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The cover uncovered: Bark control over wood decomposition

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Abstract

1. Woody debris (WD) represents a globally significant carbon stock and its decomposition returns nutrients to the soil while providing habitat to microbes, plants and animals. Understanding what drives WD decomposition is therefore important.
2. WD decomposition rates differ greatly among species. However, the role of bark in the process remains poorly known.
3. We ask how, and how much, interspecific variation in bark functional traits related to growth and protection have afterlife effects on the decomposition of wood, partly mediated by animals. We examine the roles of bark cover and bark traits throughout the wood decomposition process.
4. *Synthesis*. We find that: (1) bark effects on WD decomposition are species- and wood size-specific, (2) bark can enhance coarser WD decomposition but slows twig decomposition in some species, and (3) bark acts as an environmental filter to faunal assemblages in the early stage of wood decomposition. We highlight the need to account for bark effects on WD decomposition and offer an important complementary contribution to including woody species identity effects in biogeochemical and climate-change models via species bark traits.

KEYWORDS
arthropod, bark traits, carbon cycling, coarse woody debris, decomposition, ecosystem function, fungi, species identity effect

1 | INTRODUCTION

Woody debris (WD), comprising the dead remains of trees and shrubs, represents a large amount of organic matter, with estimates of the carbon pool in WD ranging from 36 to 72 petagrams (Pg) globally (Pan et al., 2011; Russell et al., 2015). Since most of the carbon released through decomposition is returned to the atmosphere as carbon dioxide (Chambers, Schimel, &

Nobre, 2001), WD decomposition represents a major global carbon flux, recently estimated at 8.6 Pg per year (Luyssaert et al., 2007), amounting to *c.* 0.9 times the global anthropogenic emissions (Le Quere et al., 2012). The bark covering wood makes up *c.* 13.9% (overall diameter [0.5–98 cm] median value calculated for Eurasia from Schepaschenko et al. (2017), but up to 25.2%, 16.9% and 11.49% for diameter classes of [0.5–2 cm], [2–10 cm] and [10–98 cm], respectively) of the total dry woody stem plus bark biomass. Moreover, bark represents an important tissue to consider because of its potential role in determining the rate of WD decomposition (Dossa, Paudel, Cao, Schaefer, & Harrison, 2016) and the amount of wood that may become buried in the soil (Moroni et al., 2015; Oberle et al., 2017), which considerably extends the residence time of carbon as biomass.

Studies of WD decomposition have usually considered wood and bark as a single plant organ. While this approach has enhanced our general knowledge concerning the overall rate of decomposition for WD, it has not provided the mechanistic understanding needed to make predictions for this important ecological process. In particular, studies on the decomposition of WD have revealed a strong species effect, even when controlling for critical traits such as wood density or diameter (Freschet, Weedon, Rien, van Hal, & Cornelissen, 2012; Liu et al., 2015; Pietsch et al., 2014; Weedon et al., 2009; Zanne et al., 2015), but our understanding on what drives this species effect has been held back by the lack of distinction between wood and bark.

Ecologists have long speculated on the potential effects of bark as a barrier or filter for fungal or arthropod establishment on dead tree trunks and branches and thereby for wood decomposition (Kaarik, 1974; Ulyshen, 2016). Species-specific bark traits were recently found to strongly determine the faunal assemblage on WD with knock-on impact on at least the early stages of wood decomposition (Zuo, Berg, et al. 2016). Other recent studies have looked directly at the effects of bark on the decomposition of the wood inside it (Dossa et al., 2016; Ulyshen, Müller, & Seibold, 2016). In combination, these studies have revealed some of the processes underlying the species identity effect, but general patterns remain elusive. For example, manipulative experiments showed that the presence of bark either had no effect on the rate of wood decomposition (Oberle et al., 2017), or enhanced the rate of wood decomposition in comparison with wood without bark (Dossa et al., 2016; Ulyshen et al., 2016). Moreover, such a bark effect can be species specific (Dossa et al., 2016). An important role of bark in wood decomposition is to be expected, given the large differences in the chemistry of bark and wood (Cornwell et al., 2009; Johnson, Siccama, Denny, Koppers, & Vogt, 2014). However, we need a conceptual framework (Figure 1) to synthesize the available literature related to bark effects on wood decomposition meaningfully. Here, to advance our mechanistic understanding of the decomposition of WD, needed for improving models of local, regional and global carbon cycles, we apply the "trait afterlife concept" (sensu, Cornelissen et al., 2004) by which variation in plant functional traits between or within species is linked to carbon and nutrient release processes through the legacy of these traits in senesced plant parts. This concept has previously been applied to other plant organs such as leaves, stems and roots (e.g., Cornwell et al., 2008; Freschet, Aerts, & Cornelissen, 2012; Reich, 2014), but has only been touched upon briefly for bark (Cornelissen et al., 2017). Moreover, the concept has never been applied in terms of afterlife effects of an organ or tissue (such as bark) on a carbon release process of another organ or tissue (such as wood decomposition). In order to fulfill this objective, we attempt to answer the following questions: (1) How is bark as a resource utilized differently from the wood inside it by the decomposer community? (2) What are its time-dependent effects on decomposition of the underlying wood? (3) How do animals mediate bark effects on wood decomposition? And, (4) which bark-related research gaps need to be filled for a robust understanding of the decomposition of woody debris?

We focus on a small shortlist of specific hypotheses owing to the lack of sufficient empirical data (Figure 1). We illustrate the (importance of the) effects of bark on WD decomposition with a novel case study in which, through experimental bark removal, we investigated effects of bark presence on twig decomposition across 15 subtropical species (representing 12 families). We asked: (1) Does bark presence enhance wood decomposition? (2) Does bark decompose slower than wood (i.e., twigs without bark)?

2 | WHAT IS BARK ACTUALLY?

