

Chapter 22

It's the End of the Wood as We Know It: Insects in Veteris (Highly Decomposed) Wood



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Living trees are all alike, every decaying tree decays in its own way.

—with apologies to Tolstoy

Abstract The final decay stage of wood, termed veteris wood, is a dynamic habitat that harbors high biodiversity and numerous species of conservation concern and is vital for keystone and economically important species. Veteris wood is characterized by chemical and structural degradation, including absence of bark, oval bole shape, and invasion by roots, and includes red rot, mudguts, and sufficiently decayed wood in living trees and veteran trees. Veteris wood may represent up to 50% of the volume of woody debris in forests and can persist from decades to centuries. Economically important and keystone species such as the black bear [*Ursus americanus* (Pallas)] and pileated woodpecker [*Dryocopus pileatus* (L.)] are directly impacted by veteris wood. Nearly every order of insect contains members dependent on veteris wood, including species of conservation concern such as *Lucanus cervus* (L) (Lucanidae) and *Osmoderma eremita* (Scopoli) (Scarabaeidae). Due to the extreme time needed for formation, veteris wood may be of particular conservation concern. Veteris wood is ideal for research because invertebrates within it can be collected immediately after sampling. Imaging techniques such as Lidar, photogrammetry, and sound tomography allow for modeling the interior and exterior aspects of woody debris, including veteran trees, and, if coupled with faunal surveys, would make veteris wood and veteran trees some of the best understood keystone habitats.

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22.1 Introduction

The study of deadwood is in its infancy, and researchers are currently staggering under the immense variety of microhabitats (decay stage, size, position, sun exposure, etc.) made possible by deadwood. The purpose of this chapter is to comment on insects found in the final decay stage of wood, an often overlooked habitat of little immediate economic value. The term “veteris,” invented and defined below, is meant to collect related things—a rotting log half buried under leaf litter, a dead limb still in the canopy, heartrot almost entirely encased in a living trunk, exposed deadwood in a living tree, and a tree hole itself—and bring them together. The following is both an overview of the collective “final decay stage of wood” (herein “veteris wood”) as it relates to insects and in part a larger argument for the next stage of saproxylic research, one that seeks to be more universal and allow for realistic comparisons across studies.

22.2 Beginnings

Much like the growth of a baby bird, the study of saproxylic environs and organisms has progressed from a generalized egg stage, with its grand potential fully recognized but not fully known, through the downy squawk of adolescence reeling about trying to understand limits and possibilities, to a full-fledged adult bound in a seeming infinity of feathers, and revealing further infinities of interactions, behavior, and song.

Early authors provided tantalizing but general descriptions of rotting logs and dead trees: Beebe’s (1925) description of diversity of insects associated with the early stages of tree decay reads like an adventure novel; Hubbard (1899) similarly described collecting insects from decaying Saguaro (*Carnegiea gigantea* (Engelm.) Britton and Rose) like a child opening Christmas presents; Morley (1935) provided a list of the myriad species and their parasites found swarming a beech snag; Adams (1915), Shelford (1913), Silvestri (1913), Wallwork (1976), and Wilson (1959) gave a general overview of log decay, listed species, and designated successional stages; Fager (1968) studied invertebrates in decaying oak wood and “synthetic logs”; Hickin (1963) highlighted insects as decay agents in structural wood; Blackman and Stage studied insect succession in American larch (1918) and Hickory (1924); Howden and Vogt (1951) did the same for standing dead pine (*Pinus virginiana* Mill.); Graham (1925) reported the effect of abiotic differences (especially temperature and moisture) on insects in logs; Savely (1939) provided a well-rounded expedition into biotic and abiotic aspects of succession in pine and oak logs; Mamaev (1961) began classifying succession and quantified insect use of logs; the descriptions of wood decay by Käärik (1974) and Swift et al. (1979) concentrated on nutrients, the fate of macromolecules, and microorganisms; Shigo and Marx (1977) and Shigo (1979) demonstrated how trees react to damage and set the stage for

understanding creation and maintenance of saproxylic habitats within living trees; Hamilton (1978) forced us to reconsider the deadwood habitat beyond simple succession and place it within an evolutionary context; and finally Elton (1966) placed rotting wood within the framework of the surrounding forest, clearly demonstrated the importance of the habitat, asked more questions than he answered, and inspired a future generation of students.

After Elton (1966), researchers began to move beyond the rotting log as an independent unit (an island in the ocean) and began to recognize it as a dynamic component that creates a part of the landscape, rather than simply residing within it (the same quality as, say, a stream in the woods). Harmon et al. (1986) provided perhaps the first and last review of coarse woody debris that could encompass every aspect of the subject and still adequately reflect the extent of the literature available. Thomas (1979), Triska and Cromack (1980), Maser et al. (1979), Maser and Trappe (1984), and Maser et al. (1988), all working in the Pacific Northwest of the USA, characterized deadwood with increasing breadth and specificity and illustrated that it was a necessary component of a functioning forest. In the USA, the Forest Service expanded their conception of deadwood beyond salvage and fuel for fires to include many aspects such as ecosystem services and use by invertebrates and fungi (e.g., Bull et al. 1997; Laudenslayer et al. 2002; McMinn and Crossley 1996).

The recognition that deadwood was more than a curio, nuisance, or a wasted resource—but actually a component of a healthy forest, as important as the living trees themselves—resulted in a wave of specialized research. Long-term studies of log decomposition are underway in Oregon, USA (Harmon 1992), and Tasmania, AU (Grove and Forster 2011). Whereas earlier the plight of a rotting log occupied a few pages in a book (e.g., Adams 1915: 148–157), deadwood and saproxylic insects were given entire chapters and volumes (Dajoz 2000; Johsson and Kruys 2001; Lofroth 1998; Rose et al. 2001; Schlaghamerský 2000). Speight (1989) authored the foundational document that linked biodiversity loss to the loss of the saproxylic habitat. Immediately conservation of saproxylic organisms became a major research topic (e.g., Kirby 1992: habitat management for saproxylics; Kirby and Drake 1993, “Dead wood matters!”). Initially “general” research was conducted on the more specific topic of saproxylic invertebrates, for example, linking amount or quality of deadwood to saproxylic diversity at the stand level (see Tables 2 and 3 in Grove 2002). More specific research into the subsets of saproxylic habitats, their origin and fate, their place within the landscape, and the organisms involved followed (e.g., Grove 2002; see Ferro et al. (2012b) for a partial review). Ferro et al. (2012a) provided a review of research on downed coarse woody debris in the final stage of decay.

Presently the study of biodiversity in deadwood, and the conservation and management thereof, has matured into a fully developed and independent discipline. Harmon (2002) proposed “morticulture”—management of woody debris for future needs—and Cavalli and Mason (2003) showed the practical application of that idea in Bosco della Fontana Nature Reserve in Italy. Lonsdale (2013, and references therein) provided management advice to maintain and enhance saproxylic habitats at the level of the individual tree! A series of meetings specific to European saproxylic beetles of conservation concern began (e.g., Bowen 2003) and continues; the ninth

was held in Belgium in 2016. Some flagship saproxylic species of conservation concern are particularly well studied (e.g., *Osmoderma eremita* (Scopoli) (Coleoptera: Scarabaeidae), Chiari et al. 2012, 2013a, b; Ranius et al. 2005, and references therein). For some specific topics related to saproxylic biodiversity, published literature is sufficient to warrant a review and synthesis (e.g., canopy habitat, Ulyshen 2012; a decade of “deadwoodology,” Grove 2009). Book-length works illustrating the importance of deadwood and its role in particular landscapes are available (Maser et al. 1988, well ahead of its time; Cavalli and Mason 2003; Bobiec et al. 2005). Finally, Stokland et al. (2012), a text devoted entirely to biodiversity in deadwood, simultaneously serves as the capstone of the present era and as the foundation for future studies.

22.3 Definitions

...we expect the world to be classifiable. For most of us it requires almost a change of creed to admit that it is not. . .
—Hynes 1975

To ease communication, or reduce overwhelming complexity, we create definitions—a small set of “boxes” that, together, hold the majority of the entities within a particular system. Because of the simplification or generalization that takes place when a definition is created, it’s unlikely that a single definition will work equally well in all situations.

Saproxylic Numerous definitions of saproxylic exist. Speight (1989) provided the most popular definition of saproxylic, and Alexander (2008) provided a well thought-out refinement. Both definitions take a “positive” or “resource-centric” approach, attempting to encompass organisms that require deadwood. An alternative definition could take a “negative” or “community-centric” approach: Saproxylic species—*any species that would no longer be present in a community if deadwood were no longer available, including deadwood in live trees*. Stokland and Siitonen (2012b: 249) describe a similar approach. The definition removes the awkward necessity to highlight species that indirectly use deadwood but are ultimately dependent upon it (e.g., a hyperparasite of a parasite of a beetle that eats fly larvae on the fruiting body of a fungus that consumes the decaying heart wood of a living tree). Of course any given species will still fall on a spectrum from obligate to facultative.

Wood For our purposes, a meaningful definition could be *tissue of a plant, usually part of a stem, trunk, or limb, composed of a combination of cellulose, lignin, and hemicellulose*. Some plant parts that may or may not be covered by that definition include the flowering stalk of an agave, “trunk” of a banana tree (composed of leaves), and/or the petiole of a palm leaf (rigid, similar to a limb).

Dead Occasionally there is confusion between “living,” “dead,” and “functional,” for example, in some trees, cells may be “dead” but still functional for support and transportation of water; in birds, feathers are functional despite being “dead.” Shigo (1991) divided trees into dynamic mass (“alive,” requiring energy) and static mass (“dead,” no longer requiring energy). Ideally “dead” plant material *lacks the ability to metabolically react to stimuli*. Exceptions may include “live” but frozen material, a fresh-cut limb which contains cells that react to stimuli but with little intensity or short duration (not dead but “dying”), and heartwood with no metabolism but containing compounds that remain active to confound insects and fungi.

Deadwood *Tissue composed of cellulose, lignin, and hemicellulose that can no longer metabolically react to stimuli*. Based on the above definitions, what answer would be given to the following question: How much deadwood is in a forest?

Multis wood *Deadwood available to saproxylic organisms*. Every year, a new tree grows over the old (core-skin hypothesis, Shigo 1991), and in many tree species, the inner portion of the tree consists of “deadwood” as defined above. Deadwood sheathed in living wood is generally not available to saproxylic organisms. Therefore the amount of (1) deadwood in a landscape and (2) deadwood available to saproxylic organisms differs greatly. This distinction has not been encountered in the literature by the author; therefore it is introduced here. While not given a specific term, the concept of “multis wood” has existed for a while, e.g., high stumps and other strategic tree wounding to make already deadwood available (see Birtele 2003). The term “multis” is Latin meaning “many,” referring to the many organisms that utilize it as a resource.

Veteris wood *The final decay class of wood*. Decay stages are designated and defined in a variety of ways (see below), but all decay classifications contain a final stage. A single term (keyword) used to designate that stage facilitates online alerts and literature searches. The terms “really rotten,” “highly decayed,” “advanced decay,” and “final decay” are restricted to English and too generalized, whereas “veteris” provides an unambiguous designation and is useful across multiple languages. The term “veteris” is taken from Latin meaning old or ancient.

The conception of veteris wood, based on decay class descriptions below, is of wood that has undergone both structural and chemical degradation. Generally, veteris wood is *not structurally sound and has undergone chemical decomposition due to weathering or mechanical and/or enzymatic action of decomposer organisms*. Cells in a wooden ax handle may be devoid of virtually all their cell contents, but as long as the wood maintains structural integrity, it would not be considered veteris. Similarly a fresh-cut log that is chipped to smaller pieces would not be considered veteris because of its “fresh” chemical composition.

