms involved and environmental conditions such as rainfall patterns (Kajak, 1995; Lawrence & Wise, 2000, 2004; Lensing & Wise, 2006). In Costa Rica, McGlynn & Poirson (2012) found ants to accelerate litter decomposition, presumably by reducing populations of invertebrates that graze on microbial decomposers.

(ii) Invertebrate community characteristics. Competitive exclusion, apparent competition and other forms of interference among invertebrate taxa also have the potential to alter decomposition rates, especially when involving major wood-boring taxa. Gardiner (1957) studied the colonization patterns of beetles following a severe burn in Ontario and found *Monochamus* sp. to avoid laying eggs on the bark of trees already heavily infested by bark beetles. Because *Monochamus* spp. have been shown to promote wood decay, the exclusion of this genus by phloem-feeding bark beetles may affect decomposition rates. Conversely, *Monochamus titillator* (Fabricius) larvae have been shown to compete strongly for phloem resources with larval bark beetles (Coulson *et al.*, 1976), underscoring the importance of life stage in determining the nature of interspecific interactions among such species. Termites are also likely to exclude other insects from dead wood. In Malaysia, for instance, Abe (1980) suspected that certain beetle taxa promoted wood decomposition but these species became scarce following colonization by termites. Moreover, Linsley (1959) suggested that competition from termites may explain why a greater proportion of cerambycids in tropical forests are live-stem borers as larvae and why cerambycids are more common in mangrove swamps where termites are less active.

(4) Nitrogen fertilization

Nitrogen is among the most limiting nutrients in many terrestrial ecosystems and, as discussed previously, is present at particularly low concentrations in woody tissues. Nitrogen limitation seriously constrains wood decomposition rates, in part because the enzymes used by microbes to break down wood are particularly nitrogen rich (Cornwell *et al.*, 2009), and experimental addition of nitrogen to wood has been shown to accelerate decomposition by fungi (Findlay, 1934; Allison *et al.*, 2009; Bebbler *et al.*, 2011). Decomposers are not limited to the nitrogen available in wood tissues, however. A wide variety of imports and exports determine the actual concentration of this element available during the decomposition process (Swift & Boddy, 1984). Dead wood is thought to act as a nutrient sink in the early stages of decomposition, as nitrogen is introduced and immobilized by fungi and other organisms (Swift *et al.*, 1979; Boddy & Watkinson, 1995). One of the most important examples of this involves the translocation of nitrogen from the soil into the wood by cord-forming fungi (Boddy, 1999). Additional, though less important, movements of nitrogen into wood involve precipitation and colonizing arthropod and microbial propagules (Ausmus, 1977). Only later in the decay process is dead wood thought to become a source of nutrients, a transition thought to be facilitated greatly by arthropod activity (Swift, 1977*a,b*; Swift & Boddy, 1984; Takamura & Kirton, 1999; Takamura, 2001). Additional, although less important, exports of nitrogen include transport by mycelial fungi to less nutritious substrates, and dispersing arthropods and microbes (e.g. spores) (Wood, 1976).

In addition to the accumulation and redistribution of nitrogen from the existing nutrient pool, decomposing wood indirectly acts to input nitrogen to the system by providing a resource for free-living nitrogen-fixing bacteria. Although the importance of wood to these organisms relative to other substrates is not known, it is clear that many bacteria within wood are capable of fixing nitrogen and contribute to the availability of this essential element (Larsen, Jurgensen & Harvey, 1978; Hendrickson, 1991; Brunner & Kimmins, 2003). Of 130 Gram-negative bacterial isolates recovered from decaying white fir [*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.] trees, for instance, over half were found capable of fixing atmospheric nitrogen (Aho *et al.*, 1974). As discussed previously, the comminution of wood by invertebrates is thought to promote bacterial activity, including nitrogen fixation. For example, Ausmus (1977) compared nitrogen fixation rates among the full range of wood decay classes and found them to be greatest during the channelization phase during which termites, ants, passalid beetles and other insects were actively tunnelling through wood. Nitrogen fixation appeared to be highest in the frass-filled tunnels of these insects, leading the researcher to surmise that frass was a preferred substrate for nitrogen-fixing bacteria. Subsequent laboratory studies provided some support for this idea, showing that carbon to nitrogen ratios decrease substantially when termites are present (Kitchell *et al.*, 1979).