Bark forms the outermost tissues of the tree stem, branches and roots of vascular plants (Rosell, 2016). Above-ground for living plants, it encompasses the corky, mostly dead outermost tissue and the underlying living tissue that together separate the outside environment from the cambium (Rosell, 2016). Gymnosperms often have thicker outer barks than angiosperms (Rosell, Olson, Anfodillo, & Martinez-Mendez, 2017). Below-ground bark tissues form the interface between the soil medium and the living cells of roots (Lev-Yadun, 2011). Inner and outer bark tissues may play distinct roles in the decomposition of woody debris, as they do during the tree's lifetime. However, in woody debris, living cells in the inner bark likely die within a month or so after tree death. The presence of outer bark is visible in some species at any stage of growth but some species have acquired ways of shedding their outer bark as they grow (e.g., *Commiphora*, *Eucalyptus*, *Psidium guajava* [guava]). The reasons for this behaviour are not fully understood (Crockford & Richardson, 1998; Grootemaat, Wright, Bodegom, Cornelissen, & Shaw, 2017). Throughout this article the term "bark" refers to total bark or at least that part remaining on the outside of a piece of dead wood. Bark is structurally diverse and the highest diversity of bark structures is found in the tropics (Paine et al., 2010). Morphologically, for example, one may distinguish barks by their different surface textures, by the depth or pattern of fissures, by the thickness of the corky layer, by the pattern of shedding or flaking, by colour, tissue density, water holding capacity and the presence of lichens or mosses. Barks also vary

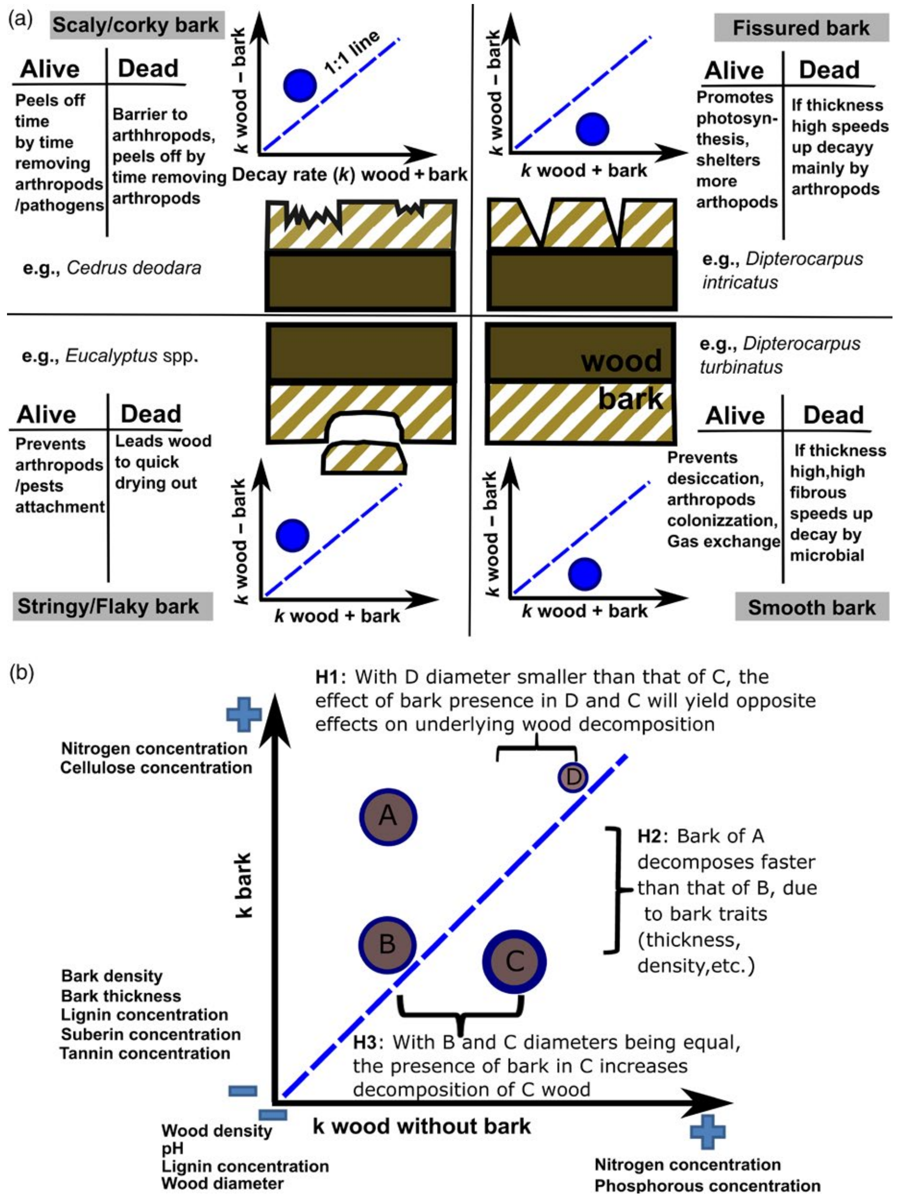

FIGURE 1 Conceptual framework of bark traits afterlife effects on woody debris (WD) decomposition. Panel a explores possible specificity of four different bark types (corky, fissured, flaky and smooth) as examples. Although, all barks in general have common roles while alive (e.g., a protective plant 'skin', sugar transport), we sought to talk about particularity that differs from one particular bark to the other as well how this specific functions would affect WD decomposition when bark dies. The bark drawing follows a longitudinal cross-cut. In panel b, we summarise two broad axes (*x*-axis, the factors driving decomposition rate of wood, and *y*-axis those of bark decomposition). We then pose particular example of hypotheses that could be tested based on what we already learnt from the bark effect on wood decomposition

substantially in chemistry (Cornwell et al., 2009) and pH (Zuo, Berg, et al. 2016).

3 | BARK CHEMISTRY VERSUS WOOD CHEMISTRY

Relative to wood, bark is a high quality substrate for decomposers. Bark has ten times more minerals than wood, mainly attributable to calcium (Ca), silica (Si), phosphorus (P) (Jensen, Fremer, Sierila, & Wartiowara, 1963). In general, in bark the proportions of galactose, mannose and starch are higher in bark than in wood (Romero, 2014). Among five tropical tree species, bark had more N and P than wood and less cellulose and C than wood in four out of five species (Dossa et al., 2016). Bark extractives such as fatty acids, alcohols, resins, pigments and tannins make up about 20%–40% of bark dry mass, while the suberin, lignin and phenolic acids form the remainder. The presence of allelopathic substances, and chlorophyll in bark also sets bark apart from wood. Bark lignin is much more complex in structure than wood lignin (Romero, 2014). Gymnosperm barks have lower ash content than angiosperms.