Types of veteris wood may include (Fig. 22.1) all or part of logs, stumps, and roots, portions of snags and canopy wood such as limbs, heartrot within healthy trees, sufficiently decayed material within and on the side of tree hollows, and the outer covering of exposed deadwood within living trees—which may range from a few millimeters to centimeters thick but still offers protection to organisms in the

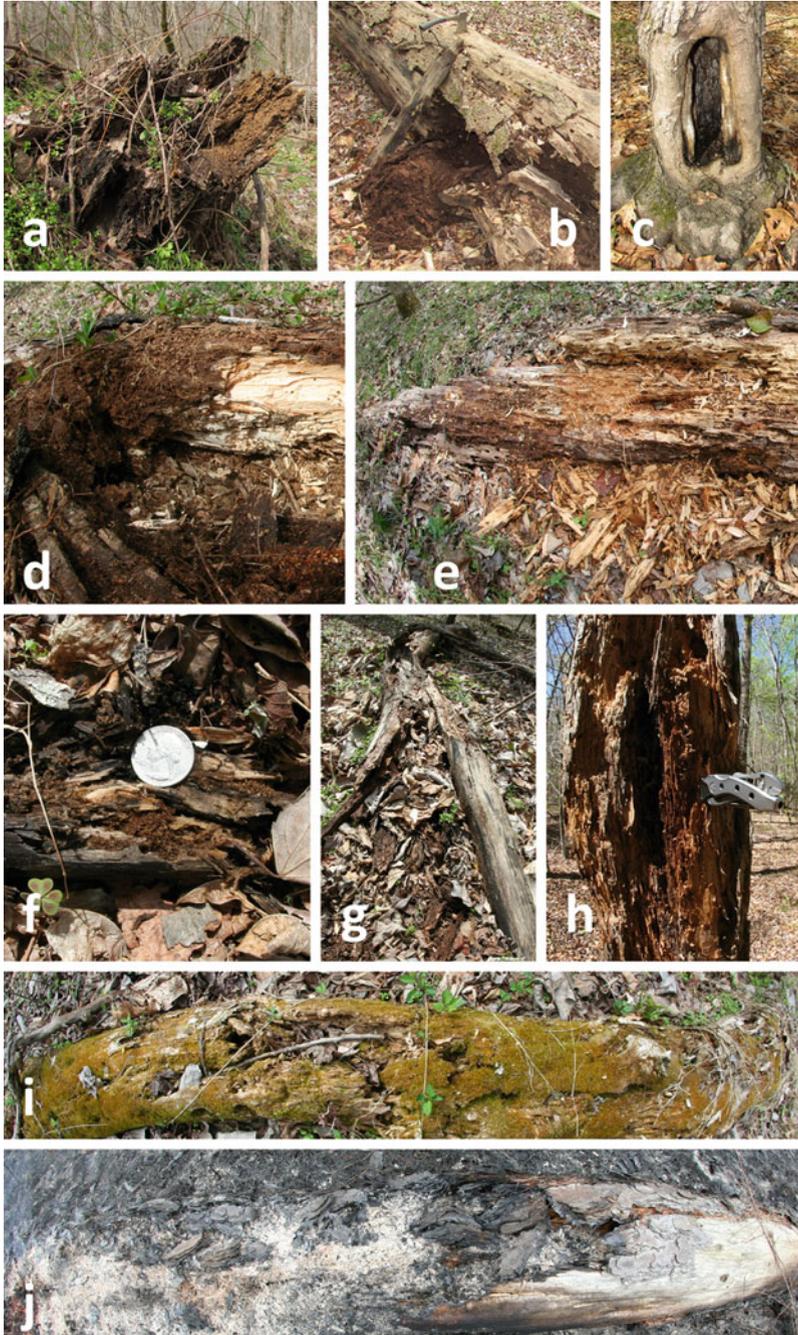


Fig. 22.1 Examples of veteranis wood. (a) Stump; (b) log with a structurally sound exterior, but with interior highly decomposed, dissected to show anatomy; (c) tree hollow; (d) log with highly

less-decayed wood beneath. Organisms that rely on external fruiting bodies of fungi that cause inner heartrot may be considered veteris wood dependent, as well. Tree holes or tree hollows could be thought of as “veteris structures.”

As is obvious above, veteris wood is a broad concept that includes many varieties of wood that have reached a highly decomposed state in a variety of ways. The concept of veteris wood is partially an artifact of human ideas and partially a natural grouping. It is a human-derived and meaningful concept in the same way that the term “tree” is human-derived and meaningful.

22.4 Decay Class and Veteris Wood

Decomposition of wood is divided into useful subsets through the concept of decay class (e.g., overview in Stokland and Siitonen 2012a: 126). How to measure decay class and how many decay classes exist depend on the woody species, environment, and question being asked (fuel quality, structural integrity, nutrient content, biodiversity supported, etc.; see Feller 2003); thus many valid decay classifications exist. Based on the decay classifications surveyed (Table 22.1), the criteria used to designate veteris wood include (1) structural aspects (bark absent, wood easily broken or crushed, oval bole shape, integration with the soil); (2) overgrowth by mosses, herbaceous plants, or trees; (3) invasion by roots; and (4) the presence of worms and other organisms associated with the soil.

Further refinements of decay class will be necessary as researchers strive to increase the accuracy and precision of their observations. Enrong et al. (2006) reviewed the concept and definition of coarse woody debris and recommended a three-part classification system where deadwood was classified by (1) size (coarse, fine, etc.), (2) position (standing, fallen, etc.), and (3) decay class. Pyle and Brown (1999) recognized that while any given log could be designated a particular decay class (e.g., 3 on a scale of 1–5), the log actually consisted of a mosaic of decay classes with pockets and sections of less or greater decay. A living tree with exposed deadwood would add an additional tile to the mosaic (to expand on the analogy). Grove et al. (2011), working in Tasmania, surveyed *Eucalyptus obliqua* logs across all decay stages and designated 27 types of rotten wood, but concluded that a system of five externally derived classes was sufficient to accurately describe decomposition in their study area. Yee et al. (2006), dissecting long-dead *Eucalyptus obliqua* logs,



Fig. 22.1 (continued) decomposed exterior, but with structurally sound interior, dissected to show anatomy; **(e)** fragmentation of a decomposed log by woodpeckers; **(f)** veteris fine woody debris; **(g)** log with central portion completely humified; **(h)** snag with at least outer 8 cm composed of veteris wood based on knife penetration definition (García-Lopez et al. 2016); **(i)** veteris log covered in moss; **(j)** log with a portion highly decomposed by fire. All images from Sumter National Forest, Laurens Co., SC (~N 34.549°, W 81.709°), except **(h)**, from Clemson Experimental Forest, Anderson Co., SC

Table 22.1 Definitions of veteris wood based on various classification systems

Class	Veteris definition	Region	Citation/notes
2	Rotten: “. . .the piece at the intersection is obviously punky or can be easily kicked apart”	Western NA	Brown (1974). CWD
2	Rotten: “Rotten material includes downed pieces that show rot visibly on the outside”	Rocky Mountains, NA	Brown and See (1981), in relation to fire fuel. CWD
2	Decayed: “If the outer layer could be fragmented by hand, and the branches could be pulled free from the bole, including heartrot”	Boreal NA	Sturtevant et al. (1997). CWD. Based on Brown (1974)
3	3: Combination of classes 4 and 5 from Maser et al. (1979) [Structural classes for wildlife use (vertebrates)]	Oregon, Washington, USA	Bull et al. (1997). CWD. Based on Maser et al. (1979). Used by Rose et al. (2001)
3	3: “Knife penetrates the wood without resistance, bark loose and mostly gone”	Chile (central)	García-Lopez et al. (2016). CWD. Based on Franc et al. (2007)
3	3: <60% log covered by bark; >30% log covered by nonvascular and vascular plants; >60% of cross-sectional area showing decay	Western Canada	Hammond et al. (2004). CWD, <i>Populus</i>
3	III: “More than 75% of the wood soft and rotten, can be kicked into pieces”	Chile (central)	Schlegel and Donoso (2008). CWD
3	Humification phase: wood has been converted into a red-brown friable mass, composed largely of the feces of saproxylics. Species from the soil invade	Europe, general	Speight (1989). CWD
4	4: “Knife penetrates the wood without resistance, bark loose and mostly gone”	S. Sweden (temperate)	Franc et al. (2007). CWD
4	Age class 4: “The form is amorphous, several wood pieces are still maintained, but overall the wood is more or less totally rotted”	Germany	Irmeler et al. (1996). CWD. Based on Brauns (1954); Schimitschek (1953); and Szujecki (1987)
4	IV: “Wood soft and rotten, partly integrated to the forest soil (humus)”	Benin, Africa	Lachat et al. (2006). CWD
4	Earthworm: “Lumbricidae, Enchytraeidae, and other invertebrates of the fourth complex repeatedly digest the wood dust formed and can be regarded as humifiers”	Caucasus, Russia	Mamaev (1961). CWD. See also Dajoz (2000) for English summary

(continued)

Table 22.1 (continued)

Class	Veteris definition	Region	Citation/notes
4	4: "The bark fallen off; the log a mere mass of rotten wood"	Temperate, USA	Shelford (1913). CWD
4	IV: Mean relative density <45% of initial density	Germany	Spänhoff et al. (2001). FWD, aquatic
5	Much decayed wood: "...the tree trunk decays and naturally sinks lower and lower, the woody fibers disappear, the debris becomes darker in color, the autumn leaves, twigs, and other litter of the forest gradually add layer to layer, and finally the remains of the log become blended with the humus of the forest floor"	Chicago, USA	Adams (1915). CWD
5	V: "Leaves, twigs, and bark absent; bole shape oval to flat; wood consistency soft; other wood properties, fragmented to powdery"	Chile (central)	Carmona et al. (2002). CWD. Based on Sollins (1982) and Spies et al. (1988)
5	5: Structural integrity soft; leaves, branches, bark absent; bole shape oval to flat; wood consistency fragmented, powdery; color of wood heavily faded; all of log on ground; invaded by roots throughout; knife blade penetrates all the way	General	Enrong et al. (2006). CWD. Based on Carmona et al. (2002); Maser et al. (1979); Spetich et al. (2002); Sollins (1982); and Rouvinen et al. (2002)
5	No formal definition; see p. 190	General	Harmon et al. (1986). CWD.
5	Class 5: "Logs were elliptical in cross section (indicative of advanced decay) and in many cases the wood was scattered across the soil surface"	Yucatan, Mexico	Harmon et al. (1995). CWD. Based on Harmon et al. (1986). Used by Keller et al. (2004)
5	V: Bark absent; twigs <3 cm absent; texture soft and powdery; shape oval; color of wood red brown to dark brown; all of tree on ground; invading roots in heartwood	Oregon, Washington, USA	Maser et al. (1979); Maser and Trappe (1984). CWD, Douglas fir. Used by Shifley et al. (1997); Bobiec et al. (2005)
5	V: Bark not firmly attached; wood without has fresh color; branches without small twigs; log not a solid piece; log shape may be oval; no hard chunks remaining; kicked log will not cleave into large pieces; log may crush when thudded with a foot; log is	Eastern USA	Pyle and Brown (1999). CWD. Used by Ferro et al. (2012a, b). Modified by Woldendorp et al. (2002a, b)

(continued)

Table 22.1 (continued)

Class	Veteris definition	Region	Citation/notes
	predominantly powdery wood; log shape may be flattened		
5	5: Bark absent; no structural integrity; twigs <3 cm absent; texture of rotten portions soft, powdery when dry; color of wood red- to dark-brown; invading roots throughout; vegetation— <i>Tsuga</i> up to 200 cm dbh; shrubs, some large, moss; fungal fruiting; mycorrhizae present	Oregon, Washington, USA	Triska and Cromack (1980). CWD, Douglas fir. Used by Sollins (1982); Sollins et al. (1987); Spies et al. (1988); Hale and Pastor (1998); Hardt and Swank (1997)
5	V: Description, very decayed; leaves absent; wood punky; shape and form <oval, collapsed	Wisconsin, USA	Tyrrell and Crow (1994b). CWD
5	V, Staphylinid stage: “The bark has mostly or entirely fallen off, and the entire log may be covered with moss or herbaceous plants. Wood adjacent to the ground has deteriorated to the point of mingling with the soil”	Tropical, New Guinea	Wilson (1959). CWD
5	No longer retains original shape; wood very soft or largely disintegrated; sometimes only outline visible beneath moss, invading roots, etc.	Australia	Meggs (1996). CWD. Used by Grove et al. (2011)
5	V: Soft and powdery (when dry), often just a mound; log does not support own weight; does not hold original shape, flattened and spread out on ground; moss, herbs, fungal bodies may be present; invading roots (when present) are throughout; hollow log from termite damage may have collapsed or be a thin shell	Australia	Woldendorp et al. (2002b). CWD. Based on Sollins et al. (1987); Pyle and Brown (1999); Spetich et al. (1999)
5	5: Wood very soft, almost completely decomposed, and easily crushed between fingers, trunk considerably shrunken, mostly covered with ground floor cryptogams and/or shrubs. Spruce trunks often bearing spruce seedlings	Finland	Renvall (1995) (Knife method). CWD. Used by Kuuluvainen et al. (2001)
6,5	Yellow cedar, 6: “Bole broken at soil level.” Western Hemlock, 5: “Integrated into soil”	Western NA	Hennon et al. 2002. CWD
6	DC 6: Diameter hard to measure; no bark; wood texture soft; oval	Boreal NA	