Nitrogen fixation also occurs within the guts of wood-feeding invertebrates as first detected in termites (Benemann, 1973; Breznak *et al.*, 1973) and since shown for the cockroach *Cryptocerus punctulatus* Scudder (Breznak, Mertins & Coppel, 1974), the lucanid *Dorcus rectus* (Motschulsky) (Kuranouchi *et al.*, 2006), scolytine curculionids of the genus *Dendroctonus* (Bridges, 1981; Morales-Jiménez *et al.*, 2013, 2009), and the scarabs *Osmoderma eremita* (Scopoli) (Jönsson *et al.*, 2004) and *Cetonia aurataeformis* Curti (Micó *et al.*, 2011). Some of this nitrogen is incorporated into the tissues of the host (Bentley, 1984), thus relieving the limitations imposed by the high carbon:nitrogen ratios encountered by wood-feeding invertebrates (Tayasu *et al.*, 1994; Nardi, Mackie & Dawson, 2002). The remainder of the nitrogen is apparently excreted along with the frass. Several studies have shown the frass of scarab larvae to contain higher nitrogen contents than the consumed material in decomposing wood, for instance (Jönsson *et al.*, 2004; Micó *et al.*, 2011). Whereas for beetles this material becomes externally available to microbes and other invertebrates, the nitrogen fixed within termite guts is somewhat conserved within the colony due to the habit of proctodeal trophallaxis common among these species (Bentley, 1984; Machida *et al.*, 2001). The nitrogen fixed from the atmosphere and incorporated into the tissues of wood-feeding insects is either leached into the soil locally or gets disseminated widely as these organisms disperse (e.g. winged reproductive termites) or becomes incorporated into higher trophic levels.

The importance of insect-mediated nitrogen fixation to wood decomposition and long-term forest fertility are important yet poorly resolved questions (Nardi *et al.*, 2002). Curtis & Waller (1998) estimated that the gut symbionts of *Reticulitermes* spp. fix several grams of nitrogen per log per year in the southeastern USA. In Thailand, Yamada *et al.* (2006) only detected nitrogen-fixing activities from wood/litter-feeding termites and not from fungus-growers or soil-feeders. At an ecosystem scale, the researchers estimated the amount of nitrogen fixed by termites in dry deciduous forests and dry evergreen forests to be 0.21 and 0.28 kg ha⁻¹ year⁻¹, respectively, which amounts to 7–22% of the total nitrogen fixation occurring in plant debris on the forest floor. Yamada *et al.* (2006) suggested that although the amount of nitrogen fixed in termite guts is relatively small compared with other inputs (e.g. precipitation, plant symbionts), nitrogen-fixing termites are likely to have an important fertilizing effect on decomposers at the centres of fresh logs, thus promoting decomposition.

IV. CONCLUSIONS

(1) Writing nearly two centuries after Kirby (1800) reached the same conclusion (see Section I), Speight (1989) stated that ‘the silent majority of the saproxylics, performing their age-old task of recycling wood through the forest ecosystem, fade into oblivion, their role unrecognized and their fate unremarked. Their contribution to the dynamics of natural forests has indubitably been generally

under-appreciated, and recognition of the need to conserve them has dawned late’. These words demonstrate how little progress has been made in changing our perceptions about the ecological importance of dead wood invertebrates. This is now beginning to change, as evidenced by the body of literature reviewed herein. Indeed, enormous strides have been made in our understanding of the diversity and ecology of invertebrates associated with dead wood, their interactions with microbial decomposers and how they influence wood decomposition.

(2) Wood decomposition is largely driven by microbial activity in most terrestrial environments but invertebrates also play a significant role. Four broad mechanisms by which they are likely to influence the process include enzymatic digestion, substrate alteration, biotic interactions and nitrogen fertilization. The effects of individual invertebrate taxa or functional groups can be accelerative or inhibitory but the net cumulative effect of all invertebrates is almost certainly accelerative, at least during the early stages of decomposition. Some taxa appear to be particularly influential with respect to promoting wood decomposition. These include large wood-boring beetles and termites, especially fungus-farming macrotermitines. The presence or absence of these species may be more consequential than species richness or other community metrics.

(3) Although the literature currently available strongly supports the contention that invertebrates contribute substantially to wood decomposition, much remains unknown about the nature, magnitude and wider implications of this influence. Three research areas are of particular interest. First, there is great need for long-term studies addressing the role of invertebrates in wood decomposition. Whereas wood often requires many decades or even centuries to decompose completely, studies attempting to quantify the contributions of invertebrates to the process have been almost entirely limited to the first 3 years. Due to the succession of organisms and changing nature of the substrate over time, it is impossible to predict the effect of invertebrates over the entire process. Secondly, the unequal importance of different invertebrate taxa to wood decomposition and the uneven distribution of these species across the globe (Eggleton & Tayasu, 2001; Jones & Eggleton, 2011; King, Warren & Bradford, 2013) suggest that the contributions of invertebrates to wood decomposition are likely to vary biogeographically. Research aimed at identifying the most influential taxa and elucidating distributional patterns would benefit efforts to improve global decomposition models. Finally, efforts to explore the connection between invertebrate-accelerated wood decomposition and forest productivity would be of great interest.

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