4 | BARK'S ROLE IN LIVING TREES

Tree bark develops as the tree grows and consequently differentiates within itself to accomplish its different functional roles. Bark emerges from three types of meristems: cambium initiates the phloem, phellogen initiates the corky layer and the dilatation meristem initiates the parenchyma which provides the rigidity that holds the underlying wood within either branch or stem or root (Lev-Yadun, 2011). The most updated consensus among scientists about the role of outer bark in living trees is that it protects the underlying living tissue from fire (Pausas, 2016), from injury and from herbivory and pathogens (Paine et al., 2010). In contrast, the inner bark has an important role in water storage and in the transportation of organic compounds, especially photosynthates (Ryan, Asao, & Way, 2014). To date, the best studied role of bark is its protection against fire in fire prone environments (Rosell, 2016). As a consequence, bark thickness represents the most used bark trait in bark functional studies (Midgley & Lawes, 2016). Recently, scientists proposed the existence of a trade-off between bark thickness and tree growth (Pausas, 2016). Bark water content varies with its thickness and density. For example, in large trees with thick bark, bark water content can sometimes exceed 50% (e.g., on average 51% in *Prunus africana* and 59% in *Rytigynia* spp. (Kamatenesi, Hoft, Hoft, Cunningham, & Ziraba, 2014; Williams, Witkowski, & Balkwill, 2014). In contrast, trees characterized by thin and dense bark have low bark water content. Since bark can accumulate a substantial amount of water, it helps to protect the tree from desiccation (Romero, 2014). The storage role of bark also extends to organic materials. In addition, bark can have an important photosynthetic role, especially the bark on twigs in the canopy but in several taxa extending to the whole tree (Rosell & Olson, 2014). In some ecosystems, especially the arid ones, trees have adapted to water stress by either producing small leaves or becoming leafless, and relying on the bark for photosynthesis (e.g., *Euphorbia*, *Boswellia papyrifera* and Cactaceae) (Girma, Skidmore, de Bie, Bongers, & Schlerf, 2013; Lev-Yadun, 2011).

Bark acts as a mechanical defense and also plays a role in protection against pathogens and in deterring attacks from herbivores (Paine et al., 2010). For example, conifer bark contains terpenoids, resins and polyphenols that form a chemical line of defense against pathogens (Franceschi, Krokene, Christiansen, & Krekling, 2005; Wainhouse, Rose, & Peace, 1997). Contrary with some earlier suggestions, smooth bark can also act as a defensive barrier against insects and pathogens (Ferrenberg & Mitton, 2014) and when very smooth, may also prevent epiphytes from establishing and seed predators from climbing branchless tree trunks. Last but not least bark has a role in wound repair. Indeed, internally, bark structure and chemistry are geared towards wound healing. Ducts react by exuding resins, gums or latex that are involved in sealing a wound and repairing damaged tissue (Wainhouse et al., 1997).

In summary, bark has several functions in living trees including (1) physical protection against fire, herbivores and pathogens, mechanical damages and desiccation; and (2) physiological function: photosynthesis, storage of water and organic compounds and wound repair. However, to what extent these functions affect the properties of wood after death is not yet well-understood.

5 | BARK'S ROLE IN THE DECOMPOSITION OF WOOD

Trees shed dead branches or die entirely. Shed branches may still have their bark or not. What determines interspecific and intraspecific variation in how long trees hold on to their bark after death is poorly known. Furthermore, some tree species die and lose their bark while still standing (Figure 2), whereas trees that die through treefall do so with their bark intact. Whether one refers to snags or downed WD, the condition of the bark is widely used as one of the indicators for grouping WD into wood decay classes (Pyle & Brown, 1998). This correlative use of bark intuitively points to an important role of bark in the decomposition of wood. While researchers already speculated long ago on the role of bark in wood decomposition, mainly as a physical barrier to decomposers during the early stages of decomposition (Kaarik, 1974; Pearce, 1996), only recently was this idea tested experimentally. Through comparing the decomposition of 11 temperate tree species and through temporal observation of faunal assemblages on decomposing logs, Zuo, Berg, et al. 2016 showed that bark can serve as a physical barrier during the early stage of decomposition, and thereby determines the composition of the decomposer community; with possible but unknown knock-on effects on the rate of decomposition. They showed how the combination of several bark traits, such as bark looseness, bark thickness, bark fissure index, bark pH, and bark water storage may determine fauna assemblages on dead wood at least during the early stages of the decomposition process (Figure 1 and Table 1). Similarly for micro-organisms, spores from the basidiomycete *Heterobasidion annosum*, an important fungal decomposer in aerobic environments, were prevented from reaching the xylem by bark (Strid, Schroeder, Lindahl, Ihrmark, & Stenlid, 2014). This role of bark as a barrier to some wood-decaying fungal species is likely to be widespread (Rayner & Boddy, 1982).

Recent studies found that the presence of bark enhances decomposition rates in some species (Dossa et al., 2016; Ulyshen et al., 2016). These researchers speculated that bark creates a favourable microenvironment surrounding the dead wood, in particular increasing moisture retention, and provides nutrition, as a high quality substrate, which favours the establishment of fungi (possibly through hyphal growth) and detritivores.