(continued)

Table 22.1 (continued)

Class	Veteris definition	Region	Citation/notes
	cross section; needles, branches absent; ground contact, >50% sunken, >30% covered in plants, mostly covered in moss		Lee et al. (2014). CWD, white spruce. Based on Hofgaard (1993)
6 (0–5)	5: “Little visible structure remaining, the wood having mostly degraded into soft, particulate matter,” exterior no longer intact	NSW, Australia	Barclay et al. (2000). CWD
8	8, Incorporation: Wood no longer recognizable by species, 20–30% soil mixed into wood, mass of mycelia, fibrous and woody root systems colonizing throughout the area	Eastern USA	Ausmus (1977). CWD. Used by Hendrix (1996)
8	Stage 8: Ten years dead and over—“Trees with sapwood reduced almost to pulp, and with only a small hard core of the heartwood remaining”	Virginia, USA	Howden and Vogt (1951). CWD, standing dead <i>Pinus virginiana</i>
8,8,5	Three systems. System A, 8: Pulverized wood, log buried. System B, 8: Completely soft without evidence of hard wood, outline indeterminable. System C, 5: Fragmented, overgrown with contours of completely decomposed log	Norway	Storaunet and Rolstad (2002). CWD, Norway spruce. Based on multiple authors

Class = total number of classifications the woody debris was separated into. Veteris definition = verbatim or paraphrased description of the final decay stage within that classification system. Notes include the type of woody debris and association with other research

designated 11 “rotten wood types,” of which all would probably be considered veteris. Most practical applications of decay class designation have only been applied to down woody debris, snags (Thomas et al. 1979), and occasionally stumps; few exist for twigs (but see Mertl et al. (2009)), roots, or deadwood within living trees. However, decay in living trees has been well studied from the standpoint of trees as a renewable resource (e.g., Shigo 1979; Shortle and Dudzik 2012), but that work has not been incorporated by the larger saproxylic research community.

While a few researchers have conducted research specific to wood decay in relation to habitat (Grove et al. 2011; Pyle and Brown 1998, 1999), historically the creation, definition, and study of decay classes have been subservient to initial study questions such as fuel loads or biodiversity use. Ultimately description of types, states, classes, etc. of saproxylic habitat will probably become much more complicated than the simplistic decay classes presented here. There is no reason to believe that classification of wood decay cannot/will not become as refined as, for example,

the modern soil classification system which employs a six-level hierarchy and lists 19,000 series (most refined unit) in the USA alone (USDA 1999).

22.5 Amount of Veteris Wood

Many publications provide measures of the amount of woody debris at a location or study site (see Goodburn and Lorimer 1998, Table 4 for a brilliant example). Often they provide the wood type (coarse, fine, dead limbs in standing trees, hollow trees, etc.), disposition (standing, fallen, partially submerged, etc.), state of decay (multiple classes used), site characteristics (unlogged, selectively logged, clear-cut, fire, hurricane, etc.), time since disturbance, tree species present, tree species absent, tree species studied, etc. (see references in Table 22.2). Findings are typically reported as a measure of volume, mass, or percentage, and a wide variety of units are used (board feet per acre, Mg ha^{-1} , etc.). Needless to say, a summary or meaningful comparison of amount of deadwood, much less veteris wood, across sites is difficult to compile. Feller (2003) provides a good case history for British Columbia, Canada. The “community” of publishers and researchers should develop a standard set of measurements and units that must be taken at a study site and reported in the resultant publication, whether all are necessary for the particular research or not. Similar standards already exist for reporting biodiversity data (e.g., Darwin Core, Wieczorek et al. 2012).

Table 22.2 summarizes 17 studies, ranging from 3° to 65° from the equator, in which amount of veteris wood was measured. Virtually all studies looked at coarse woody debris logs, while a few included snags or stumps. None listed estimated amount of attached deadwood (multis) within living trees (but see Nordén et al. (2004) for a rare example). The volume of veteris ranged from 0 to $54.4 \text{ m}^3/\text{ha}$ (average $13.5 \text{ m}^3/\text{ha}$), and percentage of deadwood that was veteris ranged from 0 to 53.3% (average 18.2%).

The relationship between the amount of veteris and disturbance (logging, fire, etc.) is not straightforward (Table 22.2; Feller 2003). Within studies where multiple locations were compared, four studies (Table 22.2; #1, 8, 17a-reduced impact, 17b) showed an increase in veteris after selective logging (either by volume or percentage), and four showed a decrease (Table 22.2; #12, 13, 16, 17a-conventional). However, measurements at a single time may be misleading. Woody debris volume often follows a U-shaped trend after a disturbance because of carryover woody debris—debris in the present stand that originated in the previous stand (Carmona et al. 2002; Feller 2003; Maser et al. 1988). A large reduction of veteris was reported in a Newfoundland forest chronosequence study 60–70 years after disturbance (Sturtevant et al. 1997) and in hemlock-hardwood forests 200–250 years after disturbance (Table 22.2; #6). A postfire chronosequence in Quebec (Table 22.2, #5) showed a complete loss of veteris during ~55–75 years postfire; however, other decay classes were available throughout the entire 90-year period studied. These findings indicate that maintaining continuity of specific decay classes at a site is not a simple matter and may require decisions decades in advance.

Table 22.2 Amount of veteris wood reported from various locations arranged from furthest to nearest equator

#	Amount of veteris		Substrate	History of site	Forest type	Lat.	Location	Citation
	m ³ /ha	Mg/ha						
1	8	15.6	CWD, logs	Primary	Boreal, Norway spruce dom.	65°N	Finland, eastern	Sippola et al. (2001)
1	9.4	32.3	CWD, logs	Selective logging ca. 1930–1960	Boreal, Norway spruce dom.	65°N	Finland, eastern	Sippola et al. (2001)
2	5	5.7	CWD, logs	Primary	Northern Boreal	63°N	Russia, Vodlozero NP	Sitonen et al. (2001)
3	36.9	31.5	CWD, logs	Primary	Southern Boreal	61°N	Russia, near Ural Mountains	Kuuluvainen et al. (2001)
4	10	16.9	CWD, logs	Minor—no human disturbance	Temperate Norway spruce	49°N	Poland, Tatra NP	Zielonka and Niklasson (2001)
5	20	39	CWD, logs	40 years since fire	Jack pine	49°N	Canada, Quebec	Brais et al. (2005)
5	0	0	CWD, logs	65 years since fire	Jack pine	49°N	Canada, Quebec	Brais et al. (2005)
5	13	25	CWD, logs	85 years since fire	Jack pine	49°N	Canada, Quebec	Brais et al. (2005)
6	13	40.6	CWD, logs	Stand age <200 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
6	7	20	CWD, logs	Stand age 200–250 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
6	11	18	CWD, logs	Stand age 250–300 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
6	10	12.2	CWD, logs	Stand age >300 year	Hemlock-hardwood	46°N	USA: WI, MI	Tyrell and Crow (1994b)
7	0.7		CWD, logs	Primary	Douglas fir, western hemlock	46°N	USA: Cascade Range, OR, WA	Sollins et al. (1987)
8		17	CWD, logs	Primary	Maple-oak hardwood	45°N	USA, Minnesota	Hale et al. (1999)
8		26	CWD, logs	Managed, 80–120 years old	Maple-oak hardwood	45°N	USA, Minnesota	Hale et al. (1999)

(continued)

Table 22.2 (continued)

#	Amount of veteris		Substrate	History of site	Forest type	Lat.	Location	Citation
	m ³ /ha	Mg/ha %						
9a	16.8	3.3	CWD, stump	Selective logging	Cool temperate wet forest	43° S	Australia, Tasmania	Woldendorp et al. (2002b)
9a	54.4	11.1	CWD, logs	Selective logging	Cool temperate wet forest	43° S	Australia, Tasmania	Woldendorp et al. (2002b)
10		4	CWD, logs	Primary and secondary	Temperate forest	42° S	Chile, Chiloe Island	Carmona et al. (2002)
11		27.7	CWD, logs and snags	Primary	Temperate rainforest <i>Nothofagus</i> dom.	39° S	Chile, Valdivian Andes	Schlegel and Donoso (2008)
11		20.1	CWD, logs and snags	Primary	Temperate rainforest mixed spp.	39° S	Chile, Valdivian Andes	Schlegel and Donoso (2008)
12	3.23		CWD, logs	Old growth, minor human disturbance	Oak-hickory, oak-maple	38° N	USA, Missouri	Shifley et al. (1997)
12	1.75	1	CWD, logs	Secondary, selectively logged ca. 1920	Oak-hickory, oak-maple	38° N	USA, Missouri	Shifley et al. (1997)
13	25.2	16.7	CWD, logs	Primary	S. Appalachian	35° N	USA, North and South Carolina	Hardt and Swank (1997)
13	27.4	21.8	CWD, logs	Maturing, selective logging ca. 1920	S. Appalachian	35° N	USA, North and South Carolina	Hardt and Swank (1997)
13	13.3	11.7	CWD, logs	Young, clear-cut ca. 1960	S. Appalachian	35° N	USA, North and South Carolina	Hardt and Swank (1997)
9b	10.4	2.5	CWD, logs	Selective logging	Temperate rainforest	35° S	Australia, New South Wales	Woldendorp et al. (2002b)
9b	7.1	0.3	CWD, stumps	Selective logging	Temperate rainforest	35° S	Australia, New South Wales	Woldendorp et al. (2002b)
14	3.5	2.4	CWD, logs	Primary	Mediterranean, <i>Cryptocarya</i> dom.	33° S	Chile, Rio Clarillo National Reserve	García-López et al. (2016)

14	13.6		19.7	CWD, logs	Primary	Mediterranean, <i>Quillaja</i> dom.	33°S	Chile, Rio Clarillo National Reserve	García-López et al. (2016)
14	59		33.9	CWD, logs	Primary	Mediterranean, <i>Lomatia</i> dom.	33°S	Chile, Rio Clarillo National Reserve	García-López et al. (2016)
9c	4.8	1.23	25.7	CWD, logs	Minor human disturbance	Temperate	25°S	Australia, Queensland	Woldendorp et al. (2002b)
9c	0.2	0.08	53.3	CWD, stumps	Minor human disturbance	Temperate	25°S	Australia, Queensland	Woldendorp et al. (2002b)
15		2	1.7	CWD, logs and snags	Moderate hurricane and fire	Tropical dry	19°N	Mexico, Yucatan Pen.	Harmon et al. (1995)
16	8.4		27.8	All dead wood	Minor human disturbance	Tropical dry	6°N	Benin, Lama Forest Res.	Lachat et al. (2006)
16	0		0	All dead wood	Teak Plantation, planted ~1960	Tropical dry	6°N	Benin, Lama Forest Res.	Lachat et al. (2006)
16	0		0	All dead wood	Fuelwood plantation, planted ~1990	Tropical dry	6°N	Benin, Lama Forest Res.	Lachat et al. (2006)
17a	11.9		10.9	CWD, DWD	Primary	Tropical dense moist	3°S	Brazil, Fazenda Cuaxi	Keller et al. (2004)
17a	12.5		8.8	CWD, DWD	Reduced impact logging	Tropical dense moist	3°S	Brazil, Fazenda Cuaxi	Keller et al. (2004)
17a	1.8		0.9	CWD, DWD	Conventional logging	Tropical dense moist	3°S	Brazil, Fazenda Cuaxi	Keller et al. (2004)
17b	22.4		20.6	CWD, DWD	Primary	Tropical dense moist	3°S	Brazil, Tapajós NF	Keller et al. (2004)
17b	31.5		20.4	CWD, DWD	Reduced impact logging	Tropical dense moist	3°S	Brazil, Tapajós NF	Keller et al. (2004)

22.6 Residence Time of Veteris Wood

While deadwood is considered to be an ephemeral habitat, described as a “sinking ship” (Jonsson 2012), or “spatiotemporally dynamic habitat” (Seibold et al. 2017), some forms of deadwood are among the most persistent habitats in a landscape and stubbornly hold their ground for generations. Angers et al. (2010) studied degradation of four species of snags in Boreal North America, each of which had a half-life of more than a decade, and some individual snags stood for half a century. Ranius et al. (2009) showed that tree hollows in European *Quercus robur* L. persist for centuries. Rotting logs in two long-term decomposition studies in Oregon, USA (Harmon 1992), and Tasmania, AU (Grove 2009), are both expected to last several centuries (some nearly a millennia; see Foster and Lang 1982). Feller (1997) used radiocarbon dating to estimate date of death and found a coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.: Pinaceae) in British Columbia that died approximately 1200 years previously. Kelly et al. (1994) developed a 1397-year-old chronology using live trees, snags, and exposed logs of *Thuja occidentalis* L. (Cupressaceae) in Ontario, Canada. Veteran trees may survive from centuries to more than a millennium, and multis wood within them may persist for centuries after tree death (Lonsdale 2013). Other than a cave, deep soil, or a piece of exposed granite, it’s hard to imagine a more stable habitat than veteris wood.

Residence time specific to decay classes is poorly studied. Typically larger wood lasts longer, and the time spent in decay classes increases as decay increases (Harmon et al. 1986: 213). Using a five-class system, Tyrell and Crow (1994a) found residence time of hemlock logs in Wisconsin and Michigan to be 2, 10, 20, 35, and ~15–100 years, respectively. In a globally extreme example, Daniels et al. (1997) studied residence time of western red cedar, *Thuja plicata* (Donn ex D. Don in Lamb.), in coastal British Columbia. In a four-class system, logs averaged 2, 47, 141, and 780 years since death for each class, respectively. Swift et al. (1979) point out that ultimately decomposed plant matter may persist for hundreds to thousands of years in the form of soil organic matter and humus. Thus the “end,” “death,” or “loss” of veteris wood is dependent on an as of yet undetermined cutoff point. Currently the “end” of a log is generally based on visual clues as no formal descriptions, such as physiochemical measurements or comparisons of soil quality or structure, could be found in the literature.

22.7 Wood Structure and Digestion

Extended overviews of this subject are found in Dajoz (2000: Chap. 14), Käärik (1974), Stokland (2012c), and Swift et al. (1979). Unless indicated, the following is taken from them. See Ulyshen (2016) for a detailed account of invertebrate influence on wood decomposition. Wood is composed of three classes of carbohydrates: cellulose, hemicellulose, and lignin. Digestion of cellulose requires the synergistic

effect of three types of enzymes and is accomplished only by a few fungi, bacteria, marine organisms, and insects. Within insects there are four mechanisms for cellulose digestion: use of protozoan symbionts in the hindgut, use of bacteria in the hindgut, use of fungal cellulases originating in the food, and, rarely, creation of the full cellulose system by the insect (Martin 1991). Hemicelluloses and lignin each require specialized enzymes for digestion, and as the composition of the molecules differs greatly between conifer and broadleaf trees, so do the enzymes needed for digestion.

Fungal digestion of wood is often lumped into three major categories: white, brown, and soft rot. White rot is the digestion of all three components (cellulose, hemicellulose, and lignin), although the rate of digestion may not be equal for all molecules. "Brown rot" is the preferential digestion of cellulose and hemicellulose leaving lignin intact and is found principally in conifers in boreal forests, although exceptions exist. Soft rot preferentially digests cellulose and hemicellulose but occasionally lignin as well. Soft rot typically occurs in water or high-moisture situations and has been found in initial decay of oak heartwood.

When plant matter dies, it often initially undergoes "microbial conditioning" (Swift et al. 1979), a process where microorganisms, including bacteria and fungi, begin digesting the material. During this process, the material is often softened, nitrogen is fixed, secondary compounds are detoxified, etc. The conditioning creates a "detritus-buffered system" (Nalepa et al. 2001a) where arthropod detritus feeders are not exposed to the full force or variety of plant defenses. Additionally the predigestion and the presence of the microorganisms, which possess nutritive value themselves, make the substrate more favorable to arthropod consumers.

Feces are not much different from rotting organic matter, and reconsumption of feces, coprophagy, allows for additional digestion of the originally consumed material and digestion of any microflora that grew after defecation. Many cockroach species will engage in coprophagy when available, but fungus-gardening termites (Blattodea: Isoptera) and passalid beetles (Coleoptera: Passalidae) take the practice to an extreme. They use an "external rumen" technique: material is eaten, inoculated with microbes, and voided. Continued "digestion" of the material by the microbes takes place in the feces which are then reingested, and nutrients and energy are absorbed by the arthropod (Mason and Odum 1969; Nalepa et al. 2001a; Swift et al. 1979). An external rumen can be used to "burn off" excess carbon and decrease the carbon to nitrogen ratio (Eggleton and Tayasu 2001).

22.8 Hypothetical Paths to Creation of Veteris Wood

Many paths lead from wood in a living tree, through death, to loss of individuality, and complete evaporation/mineralization, but several predictable paths specific to veteris formation and/or "long-term" use can be highlighted. A conceptual model of woody debris decay is presented in Fig. 22.2a, where the structural and chemical qualities of the wood are tracked from life (green line on left, 100%) through decay

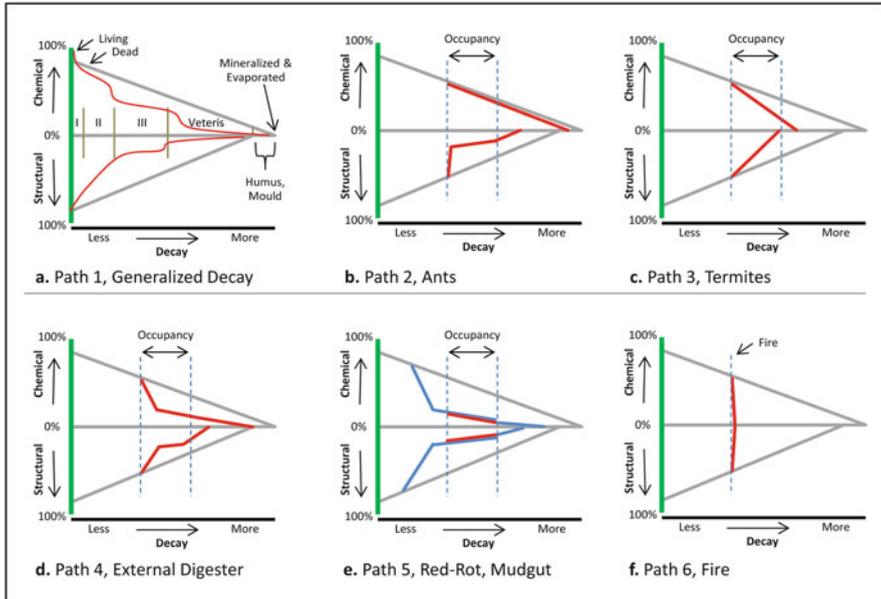


Fig. 22.2 Predictable paths to creation and use of veteris wood. Exterior gray lines represent “idealized” decay, while red lines represent “actual” decay. (a) Generalized decay, (b) excavation of a log by ants, (c) consumption of wood by termites, (d) excavation and occupation by external digesters such as Passalidae, (e) alterations of wood made by fungi (blue lines) and subsequent use by red-rot inhabitants such as Micromalthidae, (f) degradation by fire. See text for details

until complete loss (on the right, 0%). More specific aspects (e.g., lignin content, density) could be tracked on each side in a qualitative or quantitative manner but are not shown here. Use of a standardized figure similar to this would allow comparison across sites and studies. As decay occurs, the woody material passes through decay stages until it enters the veteris stage. After all structural quality is gone, the remainder of the woody debris consists of humus, wood mold, etc. The outer gray lines represent the total “decay space” of the model, while the red lines illustrate the deviation from typical decay by the proposed scenario. Path 1 (Fig. 22.2a) might be typical for many pieces of woody debris that experience biotic and abiotic processes that degrade the wood in an incremental manner and where no single taxon drives the decay.

Path 2 (Fig. 22.2b) is a hypothetical example of veteris formation by log-dwelling ants. Immediately after occupancy, removal of the material (but not consumption) for nest building results in rapid structural damage, but little chemical degradation, as illustrated by the red lines. Minimum structural integrity must be maintained while the colony is in the wood, and once that is gone, the colony must move on.

Path 3 (Fig. 22.2c) is a hypothetical example of rapid decay by termites which remove and consume wood (that may or may not be infected with fungi) which is digested in the termite body. Structural and chemical decomposition occurs nearly

symmetrically. Depending on the type of termite, the log may be fully consumed while the colony resides elsewhere, or if the colony resides in the logs, an outer protective shell must remain intact for protection (see below).

Path 4 (Fig. 22.2d) is a hypothetical example of decay by taxa that initially cause a large amount of structural and chemical degradation but maintain a residency within the wood for a long period of time, during which rate of chemical and structural change is greatly reduced (e.g., Passalidae (Coleoptera), *Cryptocercus* spp. (Blattodea), etc.). These taxa remove and consume wood but reconsume partially digested wood that has been inoculated with other organisms (external rumen *sensu* Mason and Odum 1969). The outer shell of the wood must maintain a minimum of external structural integrity to remain suitable for the colony.

Path 5 (Fig. 22.2e) is a hypothetical example of a situation involving arthropods [e.g., *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae), *Prostomis atkinsoni* Waterhouse (Coleoptera: Prostomidae)] that live within veteris wood that has been specially conditioned by fungi, sometimes called brown or red rot, and that directly consume the substrate created by the fungi. An extreme version of that rot type found in Australia is called mudguts (Grove 2007). Here the majority of chemical and structural decay are initiated by the original fungi, illustrated by the blue lines, and little to no meaningful chemical and structural changes are made by the arthropod taxa within (red lines).

Path 6 (Fig. 22.2f) is fire. Both chemical and structural quality are simultaneously driven to 0%, or nearly so, in a very short amount of time. Unlike other “natural disasters,” such as floods, hurricanes, and mudslides, fire is unique in that it causes chemical rather than physical changes. Fire can be thought of as a “proto-life,” a metabolism without a body. Fire is a form of autocatalytic reaction (one product of fire, heat, is also a reactant); it grows, reproduces, digests organic material, and respire CO₂. Ash is fire “feces” (especially important for fungi), and scorched items can be thought of as “partially digested.” Fire is a “universal omnivore” that readily digests fats, proteins, and carbohydrates including cellulose, hemicellulose, and lignin (no enzymes needed!). Fire cannot adapt or evolve, but populations of organisms can evolve in relation to fire, and saproxylic organisms are obviously in competition with fire.

Two trends are noticeable: (A) from high structural damage (Paths 2, 3) to low or no meaningful structural damage, because the previous rot had already degraded the wood (Paths 4, 5), and (B) from no consumption of the wood (Path 1) to consumption with internal digestion (Paths 3, ~4) to an increasing requirement for external pre-digesters (Paths ~4, 5).

22.9 Insects in Veteris Wood I: The Bestiary

Entomologists are a necessary evil!

—Harding and Alexander 1993

The following is a general survey of insects that are known or suspected to use veteris wood. In many cases, the reported habitat (“in logs”) is too general to fully judge if a specimen was collected from veteris or less-decayed wood. Insects in many orders (Phasmatodea, Mantodea, Lepidoptera, etc.) exploit the existence of deadwood by using cryptic colors, textures, and shapes to look like bark, twigs, etc. but don’t necessarily rely on the existence of deadwood per se. Additionally, as was pointed out above, no distinct boundary separates veteris wood from well-humified soil; therefore the case could be made that any number of soil-dwelling organisms that specialize on humus utilize “extreme” veteris wood. All insect orders are covered for completeness so that a sense of what is and isn’t known is available.

22.9.1 *Protura*

Protura are a poorly known group of incredibly abundant, very small hexapods with a worldwide distribution (Pass and Szucsich 2011). About 790 species are known, with many more undescribed. They are generally found anywhere sufficiently moist organic matter is present and have been reported from tree holes, “moist woodland humus,” and “moldering timber” (Copeland and Imadaté 1990; Pass and Szucsich 2011). Protura are known to feed on fungal mycorrhizae; other feeding habits are suspected but unknown. Certainly Protura will be present in veteris wood, but beyond that, all else remains a mystery.