However, in one of these studies the bark effect on wood decomposition was found to be species specific, with some species showing positive effect of bark on the rate of wood decomposition and other showing no effect (Dossa et al., 2016). In another study on twigs (*c.* 0.5 cm diameter of 15 tree species), presented here for illustration (Figure 3 and Table 2, see Data S1 for details), twigs without bark actually decomposed faster than those with bark, indicating an inhibitory effect of bark on WD decomposition (Figure 3b and 4a, and Figure S1 in Data S1 and Table 2). We conclude that bark is therefore partly responsible for the "species identity effect" in wood decomposition. This is a logical deduction from the above mentioned diversity of functions and attributes of bark in the living plant. However, a better understanding of the contribution of time, i.e., decomposition stage, to the effects of different bark characteristics on the rate of decomposition is required, so that we can move beyond the characterisation of vague overall species identity effects. Here, we propose a new method of including the species identity

FIGURE 2 Collection of photos on diverse tree barks in their environmental context from life to death. (a–e) Examples of different bark surface types in living trees. (a) Smooth and patchy bark of *Dipterocarpus turbinatus*, (b) Bark with adherent scales (*Cedrus deodara*), (c) Fissured bark of *Dipterocarpus intricatus*, (d) Flaking bark (outer bark of *Eucalyptus* sp.), (e) Bark of *Melaleuca* sp. (f–m) Various types of woody debris (WD) at different stages of decomposition and effects of arthropod/fungal interactions with WD, (f) *Castanopsis mekongensis* WD mainly eaten and filled with sand/mud by termites (photo taken after 36 month of WD incubation on the forest floor), (g) Decomposing stump showing fast decomposition of its bark, (h) Decomposing *Castanopsis mekongensis* log showing almost entire disappearance of its bark (photo taken after 36 months of WD incubation on the forest floor), (i) Decomposing twig with a specific moth buff-tip (*Phalera bucephala*) that emerged from it, (j) Decomposing dead standing WD (snag) showing quick bark turnover even while the snag still standing, (k) Advanced stage of decomposition of a log showing the disappearance of bark at the edge but its persistence towards the centre, (l–m) Decomposing twigs with fruiting bodies of fungi decomposing them. Credit courtesy to: G.G.O. Dossa (photos a–h, j, k), Steve Axford (photos l, m), internet (photo i)

effect in WD decomposition by using a "stage-wise" size-dependent approach that recognizes both the importance of bark for wood decomposition and the time dependence of bark traits afterlife effects which will be important for parameterization of bark traits in WD decomposition modelling. The approach posits that for early stages and small diameter pieces of WD decomposition bark exercises a relatively strong effect on wood decomposition and bark traits are important in quantifying the species identity effect. Whereas, there is a progressive weakening of the bark effect over time as the bark quality and structure deteriorate and bark cover diminishes (Shorohova & Kapitsa, 2014). Also, as diameter of WD increases the proportion of bark decreases and hence its importance to the overall process of WD decomposition declines.

Lately a few studies have examined the decomposition of bark as a substrate independently of wood, but these early results suggest it is a relatively fast decomposing substrate compared to wood (Dossa et al., 2016; Johnson et al., 2014; Oberle et al., 2017; Shorohova & Kapitsa, 2014)—although slow in comparison with leaves (Grootemaat et al., 2017) and in comparison to twig wood (see case study below).

6 | BARK TRAITS AFTERLIFE HYPOTHESIS

The trait afterlife concept (Cornelissen et al., 2004) has provided a framework for understanding species identity effects

TABLE 1 List of bark traits and their (potential) influence on decomposition of wood. In the column "Direction of the effect" we tried to disentangle the effect that drilling insects and fungi dissolving exoenzymes may have if considered individually although we acknowledge that such disentanglement is hard to achieve considering the strong interaction between these organisms. We chose boring insects as a well-studied representative for insects in general and fungi as the main microbial agents of wood decomposition

Bark traits	Potential function or influence on woody debris (WD) decomposition	Direction of the effect	
		Boring insects	Exoenzymes dissolving fungi
Bark looseness	Failure of establishment of fungi that require bark presence Very important. + (positive correlation with fauna) (Zuo, Berg, et al. 2016) (Ulyshen et al., 2016) − (drying out quickly delays decomposition) (Rayner & Boddy, 1982)	−/+	−/?
Bark retention status	+ for slow decomposing coarse WD (Dossa et al., 2016; Ulyshen et al., 2016) but species-specific (Dossa et al., 2016), 0 for fast decomposing coarse WD, − for fine WD (Dossa et al. present study)	−/+	−/+
Bark fissure index	Exposure of underlying wood. Allows colonization by soil dwelling detritivores (Nicolai, 1986; Zuo, Berg, et al. 2016). Permits migration and establishment of fungal mycelia	+	
Inner to outer bark thicknesses ratio	− Negative correlation with fauna detritivores, + facilitation of detritivore colonization. Higher ratios mean higher phloem rich proportion, promoting higher abundance of detritivores (Zuo, Berg, et al. 2016; Zuo, Cornelissen, et al., 2016)	−/+	
Outer bark thickness and toughness	Increases the abundance of invertebrates, inner bark galleries + because bark protects against desiccation or maintains a moist environment (Cornwell et al., 2009; Paine et al., 2010; Zuo, Berg, et al. 2016) − (correlation with fauna abundance) + (positive for outer thickness)	−/+	+
Bark relative thickness	If thin, lead to quick drying out of wood inside bark, and thus delays its decomposition. If thick, prevent drying out allowing high microbial activity (Cornwell et al., 2009; Lawes, Midgley, & Clarke, 2013)	−/+	+
Bark water storage capacity	Affects both microbial and invertebrate activity with knock-on effects on wood decomposition (Ulyshen, 2016; Zuo, Berg, et al. 2016)	0/?	+ Microbial abundance and activity
Bark pH	May filter organism assemblage on the wood inside bark (Zuo, Berg, et al. 2016; Harmon et al., 1986)	−	− (for certain values or above pH would inhibit microbial activity)
Bark chemistry	Large amounts of suberin, lignin and tannins slow down decomposition, some forms of lignin being more recalcitrant than others (Dossa et al., 2016; Kolattukudy, 1984; Pearce, 1996; Vane, Drage, & Snape, 2006) Speed up if N from proteins, P concentrations are high in the bark (Baldrian, 2017; Ulyshen et al., 2016)	−/+	− especially when there is more suberin, resins
Bark density	Important but after early stage the effect may weaken/disappear (Shorohova & Kapitsa, 2016; Shorohova et al., 2016) − with high density (Cornelissen et al., 2017; Grootemaat et al., 2017) + with low density	− high density + low density	-/? (high density would mean less diffusion of O_2, weak anaerobic activity)
Bark sloughness index	If rapid then wood decomposes slowly because of desiccation (Ulyshen, 2014; Weslien et al., 2011) [may dictate fungal community specificity (Rayner & Boddy, 1982)]	−/+	− (selection on specific community)
Bark punch resistance	− Negatively correlated with invertebrate detritivore abundance, the higher the resistance the slower might be the decomposition of wood by invertebrates, but this could enhance microbial activity (Zuo, Berg, et al. 2016)	−	

+, Stimulatory effect; −, inhibitory effect; ?, unknown effect; −/+, effects can be both stimulatory and inhibitory; 0, no relevant effect.