22.9.2 *Collembola*

Springtails are a highly diverse group (~8000 spp.) with a worldwide distribution and are some of the most abundant soil-dwelling arthropods (Hopkin 1997; Smolis and Kadej 2014). They feed on fungal matter and decomposing debris, and some are predatory on other invertebrates (Grimaldi and Engel 2005; Hopkin 1997). Teasing apart specific habitats of Collembola has only recently begun. For example, in Poland, about 40% of Collembola are associated with deadwood, and about 5% are considered saproxylic (Skarżyński et al. 2016). Skarżyński et al. (2016), in Wigry National Park, Poland, provide a good description of the community of Collembola in deadwood. They found that most species in the forest make little distinction between forest litter and deadwood; however about 20% of the species were “saproxylic” (predominantly in deadwood), and about 20% of the specimens collected from deadwood were of those species. Species richness and number of specimens increased with decay class; veteris wood (class III) was the highest. Smolis and Kadej (2014) described a new species of saproxylic Collembola from hemlock logs in Oregon, USA, that were “very rotten, soft and moist inside.” Despite searching, they could not find it in any other habitat. The presence and

influence of Collembola in veteris wood is largely unknown, but studies cited above indicate that many saproxylic and veteris-dwelling Collembola are to be expected.

22.9.3 *Diplura*

Diplura are soil-dwelling invertebrates (800+ spp.) with a worldwide distribution (Allen 2002). They can be split into two groups, the Campodeomorpha and Japygomorpha; the former are considered herbivorous, while the latter are predatory (Grimaldi and Engel 2005). Reddell (1983) lists species that were collected in rotten wood, redwood duff, and deep humus, all of which could be considered veteris wood. As members of the soil fauna, Diplura are expected in veteris wood; whether any species are obligate is currently unknown.

22.9.4 *Archaeognatha (Microcoryphia) and Zygentoma (Thysanura)*

Both orders are largely soil-dwelling insects with about 350 and 370 species, respectively (Triplehorn and Johnson 2005). They are generally considered browsers or grazers of detritus, soft plant matter, and lichens (Ferguson 1990). They have been reported from deadwood and can be found in cavities within and beneath veteris wood, but that use may be restricted to shelter. As members of the soil and leaf litter fauna, both are expected in veteris wood.

Some species of *Zygentoma* may use deadwood more consistently. Some species of the Nicoletiidae subfamily Atelurinae are associated with ant and termite nests (Triplehorn and Johnson 2005) and may follow their hosts into veteris wood. The relic taxon *Tricholepidion gertschi* Wygodzinsky (Lepidotrichidae) is known from under decaying bark or in rotten wood of fallen Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.). At a northern California site, specimens were found under decaying bark, but absent from the soil and leaf litter, despite specific searching (Engel 2006; Wygodzinsky 1961).

22.9.5 *Ephemeroptera*

Mayflies are aquatic as immatures with a short-lived, nonfeeding adult phase (Grimaldi and Engel 2005). Immatures of many species scrape/graze microorganisms growing from the surface of woody resources or use it as structure (e.g., Waltz and Burian 2008). How many could be considered saproxylic in any sense is unknown. However, immatures of the African species *Povilla adusta* Navas

(Polymitarciidae) are clearly saproxylic. They are famous for burrowing into softened wood for shelter, including pilings and boats, and then emerge at night to filter feed on planktonic algae or periphyton if available (Bidwell 1979; Petr 1970, 1971). *Povilla adusta* prefer softened wood and could be considered denizens of veteris wood.

22.9.6 *Odonata*

Dragonflies are a worldwide taxon with predominantly aquatic immatures and active flying adults; both life stages are predatory (Corbet 1999; Grimaldi and Engel 2005). Immatures of at least 24 genera and 47 species are associated with phytotelmata (plant-based container habitats) including saproxylic/veteris habitats: water-filled bamboo, tree stumps, and tree hollows (Corbet 1999; Kitching 2000, species list). Two species in the family Megapodagrionidae are obligate tree-hole breeders and immatures of the family Pseudostigmatidae, and several other genera are only known from tree holes and may be considered obligate as more is known (Corbet 1999). While traditionally not thought of as a saproxylic habitat, water-filled tree holes have been microcosms for important ecological studies and will certainly be of conservation concern in the future (Kitching 2000).

22.9.7 *Plecoptera*

Stoneflies are most prevalent in flowing freshwater in the temperate zones. Immatures of many species scrape/graze microorganisms growing from the surface of woody resources or use it as structure (e.g., Stewart and Stark 2008). Omad et al. (2015) found that *Diamphiphnopsis samali* Illies (Diamphiphnoidae) specifically fed on wood (50% of gut content) and fungal hyphae (30%) in first-order Patagonia streams. How many other Plecoptera could be considered saproxylic in any sense is unknown.

22.9.8 *Embiidina (Embioptera) (Embiodea)*

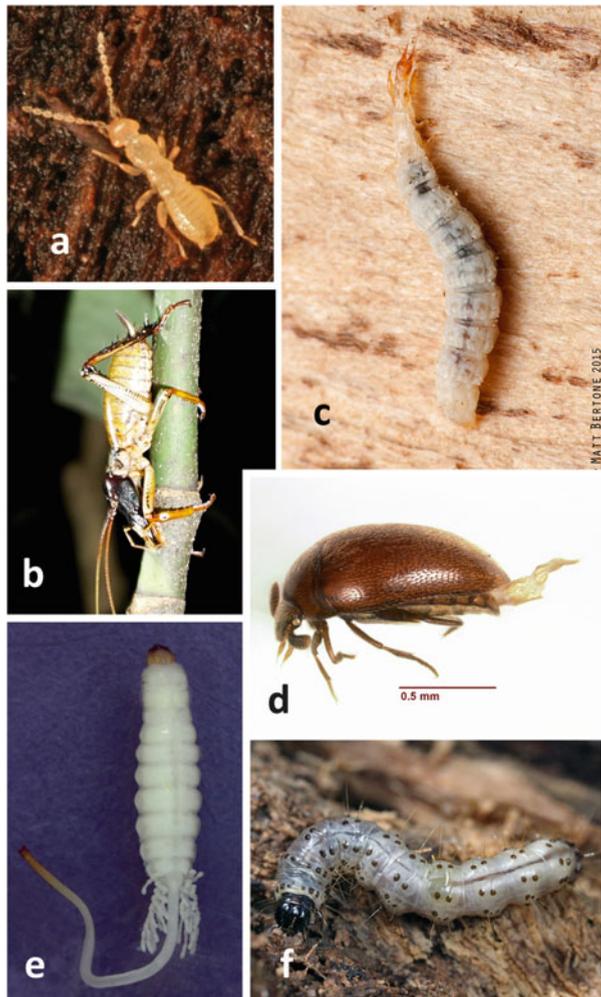
Web spinners are gregarious subsocial insects that generally live within tunnels or under sheets made of silk produced by glands in the proximal tarsomere of the front legs. About 360 species are described (although Ross (1970) reports the existence of 800+ mostly undescribed species), and most are found in the tropics, although some range into the warmer temperate zones (Grimaldi and Engel 2005). They are general detritivores and grazers of lichens, etc. Many species construct galleries under or among rocks, within leaf litter, and in the crevasses of bark. At least seven species

have been reported from under “bark of dead limbs and trunks”; on dead vines; on an old oak stump; “on bark of a high, dead stump”; and “in bark crevices of trees and dead stumps” (Ross 1944, 1984a, b). Whether association with deadwood among these species is consistent or happenstance is unknown. Probably some species will be recognized as saproxylic as more becomes known.

22.9.9 Zoraptera

Zoraptera (Fig. 22.3a) are the only order of insects that are exclusively found in deadwood (Stokland 2012a). Despite their taxonomic paucity—only 32 species are known—Zoraptera are of interest for a variety of reasons. The relationship of

Fig. 22.3 Interesting insects in veteris wood. (a) *Zorotypus hubbardi* Caudell, Zoraptera: Zorotypidae, adult (photo by Art Evans); (b) *Hemideina thoracica* (White) Orthoptera: Anostomatidae, adult (photo by Shelly Myers); (c) *Nallachus americanus* (McLachlan) Neuroptera: Dilaridae, larva (photo by Matt Bertone); (d) *Tohlezkus inexpectus* Vit, Coleoptera: Eucinetidae, adult; (e) *Axymyia furcata* McAtee, Diptera: Axymyiidae, larva (photo by M. J. Hatfield); (f) *Scolecocampa liburna* (Geyer), Lepidoptera: Erebidae, larva (photo by Kim Fleming)



Zoraptera to other orders has long remained a mystery, but recent studies have confidently placed it within the Polyneoptera (Grimaldi and Engel 2005), and Misof et al. (2014) placed them sister to the Dermaptera. Adult Zoraptera come in two forms: alate (eyed, winged) and apterous (blind, wingless). The alate form is the dispersal stage and tends to appear when resources are being reduced (Grimaldi and Engel 2005). Zoraptera eat fungal hyphae, nematodes, or minute arthropods and are often reported from rotten logs, termite galleries, and sawdust piles (Shetlar 1978).

Zoraptera have played a prominent role in the description and thoughts on deadwood: Silvestri (1913) introduced the term “saproxyllic” in his description of the order; Wilson (1959) designated his third log decay stage (of 5) the “Zorapteran stage”; and Hamilton (1978) pointed out they were one of the numerous insects associated with deadwood that exhibit flight polymorphism.

22.9.10 Orthoptera

The crickets, grasshoppers, katydids, and relatives are represented by about 23,000 species, most of which are phytophagous, while others are detritivores or predatory (Grimaldi and Engel 2005). Orthoptera associated with veteris wood include members of the cricket family Myrmecophilidae, which are obligateinquilines of ants and may be found in deadwood as they follow their hosts (Blatchley 1920; Wetterer and Hugel 2014; Wheeler 1910). Other Orthoptera may interact with veteris wood by seeking shelter within and beneath it, and some arboreal species may insert eggs within the moist veteris wood on the outside of dead limbs, although the last part is purely speculative.

The grand saproxyllic Orthoptera are the wetas or king crickets (families Anostostomatidae and Rhabdophoridae) which are endemic to New Zealand (Field 2001). Wetas represent some of the largest and most enigmatic insects alive. Many wetas occasionally use tree holes or crevices, but species in the genus *Hemideina* Walker (Fig. 22.3b) are specifically associated with tree holes where they reside during the day, presumably to avoid predation (Gibbs 2001). *Hemideina* don't excavate their own holes de novo but typically use holes previously created by larvae of *Ochrocydus huttoni* Pascoe (Coleoptera: Cerambycidae) or *Aenetus virescens* (Doubleday) (Lepidoptera: Hepialidae) (Gibbs 2001). Wetas maintain holes in live trees by nibbling the cambium at the edge of the hole to maintain an opening and can enlarge and excavate the tunnel when heartrot (veteris) exists (Field and Sandlant 2001).

22.9.11 Phasmatodea

Walking sticks or stick insects are typically cryptically colored and/or shaped herbivorous insects that reside on the plants they are consuming (Grimaldi and

Engel 2005). However some members are loosely associated with deadwood. Members of the genus *Anisomorpha* Gray will sometimes rest under loose bark or logs (fresh to veteris) possibly for protection from predators or due to a more suitable microclimate (Blatchley 1902; Conle et al. 2009; personal observation). *Eurycantha calcarata* Lucas (Phasmatidae) has also been reported to rest in rotten logs and stumps during the day (Gurney 1947b). *Dryococelus australis* (Montrouzier) (Phasmatidae), the (presumed extinct and then rediscovered) Lord Howe Island stick insect, would rest in tree holes during the day. A single tree hole might be used by multiple individuals for many generations, and the accumulation of droppings might exceed several bushels (Gurney 1947b). Hollow sections of banyan figs are currently used for rearing captive populations, and plans are under way to reestablish the species on the island (Crew 2012).

The eggs of many walking sticks have a distinct cap on the operculum called a capitulum (Clark 1976) which greatly resembles an elaiosome, a process found on plant seeds which invokes myrmecochory, dispersal by ants. Instances of ants collecting phasmid eggs and taking them back to the nest have been recorded but mostly in ground-nesting ants. Compton and Ware (1991) conducted several studies on the interaction of ants with the eggs of *Phalces brevis* (Burmeister) (Phasmatidae). Eggs with an intact capitulum were greatly preferred by ants. First instar walking sticks from eggs that hatched within a laboratory colony of *Acantholepis capensis* Mayr were ignored by the ants, and presumably the same would happen in the wild. Stanton et al. (2015) showed that ants collected and moved eggs of the walking stick *Eurycnema goliath* Audinet-Serville (Phasmatidae) specifically because of fatty acids found on the capitulum. There are more than 3000 species of walking stick known (Grimaldi and Engel 2005), and if any species have eggs that are attractive to ants that nest in rotting wood, and if the protection of the ants is important for the early development of the phasmid, then the interaction would represent an important use of veteris wood.

22.9.12 *Dermaptera*

Earwigs (~2000 spp.) prefer warm moist climates, and most species are detritivores/omnivores while a few are herbivores or predators (Grimaldi and Engel 2005). Dermaptera are subsocial; the female will often create a burrow and guard the eggs and newly hatched offspring. Dermaptera are often found in leaf litter and in, on, and under deadwood. Blatchley (1920) lists several species in eastern North America collected from half-buried logs and beneath bark of various types of dead trees. Some species may live entirely on or within veteris, or prefer to create natal burrows in veteris, but to what extent that occurs is currently unknown.

22.9.13 *Grylloblattodea and Mantophasmatodea (Notoptera)*

The ice crawlers and rock crawlers are placed in two closely related orders (Misof et al. 2014) that are occasionally combined (Notoptera). Mantophasmatodea were first described as an order during 2002 (Klass et al. 2002) and currently consist of about 15 predatory species all known from Africa (Grimaldi and Engel 2005). They have not yet been reported to interact with deadwood.

Grylloblattodea are represented by 26 species restricted to North America and Asia. North American species are known from higher elevations and are active at cold temperatures, while some Asian species occur in leaf litter and are active at “normal” temperatures (Ando 1982). North American species are famous for creeping out at night and scavenging dead insects and other debris off of snow banks. Reportedly they can be kept as “pets” in a refrigerator at 8 °C for several months (Gurney 1953, and references therein) but will become sluggish or even die from “high” temperatures (still below human body temperature). Gurney (1953) reported a specimen collected from the center of a rotten log about 2.5–3 ft (~80 cm) in diameter: “The wood was almost completely decayed and it was fairly damp in the center.” A female of a Russian species was collected from a rotten tree stump (Bei-Bienko 1951; see Gurney 1953), and in Montana, several specimens were collected in rotten logs and stumps, including one collected a foot (~30 cm) above the ground in a rotten stump (Pletsch 1946). Esch et al. (2017) collected numerous *Grylloblatta campodeiformis* Walker (Grylloblattidae) from several species of dead pine in Alberta, Canada, using emergence traps. Gut examination revealed no plant matter but plenty of saproxylic arthropods.

The extent to which grylloblattids use deadwood and for what purposes are unknown, although the findings of Esch et al. (2017) clearly show some species are saproxylic. Adults and immatures are generally soft bodied and probably don’t dig into sound wood. As climate change alters temperature regimes and reduces snow fields, grylloblattids will certainly become taxa of conservation concern, and knowing the full extent of their natural history will be important.

22.9.14 *Mantodea*

The preying/praying mantises/mantids are an order of exclusively predatory orthopteroids closely related to cockroaches, with about 2300 described species (Grimaldi and Engel 2005). Mantises are often morphologically cryptic and exhibit a variety of colors, shapes, and textures. “Bark mantids” spend most of their time on tree trunks (Prete et al. 1999) and resemble bark, lichen, etc., but there is no indication that any are found on, or exclusive to, dead trees. Certainly mantises will place their oothecae (egg cases) on or under deadwood of various sizes and decay states, but there is no indication that this isn’t simply an opportunistic use of an available substrate.

22.9.15 *Blattodea (Cockroaches)*

Many species of cockroaches (exclusive of the termites) are associated with soil and leaf litter habitats, and many are considered to be generalist detritivores and are therefore expected to be found in, near, and around deadwood of all decay stages. Bell et al. (2007: 46) list 16 species of cockroaches that are associated with rotten wood (not including members of *Panesthia* Serville (Blaberidae) and Cryptocercidae) and provide a good summary of cockroach interaction with deadwood. Some cockroach species, which are morphologically convergent with wood boring beetles, are suspected of boring into solid wood (Bell et al. 2007: 12). Myrmecophylic and termitophilous cockroaches may accompany their hosts into deadwood. Needless to say, much more research needs to be done on non-synanthropic cockroaches, and their role in wood decay may be more extensive (especially in the tropics) than currently thought.

Two cockroach genera are of special interest when it comes to creation of veteris wood, *Panesthia* and *Cryptocercus* Scudder (Cryptocercidae). *Panesthia* are subsocial and live as multigenerational groups in a variety of rotting logs that they excavate and feed on over many years (Bell et al. 2007). Additionally they can digest cellulose independent of gut symbionts (Scrivener et al. 1989).

The cockroach genus *Cryptocercus* consists of 14 species distributed in western NA (1 sp.), eastern USA (4 spp.) (Burnside et al. 1999), eastern Russia (1 sp.) (Mamaev 1973), China (7 spp.) (Grandcolas et al. 2005; Nalepa et al. 2001b; Wang et al. 2015), and South Korea (1 sp.) (Grandcolas et al. 2001). With the exception of a brief walking dispersal stage, *Cryptocercus* spends its entire life living and feeding within decayed sections of rotted logs (Nalepa et al. 1997), and where present, *Cryptocercus* may play a critical role in log decomposition (Nalepa et al. 2017). While of minor global importance for wood decay, *Cryptocercus* are sister taxa to all “termites” (Legendre et al. 2015) and represent an important link between “cockroaches” and “termites” in regard to lifestyle, gut biota, and sociality (see overview in Grimaldi and Engel 2005: 235). [Grandcolas (1994) and subsequent publications (see Grandcolas et al. 2001) maintain wildly differing views conceding the phylogenetic placement of *Cryptocercus* despite enormous evidence to the contrary (see Legendre et al. 2015; Lo et al. 2000; Nalepa and Bandi 1999).]

Cryptocercus differ from most cockroaches and are similar to most termites by (1) using deadwood as an exclusive food source, (2) dependence on protozoan gut fauna for digestion of cellulose (Martin 1991), and (3) subsocial behavior (Cleveland 1934; Grimaldi and Engel 2005). *Cryptocercus* was well studied by Cleveland (1934) who described 12 genera and 25 species of flagellate protozoa in the gut fauna, which share a common ancestor with protozoa in termites (Cleveland 1934; Nalepa 1984). *Cryptocercus* have been found living in logs of numerous species including American chestnut (*Castanea dentata* (Marsh.) Borkh.), oak (*Quercus* spp.), and eastern hemlock (*Tsuga canadensis* (L.) Carrière) (Cleveland 1934).

Cryptocercus are subsocial with a basic social unit of an adult pair and ~15–20 offspring from one (rarely two) reproductive season(s) (Nalepa 1984). Individuals of *Cryptocercus punctulatus* Scudder take 6–8 years to reach maturity after which they disperse to a new log and start a family. Adults typically remain with their brood at least 3 years (Cleveland 1934; Nalepa 1984). Multiple families may live within a single log, but galleries are separated by structural boundaries (Nalepa 1984). Nymphs acquire protozoans by proctodeal feeding from adults and may continue this activity for up to a year after hatching (Nalepa 1984).

Cryptocercus exhibits a distinct “Greyian” distribution (Grimaldi and Engel 2005; Nalepa and Bandi 1999). During the Late Cretaceous and early Tertiary, vast forests covered the Northern Hemisphere. Over time those forests were diminished, but “relic temperature” refugia remained in East Asia and eastern North America, which today share numerous relic taxa (Hsü 1983). Based on divergence of endosymbionts, Nalepa et al. (1997) estimate that the split between the eastern and western North American species of *Cryptocercus* took place 25–70 million years ago. Migration from one location to the other could have taken place during the Eocene optimum 65–34 million years ago when the forest was contiguous between both locations (Nalepa and Bandi 1999). Low vagility and the requirement for dead logs imply that current populations of *Cryptocercus* are found in places that have been continually forested since the early Tertiary (approximately 60 million years) (Nalepa et al. 1997; Nalepa and Bandi 1999). The restricted ranges and requirements of *Cryptocercus* increase the likelihood that it will become a taxon of conservation concern in the future (Nalepa et al. 2017), for example, *C. clevelandi* Beyers may already be extirpated from Washington, USA (Nalepa et al. 1997).

22.9.16 *Blattodea* (Termites)

The role of termites in deadwood is treated by Bignell (2018; see Chap. 11). The following is presented with specific attention to veteris wood.

Termites are a branch of eusocial “cockroaches” composed of about 3000 species that first evolved in the Late Jurassic to Early Cretaceous (Grimaldi and Engel 2005; Legendre et al. 2015; Lo et al. 2000; Thorne et al. 2000). They are mostly absent from boreal regions but predominate in the tropics (Abe 1987). Termites actively alter wood themselves through excavation and consumption and, by their presence, increase wood decay when predators dig out colonies; see Redford (1987) for a list of mammals that feed on termites. Strong evidence indicates that members of the Cretaceous dinosaur family Alvarezsauridae (Saurischia) preyed on wood-nesting termites (Longrich and Currie 2009), indicating termites have been dug out of logs for the past 100 million years.

Mastotermes darwiniensis Froggatt (Mastotermitidae) is sister to all other termites and contains several ancestral cockroach-like characteristics, including a full complement of wing veins and symbiotic bacteria only otherwise found in cockroaches, and it lays eggs in an oothecae-like pod rather than singly as do other

termites. *Mastotermes* is restricted to Australia but has been introduced to New Guinea. The voracity of *Mastotermes* is legion; they will eat all forms of deadwood, live trees, paper, ivory, bitumen, asbestos, creosote-soaked poles, the rubber of buried tires, and bore through lead (Grimaldi and Engel 2005; Hill 1942). Additionally they will construct short towers and tunnels tens of meters long to gain access to resources (Hill 1942). Colonies in the wild tend to be small, but in urban settings colonies (or numerous fused colonies) may reach nearly a million individuals (Grimaldi and Engel 2005; Hill 1942). No indication is given concerning the usefulness of *Mastotermes* for bioremediation of landfills, but exploration of the topic seems worthwhile.

Abe (1987) separated termite “life types” based on nest and feeding habits. Nest habits came in three varieties: one piece, nesting within a single piece of wood for the life of the colony; intermediate, living within wood but also using multiple pieces of wood; and separate, living away from the food source. For a colony to reach maturity, one-piece nesters require large pieces of long-lived wood that can provide adequate food and protection, perhaps up to 30 cm diameter or greater in the tropics (Abe 1987). One-piece nesting termites may be more heavily impacted by forest management than species with other life types.

The general evolutionary trend in termites has been to move from wood as a nest structure to soil and to move from consuming less-decayed food material (e.g., log) to more decayed material (e.g., humus) (Donovan et al. 2001; Eggleton and Tayasu 2001). Not all termites feed on deadwood, Hodotermitidae eat dead grass, and many Termitidae are humus feeding, although this might be considered “extreme” veteris wood!

22.9.17 *Psocodea*

Recently the orders Psocoptera and Phthiraptera have been combined into Psocodea. The bark lice, book lice, or bark flies (Psocoptera of old) are a largely overlooked order consisting of about 4400 described species. They feed by scraping encrusting lichens, algae, fungal hyphae, and spores. Many live on the bark surface, within decaying plant material, on deadwood, in insect galleries, with ants and termites, or associated with bird and mammal nests (Grimaldi and Engel 2005).

Psocoptera in relation to the saproxylic habitat are poorly studied. Deyrup and Mosley (2004) reported Psocoptera from fire-killed pine. Paviour-Smith and Elbourn (1993) collected nine species from deadwood in Wytham Woods, UK. Matthewman and Pielou (1971) collected 15 species within six families from sporophores of *Fomes fomentarius* (L.) Fr. (Polyporaceae). More research needs to be done to discover which species use, and what role they play in, saproxylic habitats, including veteris wood.

The chewing and sucking lice (~5000 spp., formally Phthiraptera) are exclusive parasites of bird and mammal hosts (Grimaldi and Engel 2005). Any louse species that is an obligate parasite on a species of bird or mammal that is an obligate cavity nester is just as saproxylic as a mite on a bark beetle. Presumably the vertebrate will get most of the attention.