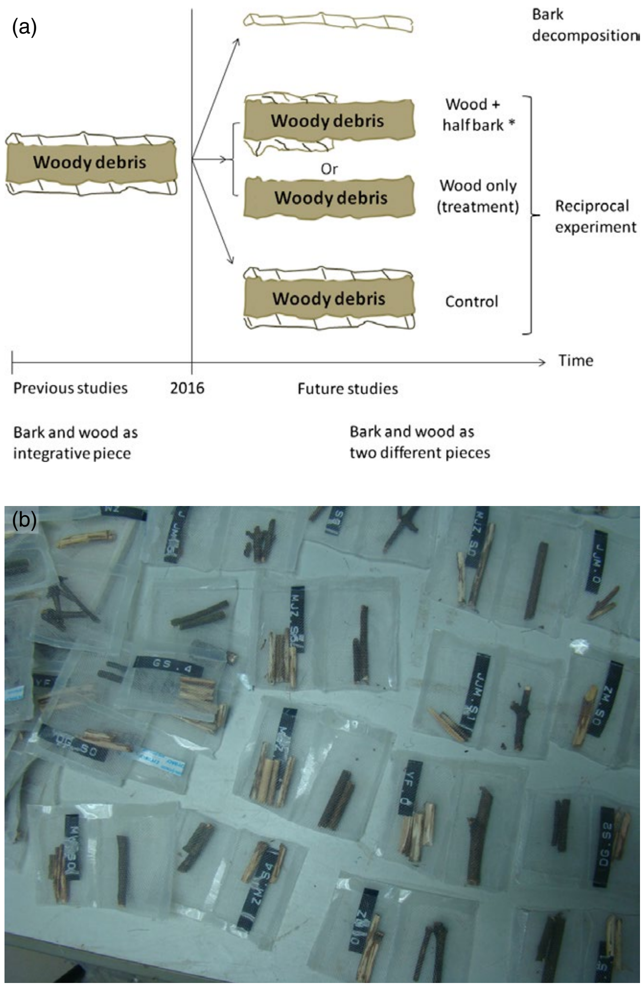

FIGURE 3 Examples of how to study the role of bark in wood decomposition. Panel a shows two methodological approaches where bark is peeled off from the woody debris (WD) and three aspects are monitored: (i) bark decomposition, (ii) WD with intact bark decomposition and (iii) wood decomposition without bark. The latter treatment can consist of removing half of the bark and comparing WD with half bark decomposition with WD with entire bark coverage or can be either on the removal of bark from the entire piece of WD as employed in Dossa et al. (2016). Multiple alternatives are possible, for instance: (i) the removal of the outer bark only, (ii) treat bark removed logs in different ways to simulate bark—such as surrounding them in a substance that retains water but is otherwise inert or painting them with a fungicidal paint. Panel b shows litterbags containing twigs with bark and without bark separated in the middle of the litterbag by gel (present case study; see Figure 4)

TABLE 2 Model results for twig decomposition in two litter beds in experimental ecology garden at Southwest China University, Beibei, Chongqing, China. Annual decay rate *k* (log transformed) was modelled over 24 months of incubation as a function of bark treatment (bark intact vs. bark removed), litter bed treatment (sandstone vs. limestone litter beds) and their interactive effects (for the full model and summary see Table S2 in Data S1). There were 15 species (see list of species on Figure 4 legend). *df* denotes degree of freedom. Denominator *df* = 367

Variables	Numerator *df*	*F*-value	*p*-value
Intercept	1	293.3313	<.0001
Twig initial mass	1	2.86207	.0915
Species	14	94.21153	<.0001
Bark treatment	1	34.95677	<.0001
Litter bed treatment	1	183.27	<.0001
Species:Bark treatment	14	11.21291	<.0001

on decomposition. The concept was first applied to leaves and has been extended to other plant organs such as stems and root (Freschet, Aerts, et al., 2012). However, has barely been applied to bark, perhaps partly because we lack comprehensive understanding of interspecific functional variation in bark traits (but see Paine et al., 2010; Rosell, Gleason, Méndez-Alonzo, Chang, & Westoby, 2014). Moreover, bark afterlife effects represent a novel extension of the concept in which the traits of one organ determine the carbon and nutrient dynamics of another organ after death (Figure 1 and Table 1). In our conceptual framework (Figure 1), explicit hypotheses can be tested to move the field forward. For example, the size dependency hypothesis posits that the effect of bark on wood decomposition will vary with the diameter of the WD. Furthermore, comparing available results from twigs and logs suggests there is a threshold at which the bark effect on wood decomposition is reversed. The time and size dependency functions of bark effects on WD decomposition are also likely to be species (bark trait) dependent. Hence, we can hypothesise that, for example, a species with rapidly decomposing bark will have a shorter phase during which bark has an important effect on WD decomposition than a species with more recalcitrant bark, although the effect may still be important if the high quality substrate provides an opportunity for decomposers to establish.

7 | ANIMALS AS MEDIATORS OF BARK EFFECTS ON WOOD DECOMPOSITION

Saprophytic animals feed on dead organic matter, to which their life cycles are intrinsically connected (Grove, 2002). These animals may exhibit different strategies in the ways they utilize organic substrates, including bark and wood. While considering such strategies, we first examine animals that occupy or consume bark when trees are still alive—including those on recently downed living trees—and then look at those using bark only after the tree has died, as the first are intrinsically linked to the latter and may have either facilitating or inhibitory effects (Weslien, Djupström, Schroeder, & Widenfalk, 2011; Zuo, Fonck, van Hal, Cornelissen, & Berg, 2014). Second, we review animal uses of dead wood by separately considering snags and downed WD and further distinguishing WD retaining bark vs. no longer retaining bark. We then conclude this section by exploring different ways animals mediate bark effects on WD decomposition.