22.9.18 *Thysanoptera*

Thysanoptera are an order of small insects, 0.5–10 mm long, that consist of about 5500 described species (Grimaldi and Engel 2005). Thrips are poorly studied as an order with the exception of economically important species, but even then, gaps in basic biology remain (Mound 2005). Recently eusocial gall-inhabiting thrips were discovered in Australia (Grimaldi and Engel 2005). While traditionally thought of as phytophagous, about 40% of known thrips are frugivorous (Mound 2005). In fact, Mound (2005) notes: “The English common name, thrips, is the Greek word for ‘woodworm,’ derived from observations by early naturalists that many species are found on dead branches.” Stannard (1968) reports at least 42 species of thrips from dead branches or under bark of dead trees or logs in Illinois, USA. Kettunen et al. (2005) collected 23 species of thrips from dead Aspen (*Populus tremula*) in Finland. Kobro (2001) found that the polypore-feeding thrips *Hoplothrips polysticti* (Mori-son) (Phlaeothripidae) was most numerous in “semi-old” forest, but markedly less numerous in younger or older forests, a rare trend. Certainly many species of saproxylic thrips exist, which of those are associated with veteris wood is unknown.

22.9.19 *Hemiptera (Including Heteroptera and “Homoptera”)*

Hemiptera represent the largest non-holometabolous order of insects (~35,000 spp.) and are characterized by possession of piercing-sucking mouthparts (Triplehorn and Johnson 2005). Few species possess morphological features that would indicate they can burrow into sound wood, but they may be able to burrow into veteris wood or utilize external features of less-decayed wood (Gossner and Damken 2018; see Chap. 9). Ulyshen et al. (2012) collected 14 species within eight families of Hemiptera emergent from less-decayed (non-veteris) wood.

The suborder Heteroptera is largely composed of predators, while a few taxa have changed to phytophagy or fungivory. The unique-headed bugs (Enicocephalomorpha) are micropredators largely associated with soil but can be found under rocks, moist detritus, and in rotten logs (Wygodzinsky and Schmidt 1991: Table 1). The group is poorly known and in need of additional study. The Aradidae are saproxylic fungivores typically associated with subcortical habitats (Deyrup and Mosley 2004); however some species are found in termite nests or exposed on dead trees or shelf fungi (Froeschner 1988). Seibold et al. (2014) found that Aradidae activity increased with increased amount of deadwood in a forest but not abundance of sporocarps in the area. Aradids may or may not be associated specifically with veteris wood, depending on the extent of decay or type of shelf fungi. The closely related morphologically reduced family Termitaphididae is fungivorous and associated with termites (Grimaldi and Engel 2005) and may enter wood with their hosts.

The extent to which Heteroptera utilize deadwood as structure is unknown. Blatchley (1926) lists at least three Reduviidae species found overwintering in oak stumps and “beneath logs, the sides of which are deeply buried in leaves and mold” [*Melanolestes picipes* (Herrich-Schaeffer), *Pygolampis pectoralis* (Say), and *Zelus longipes* (L) (as *Zelus bilobus* Say)], and one Miridae [*Fulvius imbecilis* (Say)] found beneath logs in autumn. Other associations with deadwood include *Amnestus spinifrons* (Say) (Cydnidae) taken beneath decaying wood and *Mesovelia mulsanti* White (Mesoveliidae) which “possesses an ovipositor for inserting her eggs into the stems of plants and even in the spongy wood of floating logs” (Blatchley 1926). Some *Nerthra* Kirkaldy (Gelastocoridae) burrow into rotting logs and can be carried some distance over open water (Polhemus and Polhemus 1988; Todd 1959).

The historic “Homoptera” have been divided into three suborders: Sternorrhyncha, Auchenorrhyncha, and Coleorrhyncha (Grimaldi and Engel 2005); the latter is only known from moss and leaf litter, while the other two have some members in deadwood. As with the Heteroptera, these groups probably do not burrow into sound wood and are probably limited to well-decayed wood. O’Brien (1971) reported nymphs of Achilidae, which are believed to be fungus feeding, collected from standing dead trees, “deep in a rotten log” and berlesed from “redwood duff.” Holzinger and Friess (2014) reported an adult Achilidae (*Cixidia lapponica* Zetterstedt) from “deep inside a rotten pine log.” Certainly more associations between Hemiptera and veteris wood are waiting to be found.

22.9.20 Neuropterida

The snakeflies (Raphidioptera), alderflies (Megaloptera), and lacewings (Neuroptera) are three closely related orders with members that are chiefly predators as both adults and immatures (Grimaldi and Engel 2005). Some ground- and tree-dwelling Neuropterida larvae will certainly use deadwood as structure or substrate while resting or pupating, but others are associated with deadwood, including veteris, as immatures. Larvae of more than 70 species of Raphidioptera are reported to be subcortical (Aspöck 2002). Larvae of the North American ant lion species *Glenurus gratus* (Say) (Myrmeleontidae) are known from dry tree holes, especially in oak trees (Miller and Stange 2006). In Illinois, USA, Adams (1915: 153) reported, “When a log reaches such a condition that it looks like brown meal, and is nearly level with the surface of the ground, it may during the summer become so dry that it affords a favorable haunt for myrmeleonid larvae; probably the ant-lion of *Myrmeleon immaculatus* DeG., a woodland species.” Thus veteris wood may provide a substrate for ant lion larvae in places where the soil is unsuitable. Immature pleasing lacewings (Dillariidae) (Fig. 22.3c) are associated with deadwood. Steyskal (1944) collected 6 females and 14 males of *Nallachius americanus* (McLachlan) from a “large long-dead” standing tree, and Bowles et al. (2015) reported collection of larvae emergent from deadwood. Immatures of Berothidae are hypermetamorphic predators of termites and may be found in deadwood as they follow their prey

(Gurney 1947a). Berothid larvae kill termites by emitting a fatal gas from their anal region (Johnson and Hagan 1981).

22.9.21 Coleoptera

The beetles are the largest order of insects (~350,000 described species) and the best studied group of saproxylic organisms. Gimmel and Ferro (2018; see Chap. 2) provide an overview of saproxylic Coleoptera. One of the chief adaptations of the Coleoptera is the presence of hardened forewings called elytra, which protect the flight wings and allow for movement through firm substances such as dirt, wood, and crevasses. The beginning of modern beetles may be the result of some little proto-beetle utilizing deadwood resources (Grimaldi and Engle 2005).

Some beetles associated with veteran wood and structures are some of the best known saproxylic insects, such as *Osmoderma* spp. Lepeletier and Serville (Scarabaeidae) and *Lucanus* spp. Scopoli (Lucanidae) (see Conservation, below). Additionally some of the most interesting beetles are associated with veteran wood. *Micromalthus debilis* is found deep in logs with red rot and has perhaps the most unusual and elaborate life history of any insect, but its life history is not yet fully understood (Grimaldi and Engle 2005: 363; Pollock and Normark 2002). *Titanus giganteus* (L.) (Cerambycidae) adults are the world's largest beetles by length (ca. 170 mm) and weight (although "largest" anything is always debatable), and their grubs may be the largest insects known (Acorn 2006). The larvae almost certainly feed on subterranean veteran wood but have never been found!

Large beetles, beetles in veteran trees, beetles associated with early stages of decay, and pest beetles are all actively being studied. The group of saproxylic Coleoptera most likely to be overlooked are small species associated with veteran down woody debris, essentially well-rotted logs. Leaf litter has been called the "poor man's tropical rainforest" (Giller 1996), and the temptation to concentrate collection from, and research on, such a rich environment is very high. Veteran woody debris straddling the O and A soil horizons harbors few specimens per equivalent volume of immediately adjacent leaf litter (Ferro et al. 2012a). Most studies on saproxylic insects concentrate on early stages of decay for various reasons. Therefore, veteran logs represent an overlooked habitat, spurned by leaf litter collectors and ignored by saproxylic workers.

In a singular study, Ferro et al. (2012a) compared beetles in veteran down coarse woody debris (referred to as CWD5) with beetles in adjacent leaf litter at six sites in Great Smoky Mountains National Park, Tennessee, USA. More species (170) and specimens (3471) were collected from leaf litter than an equivalent volume of CWD5 (111 and 790, respectively). However, species richness wasn't significantly different between the two habitats. Of 59 species available for analysis, 8 were significantly associated with CWD5. Those included the rarely collected *Tohlezkus inexpectus* Vit (Eucinetidae) (Fig. 22.3d), previously known from only five specimens; the genus *Sonoma* Casey (Staphylinidae: Pselaphinae), recently shown to

harbor numerous cryptic species (Ferro and Carlton 2010); and *Mychocerus striatus* (Sen Gupta and Crowson) (Cerylonidae), which, despite being the fourth most numerous beetle on the forest floor, was represented by only four specimens in leaf litter but 246 in CWD5. Clearly veteris wood contains many more surprises, even within the comparatively well-known Coleoptera.

22.9.22 *Strepsiptera*

The twisted-winged parasites are a small order of about 600 species, all of which are parasitic. At various times, the group has been placed within and/or sister to Lepidoptera, Diptera, Hymenoptera, and Coleoptera but is now generally considered to be a unique order, sister to the Coleoptera (Misof et al. 2014). Basal taxa have free-living males and females, while females of more derived taxa permanently reside within the host. Strepsiptera are known to parasitize 34 families within seven orders of insects including Zygentoma and aculeate Hymenoptera (Grimaldi and Engel 2005). Strepsiptera will be in deadwood, including veteris wood, as they follow their hosts.

22.9.23 *Hymenoptera*

How bees, ants, and wasps relate to deadwood has been treated in greater detail in this volume (Bogusch and Horák 2018, Chap. 7; Hilszczański 2018, Chap. 6; King et al. 2018, Chap. 8). Many Hymenoptera will use veteris wood—from paper wasps (Vespidae) which construct nests from chewed plant fibers, including the thin outer layer of veteris wood on snags, to sweat bees (Halictidae) that overwinter in rotting logs and stumps. Additionally, hymenopteran parasitoids are as dependent on veteris wood as their hosts. Creation and use of veteris wood by ants are highlighted here specifically because of the economic and ecological implications.

Ants (Formicidae) are a worldwide taxon of eusocial insects numbering more than 15,000 species (Antweb 2017) that probably evolved in the mid-Cretaceous about 120 million years ago (Grimaldi and Engel 2005). Since the availability of a durable nest (especially hollow logs and twigs) is considered to be an important factor in the evolution of eusociality (Nowak et al. 2010), ants as we know them (and perhaps termites) may be the product of the interplay between a proto-ant population and deadwood, an idea first proposed by Hamilton (1978). In boreal habitats, deadwood is preferred by many ants because it provides a warmer nesting environment than soil (Boucher et al. 2015; Higgins and Lindgren 2012). Wheeler (1910: Chaps. 12–13) offers an overview of ant nests including those within deadwood and cavities in plants. Ants contribute to creation of veteris wood through mechanical removal of wood and, by their presence, induce predators to further destroy the wood

resource. Redford (1987) lists 216 mammals that have been reported to eat ants or termites, 47 of which are known to break into nests.

Twig-dwelling ants live in dead, hollow twigs found in the canopy and on the forest floor (Byrne 1994) where density can be high (e.g., 0.31 nests/m² on the ground) (Fernanders et al. 2012). Arboreal twig-dwelling ants are also the subject of numerous studies concerning their use as biocontrol of pests within coffee agroecosystems (Jiménez-Soto and Philpot 2015; de la Mora and Philpott 2010) including use of artificial nests (Philpott and Foster 2005). However, no measure of the alteration of the substrate (twig) by the ants, nor destruction by predators, could be found.

Carpenter ants (*Camponotus* spp. Mayr) consist of ~1000+ spp. worldwide and are predacious, and many species excavate deadwood to create nest sites (Antweb 2017; Chen et al. 2002). They have been implicated in induced wind damage of trees in urban settings (Fowler and Roberts 1982). Chen et al. (2002) found that *C. vicinus* (Mayr) prefer to nest in logs and stumps 20–30 cm in diameter in Idaho, USA, while in New Brunswick, Canada, Sanders (1964) found that only snags greater than 15 cm DBH were colonized by *Camponotus* spp. Boucher et al. (2015) looked at postfire succession of ants in deadwood. They found that ant nest abundance peaked 30 years postfire, that the presence of wood-boring beetle holes increases the likelihood of colonization, and that ant presence within a log had an impact on carbon and nitrogen dynamics, possibly speeding decay.