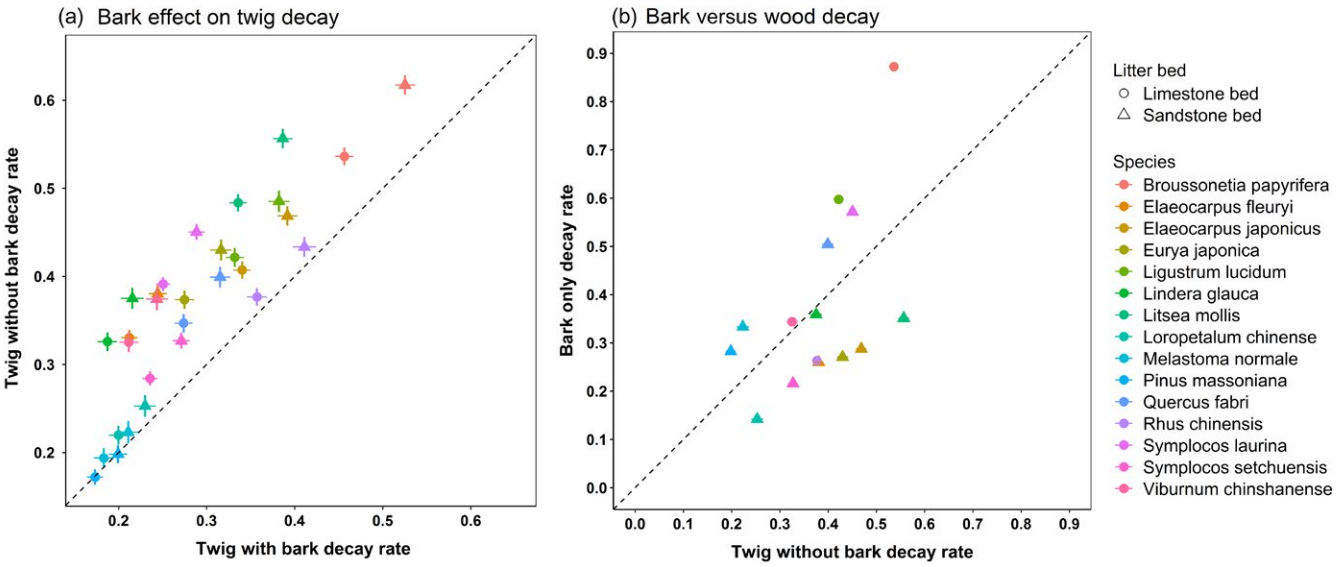

FIGURE 4 Decay rate, constant rate k (per year) of twig with bark attached, twig without bark, and bark only of 15 tree species incubated in different litter beds in an experimental ecology garden at Southwest China University, Beibei, Chongqing, China (Dossa et al., unpublished results). Dash line represents 1:1 line. Plant materials were collected from Sea-stone Park and Jinyun Mountain in Chongqing, China. These plant materials were incubated in two common litter beds built with soil from aforementioned sites at Sea-stone Park and Jinyun mountain constituting sandstone and limestone litter beds respectively. Panel a shows the decomposition comparison between decay rate of twigs with respect to bark removal treatment (bark intact vs. bark removed) as well as with respect to litter bed treatment (sandstone vs. limestone litter beds). Panel b shows the decomposition comparison between bark litter solely and twig without bark. Note that since specific bark litter was only incubated in the litter bed of their origin, only corresponding twigs without bark were considered. Data represent *M* + *SE* (Mean and standard errors). Decay rates were calculated on the basis of a negative exponential decay model and on a 2-year experiment vs. a 1-year experiment for bark decomposition. See Data S1 (materials and methods) for details of sampling, experimental and data analysis

7.1 | Animal use of bark

To animals (in general whether invertebrates or vertebrates), bark serves different purposes including habitat, food and foraging site (whether directly or indirectly as quality enhancer) (Lieutier, Day, Battisti, Grégoire, & Evans, 2004; Stokland, Siitonen, & Jonsson, 2012). Arthropods living on bark of trees are highly diverse, as they respond to heterogeneity in environmental factors, e.g., habitat types (Nicolai, 1989), thermal properties of bark (Nicolai, 1986), the percent cover of epiphytic vegetation on the bark surface (André, 1985), the size of the living trees (larger trees supporting more bark dependent arthropods (Yasuda & Koike, 2009) and physical characteristics of bark (e.g., bark types). For example, smooth bark tends to have a less diverse fauna compared to fissured or scaly bark (Nicolai, 1986). Among arthropods living in or on living bark, numerous taxa including aphids feed on phloem sap (Pointeau et al., 2012)]. Other taxa use bark mainly as habitat, e.g., Homoptera (Dungan, Turnbull, & Kelly, 2007), oribatid mites (Erdmann, Otte, Langel, Scheu, & Maraun, 2007; Fischer, Schatz, & Maraun, 2010), bark dwelling spiders (Horváth, Lengyel, Szinetár, & Jakab, 2005), bark beetles (*Coleoptera*: Curculionidae, Scolytinae) (Kausrud et al., 2011), Opiliones, Isopoda, Myriopoda (Synxenidae), Blattodea, Psocoptera, Heteroptera, Formicidae, and Diptera (Nicolai, 1989). Some species, for example, *Pseudopsocus rostocki* (K.) (Psocoptera), *Drapetisca socialis* (Aranae) and *Empicoris vagabunda* (L.) (Rhynchola) are endemic to bark habitat. The abundance of arthropods on bark attracts animals that prey on them such spiders, ants and insectivorous birds.

The consumption of bark tissue can sometimes cause the tree's death. Bark beetles are often responsible for such early attack and the severe consequences of bark beetle outbreaks are well-known (Kurz et al. 2008; Ghimire et al., 2015). Bark beetles often associate with micro-organisms, in particular fungi, and therefore colonisation by beetles may facilitate establishment of fungal decomposers (Jacobsen, Kauserud, Sverdrup-Thygeson, Bjorbækmo, & Birkemoe, 2017; Lieutier et al., 2004).

In addition, several other vertebrates, especially mammals including deer, bear, elephants and humans, strip bark from living trees to feed on the live tissues below. This sometimes causes lethal damage to the host trees (Kitamura & Ohnishi, 2011; Shibata & Torazawa, 2008). Moreover, interactions between unrelated organisms such as elephants and cerambycid beetles (Jones, 1960), or between porcupines and fire (Yeaton, 1988), can have consequences at landscape scale. Subtle effects of bark damage to savanna trees by porcupines (Yeaton, 1988), or anthropogenic disturbance, in combination with fire, periodic winds and lightning can cause a large-scale, marked increase in tree mortality (Rykiel, Coulson, Sharpe, Allen, & Flamm, 1988). Removal of bark patches results in dead wood scars which are vulnerable to periodic burning and enlarged by successive wildfires. This causes lop-sided growth and hollowing out of the trees over 20 years or so, resulting in a "chimney effect" which further speeds up the hollowing-out, eventually leading to snapping of the weakened stems in periodic windstorms. The debarking of forest trees for the commercial trade in traditional medicines has become more widespread, greatly increasing forest die-back and canopy-gap formation (Cunningham, 1991).

Coarse WD represents a primary food resource to animals. However, its nutrient content is usually not high enough to meet the nutritional needs of animals. This leads to a stoichiometric mismatch which can be alleviated through collaboration among wood borers and fungi (Filipiak & Weiner, 2014). The presence of bark puts saprophytic fungi in contact with its relatively high nutrient resource (compared to wood), which can enable the colonization of bark by wood borers (Jacobsen, Birkemoe, & Sverdrup-Thygeson, 2015; Ulyshen, 2014; Weslien et al., 2011). After the death of trees, bark tissues can be directly consumed by arthropods (e.g., beetles, termites, etc.). Bark beetles and fungi feeding on wounded bark are the first colonizers of senescing trees (Weslien et al., 2011). Often these early colonists target the phloem (Macedo-Reis et al., 2016). During direct consumption, bark beetles serve as vectors for N-fixing bacteria and fungi (see below) while termites serve as vectors for basidiomycete fungi (Schowalter et al., 1992).

Dossa et al. (2016) showed that arthropods are important decomposers of bark litter through a standard litter bag experiment. Indirect consumption of bark occurs when the animals feed on fungal tissue (hyphae, mycelium or fruiting bodies) that has established on the surface of the bark. They (e.g., ambrosia beetles) can either target sporocarps formed on bark, tree stems or branches (i.e., myelophagy) or both fungal sporocarps/mycelia and xylem/wood (i.e., xylomycetophagy) (Macedo-Reis et al., 2016). Mycelia are food sources for diverse insects (A'Bear, Boddy, Kandeler, Ruess, & Jones, 2014; Zuo et al., 2014). In addition, some vertebrates including woodpeckers may loosen or dislodge bark while foraging (Ulyshen, 2016). Bark sloughing is also commonly observed in snags.

The space between bark and wood also serves as habitat. Generally, fungal mycelia develop beneath the inner bark surface, which aids their early establishment on dead wood. Some arthropods also use the space underneath bark of dead trees as a habitat for laying their eggs (Ulyshen, 2016). For some arthropods, this rather stable habitat can protect them from extreme temperature and moisture fluctuations and from predators and parasitoids (Zuo, Berg, et al. 2016).

Some fungi have mutualistic relationships with arthropods to enable them to colonise WD (Muller, Varama, Heinonen, & Hallaksela, 2002; Persson et al., 2009). Some arthropods e.g., bark beetles (Scolytinae) and weevils (Platypodinae), have a mycetangium, an organ that helps collect mycelia and fungal spores to assist in the transport of fungi to new breeding sites (Harrington, 2005; Rayner & Boddy, 1982). Fungi manipulate beetles by emitting volatile organic compounds to attract their symbiotic partners (Hulcr, Mann, & Stelinski, 2011) or other beetles (Harrington, 2005). Fungal interactions and priority effects also play a crucial role in decomposer community dynamics and ultimately in how a substrate decomposes. For example, endophytic fungi in the sapwood initiate and sometimes dictate the decomposition pathway (Parfitt, Hunt, Dockrell, Rogers, & Boddy, 2010), in one report even increasing mass loss by 40% at 25°C (Song, Kennedy, Liew, & Schilling, 2016). There exists a highly diverse biota that uses WD (Stokland et al., 2012). Moreover, our general understanding of the different ways arthropods either access or influence resources in dead wood is substantial and richer than our understanding of their relationship with bark.

7.2 | Snags and stumps vs. downed wood

The position of WD relative to the soil surface can be very important for decomposition (Cornwell et al., 2009) and here we briefly discuss the role of bark therein. So far the main focus of this review has been on downed WD, but snags and stumps are grouped here because both represent standing woody debris. Stumps are a feature of logging of the main stems for wood extraction (Figure 2g and j). As such they represent a narrow range of economically attractive tree species, with some different distribution of bark features than tree species as a whole. In addition, during wood harvest bark, branches, tree tops and saw-dust are left behind as debris, and this again differs from unmanaged forests.

Downed WD differs from their counterpart snags and stumps on being in contact with the ground, which (1) is a source of microorganisms and (2) is a source of moisture and a sheltered environment for many organisms. Especially in larger pieces of downed wood, decomposition of the underside and top of the log may be substantially different. This may also extend to the rate at which the bark is lost and the effect of bark loss on the decomposition process.

The exposure of snags to sunlight and wind increases moisture loss from wood and bark, leading to shrinking and sloughing off of bark (Koster, Ilisson, Tukia, Jogiste, & Mols, 2009; Maser & Trappe, 1984). Compared to downed WD, snags and stumps may also be a preferred habitat for certain wood boring arthropods (Franc, 2007), which may facilitate bark sloughing and bark loss may in turn encourage arthropod attack (Buxton, 1981). However, some fungi require wood covered by bark (Jacobsen et al., 2015; Weslien et al., 2011).

8 | CASE STUDY: AN INHIBITORY EFFECT OF BARK ON TWIG DECOMPOSITION

Our case study from subtropical China, exemplifies the important role of bark for wood decomposition and is presented here for illustration (see Figure 3b, Table 2, Figure S1 in Data S1 for details). This study employed twigs (*c.* 0.5 cm diameter) collected from 15 tree species from 12 families, subjected to experimental bark removal in order to compare (1) decomposition of bark only, (2) twigs with bark and (3) twigs without bark, each incubated in two different common litter beds (limestone and sandstone beds for 24 months). In total, we used $n = 457$ litter bags. We found that twigs without bark decomposed faster than those with bark in both litter beds, indicating an overall inhibitory effect of bark on WD decomposition (Figure 4, Table 2). There was no overall difference in decay rates between twigs without bark and bark alone, but there was a substantial species effect (Figure 4b). Decay rates of bark varied from 60-150% of those of the same species of twig without bark. These results contrast with previous reports on the effects of bark on coarser wood decomposition (Dossa et al., 2016; Ulyshen et al., 2016), suggesting that the sign of the bark effect on wood decomposition could be size dependent. Otherwise these results largely confirm the limited findings for logs from previous studies indicating that (1) species effects are important and (2) bark decomposition rates are highly variable across species (Dossa et al., 2016; Grootemaat et al., 2017), At first, twigs without bark decomposing faster than twig with bark might suggest that bark itself decomposes slower than twigs only (twig without bark). However, as shown in Figure 4 (panel b), there is no consistent difference between xylem (twig without bark) and bark decomposition across species. This implies that perhaps the presence of bark serves as protective wrapping that forms a barrier to decomposers (Kaarik, 1974; Pearce, 1996) rather than bark itself being particularly slow to decay. There may be interaction: this 'wrapping function' may also depend on the decomposition stage (e.g., via moisture content) of the bark. However, slow bark decomposition compared to the wood inside has been reported previously for *Betula* spp. (birch) WD (Shorohova & Kapitsa, 2014), however, for log diameters larger than 8 cm. The authors suggested the presence of betuline and the low moisture of birch bark in natural conditions to explain this finding.

9 | KNOWLEDGE GAPS AND FUTURE DIRECTIONS

Researchers have acknowledged the important role of the quantity and quality of bark in wood decomposition but empirical data to test this role of bark remain scanty. With the current understanding two tentative conclusions can be drawn: (1) the effect of bark in wood decomposition is species specific and wood size specific; and (2) bark acts as an environmental filter for faunal assemblages at early stage of wood decomposition, with important consequences for wood decomposition. Whether bark sometimes exhibits an inhibitory effect for stem of larger diameter, as found in our twig case study, is yet to be established. Data quantifying the variation in bark decomposition rates across large pool of species as well as large pieces of wood (diameter >10 cm) is still lacking (Magnússon, Tietema, Cornelissen, Hefting, & Kalbitz, 2016). How bark chemistry affects bark decomposition (Grootemaat et al., 2017) and thereby its direct or indirect effects on wood decomposition has not been investigated in any detail; also comparisons of bark lignin and wood lignin and their effect on decomposability are missing, as are studies on how bark of roots influences root xylem decomposition. Furthermore, for the bark afterlife approach to be useful as predictive tool, a much greater understanding of the distribution of bark traits and their functional association with wood traits is required. For example, why bark in certain species (e.g., *Betula*) persists for a long time but not in others, and what effect this has on wood decomposition as decomposition progresses remains unknown? Such species specific differences in bark duration and quality may have implications for biodiversity management. In addition, harvesting may increase the amount of woody debris, including dead bark, in forests and critical treatment of this material may affect how quickly it decomposes (Shorohova & Kapitsa, 2016) and how much biodiversity it can support. Other important variables to consider are fire and drought. There are very few studies comparing decomposition of WD that has been partially burned or not (Boulanger, Sirois, & Hebert, 2011; Molinas-González, Castro, & Leverkus, 2017), even though fire resistance of trees has been linked to bark thickness (Charles-Dominique, Midgley, & Bond, 2017; Pausas, 2016; Pellegrini et al., 2017).

10 | CONCLUSIONS

Recently, Bradford, Berg, Maynard, Wieder, and Wood (2015) called for more experimental research directed to understanding factors controlling organic matter decomposition, and stressed how an enhanced mechanistic understanding was essential for improving parameterisation of the process in global climate models. One such factors is the role that bark plays in the afterlife of WD. Its presence can have positive or negative effects on the rate of wood decomposition depending on WD size. The effect sign and size may also depend on indirect biotic factors, especially how barks of different species and decay stages can serve as a habitat, food source and oviposition site for animals, especially wood decomposers, To date, findings suggest that the effect of bark traits on the faunal decomposer assemblages is strongest at the early stage of decomposition, meaning that investigation of the effect of bark traits on WD decomposition may be feasible within a typical short duration research project, at least in many species and biomes. In conceptual terms, bark represents an unconventional factor to take into account as it reflects the role of an organ on carbon release of another organ, through a process that is in addition mediated by animals and micro-organisms. For a long time, people researching WD decomposition have questioned the biological meaningfulness of a negative exponential model with a single decay constant rate *k*, with the suggestion to break the decay process into phases with changing *k* per phase rather than constant throughout the entire course of decomposition (Cornwell & Weedon, 2014). Contemporary research findings provide a basis for robust phase-wise parameterisation. Moreover, instead of using a vague species identity effect, one could give more weight to bark traits at early stages and more weight to wood traits at later stages when bark is no longer a physical barrier or source of microbial nutrition.

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AUTHORS' CONTRIBUTIONS

G.G.O.D, D.S. and R.D.H. conceived the ideas and designed the methodology; G.G.O.D, J.H.C.C. and J.-P.T. collected the data; G.G.O.D., D.S., J.H.C.C. and R.D.H. analysed the data; G.G.O.D., R.D.H., J.H.C.C., R.T.C. and D.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used for the case study is deposited in Dryad Digital Repository: https://doi.org/10.5061/dryad.cr6k97r (Dossa et al., 2018).

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SUPPORTING INFORMATION

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