Wood-nesting ants are ecologically and economically important in relation to bears and woodpeckers. In a Minnesota, USA, study, Noyce et al. (1997) found that black bears [*Ursus americanus* (Pallas)] regularly dug into stumps and logs for ants. In July, while brood is high, ants consisted of 58% of bear scat volume and were found in 96% of scats. A study on foraging habits of *Ursus arctos* L. in central Sweden showed that ants accounted for up to 16% fecal volume and that bears preferred carpenter ants (which are stump and log dwelling and have less formic acid and higher fat content) over mound-building ants (Swenson et al. 1999). In that same study, ant biomass available to bears was 10 times greater than moose biomass at the same locations. The relationship between forest management, woody debris, wood-dwelling ants, and bears is in need of additional study (Swenson et al. 1999).

Woodpeckers (Piciformes: Picidae) excavate cavities for nests, regularly tear into wood (living and dead) for arthropod prey, and have been studied in relation to use of trees and wood products (McAtee 1911). Conner et al. (1976) found that woodpeckers would often create nests in sound trees with heartrot (possibly veteris)—the sound sapwood protected the nest from predators while the soft heartwood was easy to excavate. Nappi et al. (2015) found differences in foraging behavior among woodpecker species ranging from utilization of newly dead trees to preference for highly degraded snags.

The pileated woodpecker (*Dryocopus pileatus* (L.)) feeds primarily on ants (Beckwith and Bull 1985) and is considered a keystone species because abandoned nest cavities are used by secondary cavity nesters (Newell et al. 2009). A study in Oregon, USA, where ants consist of 97% of the pileated woodpecker diet, found that 61% of logs contained ant colonies, ant colonies were more common in the larger

diameter logs, and ants preferred decay class 4 (out of 5) (Torgersen and Bull 1995). In Oregon, *Camponotus* spp. are important predators of the western spruce budworm (*Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae), an important forest pest (Torgersen and Bull 1995). Thus deadwood of the appropriate size and decay class is an important factor in management practices that promote woodpeckers (keystone species) and *Camponotus* spp. (biocontrol of western spruce budworm but also woodpecker prey).

Many of the studies cited above (and others not included) indirectly provide measures of amount and incidence of deadwood at various locations and times. Mining literature for indirect measurements of deadwood, snags, tree holes, etc. may be profitable.

22.9.24 *Mecoptera*

The scorpion flies, hanging flies, earwig flies, snow fleas, and allies are not yet known to be associated with deadwood in a meaningful way and may be the only order with no saproxylic members (?). But they are a fascinating group nonetheless (Grimaldi and Engel 2005). Immatures are unknown for many species, and some immatures are found in moss, which in some cases may be predominate on, or restricted to, rotting logs in some forests. Certainly more work is needed.

22.9.25 *Siphonaptera*

The fleas (~2500 spp.) are exclusive parasites of bird and mammal hosts (including rodents, bats, and marsupials) (Grimaldi and Engel 2005). Any flea species that is an obligate parasite on a species of bird or mammal that is an obligate cavity nester is just as saproxylic as a mite on a longhorn beetle. Presumably the vertebrate will get most of the attention.

22.9.26 *Diptera*

Diptera are represented by 120,000+ species and found in virtually all terrestrial and aquatic habitats (Grimaldi and Engel 2005) and are second to the Coleoptera (and may be first when all is said and done) in number of saproxylic species. Compared to beetles, little research has been conducted on saproxylic Diptera, much less in veteris wood. How the “true flies” relate to deadwood has been treated in greater detail by Ulyshen (2018; see Chap. 5). The following section will concentrate on Diptera known from veteris wood (including tree/rot holes) and briefly outline North American saproxylic fauna.

In a magnificent study, Hövemeyer and Schauerermann (2003) collected Diptera emergent from beech wood over a 10-year period in Germany. In total they collected 163 species within 37 families. They found that some species showed temporal patterns—77 species predominantly emerged from logs 8–10 years old (veteris?)—and number of individuals and species increased as the log aged. Rotheray et al. (2001) surveyed the saproxylic Diptera of Scotland resulting in the collection of 258 species in 32 families. Of 85 species reared, nine were certainly from veteris wood—heartrot or tree holes. Savely (1939) studied logs in North Carolina, USA, and recorded 10 fly species (three in veteris) from pine logs and 10 species (seven in veteris) from oak logs. Howden and Vogt (1951) collected 20 fly species (one from veteris wood), in 14 families from standing dead pine. Irmeler et al. (1996) collected Sciaridae and Mycetophilidae emergent from deadwood in a forest in Germany. They found flies were more numerous in veteris wood and listed 24 species of Sciaridae and 35 species of Mycetophilidae from veteris wood. Komonen et al. (2001) collected ~14 species of flies in seven families emergent from basidiocarps of two species of old-growth forest polypore fungi. The family Tipulidae certainly has many members with larvae in veteris wood. For example, an expedition to Sumatra obtained larvae of 4 species from tree holes, 48 species from saturated decaying wood, and 11 species from decaying fleshy fungi (Alexander 1931).

Syrphidae, larvae of which are often associated with saproxylic microhabitats in live trees rather than down woody debris, have been well studied in Europe (see Speight (2011) for species-level treatment). Reemer (2005) found that saproxylic syrphids may be increasing in the Netherlands, possibly due to changes in forest management and aging forests. However, several species dependent on the actions of other insects, such as wood borers, may be in decline. Ricarte et al. (2009) surveyed syrphids in a Mediterranean forest in Spain. They collected several threatened species, and, while some species were found in holes of multiple tree species, *Callicera macquarti* Rondani has only been collected in rot holes of a single tree species. Rotheray (2013) showed that in the UK, four species of syrphids, including the red-listed *Blera fallax* (L), may reduce competition by occupying distinct depths when they co-occur within tree rot holes.

Axymyiidae is one of the more extraordinary flies associated with veteris wood. The family consists of four genera and eight species distributed in the Holarctic including Taiwan and Southern China (Sinclair 2013). In general the larvae burrow into wet rotting logs and extend a siphon to the exterior of the log; see Krogstad (1959) for a diagram of the unique larval position. Wihlm et al. (2012) illustrate morphology of all life stages for *Axymyia furcata* McAtee (Fig. 22.3e). In practice the larval habitat (at least for *A. furcata*) is very specific, and they require all of the following: moderate to dense hardwood to mixed forest, small lotic habitats (such as springs or streams) that are *not* prone to flooding, deadwood greater than 3 cm diameter, generally wood without bark or moss, and wood that is light in color, soft enough to push a pencil into it but firm enough to resist prying apart; and the larvae are generally located in a part of the log near the water surface that stays perennially wet but does not get submerged (Wihlm and Gregory 2011). A recently described species from Alaska and Washington was first collected in 1962 but, despite decades

of search, is only known from two specimens, the second collected in 2012 (Sinclair 2013). Whether the specific requirements of Axymiidae will put its members in peril is yet to be seen.

At least 75 fly families worldwide are known to contain saproxylic members (Ulyshen 2018, Chap. 5), and many of these are associated with veteris wood. Members of several additional families that are ectoparasites on birds and mammals (Hippoboscidae, Nycteribiidae, Streblidae, etc.) may also qualify as saproxylic when their hosts are frequent or obligate snag or tree hole nesters. The 55 North American dipteran families known from veteris (McAlpine et al. 1981, 1987; Teskey 1976) include Acartophthalmidae, Anisopodidae, Anthomyiidae, Asilidae, Asteiidae, Aulacigastridae, Axymiidae, Braulidae, Canthyloscelidae, Cecidomyiidae, Ceratopogonidae, Chironomidae, Chloropidae, Chyromyidae, Clusiidae, Culicidae, Cypselosomatidae, Dolichopodidae, Drosophilidae, Empididae, Heleomyzidae, Lauxaniidae, Lonchaeidae, Micropezidae, Milichiidae, Muscidae, Mycetophilidae, Mydidae, Neriidae, Odiniidae, Pachyneuridae, Pallopteridae, Periscelididae, Phoridae, Platypezidae, Psychodidae, Rhinophoridae, Richardiidae, Ropalomeridae, Sarcophagidae, Scatopsidae, Scenopinidae, Sciaridae, Stratiomyidae, Strongylophthalmyiidae, Syrphidae, Tabanidae, Tachinidae, Therevidae, Tanyderidae, Tipulidae, Trichoceridae, Ulidiidae, Xylomyiidae, and Xylophagidae.

22.9.27 *Trichoptera*

The caddisflies consist of more than 14,500 species (Morse 2017) all of which have aquatic larvae. Caddisfly larvae can produce silk, and many use that to construct cases out of materials including sand, rocks, leaves, bark, and small chips of rotten wood. Few, if any, are associated with veteris wood, other than those which use it for case-making material. However, in North America, larvae in the genus *Heteroplectron* McLachlan (Calamoceratidae) are found in pools where plant material accumulates, and they create cases by excavating the center out of small twigs (Wiggins 1996). In Australia, several species of *Triplectides* Kolenati (Leptoceridae) are known to create or use hollow twigs as cases (St Clair 1994). How dead terrestrial plant matter affects caddisflies is interesting, or to put it another way, the tethering of twigs to Trichoptera is titillating.

22.9.28 *Lepidoptera*

Butterflies and moths are generally phytophagous and rarely associated with dead-wood, except when using it as structure for hiding or cocoon placement. The larvae of Cossidae and Sesiidae are wood borers but require living wood as they only digest cell contents (Stokland 2012b). The caterpillar of the eastern North American species *Scolecocampa liburna* (Geyer) (Erebidae) (Fig. 22.3f) lives in and eats

decaying logs and stumps of chestnut, oak, and hickory (Pogue 2012). Caterpillars, presumably of the western species *S. atriluna* Smith, have been found (with frass) living in veteris logs in the Chiricahua Mountains, Arizona (personal observation).

The economically important family Tineidae consists of about 3000 species (Grimaldi and Engel 2005) that eat a wide variety of dry organic matter including keratin, wool, fungi, grain, leather, and even mummified human corpses (Holland 1913; Katz 1997). Often the larvae construct and reside within cases made of debris held together by silk. The family Oecophoridae is also known for larvae that eat dead plant material including carpets and textiles. While noneconomic species of both families have traditionally been overlooked, species associated with saproxylic habits are gathering more attention (Jaworski 2018; see Chap. 10).

Ols et al. (2013) recorded five species of Tineidae emergent from stumps in Sweden, and Komonen et al. (2001) reared two species from polypores in Finland. Both studies each reported collecting one species of Oecophoridae. Lawrence and Powell (1969) provided biological information on 13 species of Tineidae and Oecophoridae associated with polypore fungi in western North America. They noted that larvae were often found in the bark or wood under the fungal fruiting body and suggest retaining the wood immediately around fungi when conducting emergence surveys. They found most species could be considered polyphagous, but at least one appeared to be host specific. Working in Poland, Jaworski et al. (2012, 2014, 2016) have studied the association between tineid species and polypore fungi. In total they have recorded over 20 species of saproxylic tineids from their study areas, many new to Poland, and associated moths with fungal hosts. In some cases, tineid species preferred red-listed fungal hosts and were of conservation concern themselves.

22.10 Insects in Veteris Wood II: Ecological Concerns

Veteris wood has received so little study that the following section is presented mostly as a series of questions and speculations. While analogies and extrapolations could be gleaned from the literature, a few simple studies would be much better.

22.10.1 Diversity

In general, studies have shown that diversity of saproxylic insects peaks around the stage where bark loosens from the trunk (e.g., Blackman and Stage 1924) and then drops as wood moves into the final decay stage. Ferro et al. (2012a, b) surveyed beetles in coarse woody debris across a decomposition spectrum of decay classes 1, 2, 3–4, and 5 (veteris) and found a humped diversity curve: 110, 156, 127, and 111 species, respectively. However Ulyshen and Hanula (2010) and Howden and Vogt (1951) found highest richness the first year of death, but Hammond et al.

(2004) found a gradual increase over many years (none surveyed the final decay stage).

There are several reasons to suspect that saproxylic insect diversity should *decrease* as decomposition occurs. Necessarily less material and energy are available to later successional individuals. Fewer distinct habitats are available (subcortical, heartwood, etc.) as the well-defined layers of the dead tree decompose into a more uniform heap. The mechanical protection provided by the wood decreases over time. And finally decomposition removes many secondary chemical compounds which makes the substrate available for generalists rather than specialists (see Wood Structure and Digestion above).

On the other hand, diversity may *increase* as decomposition occurs. Microbial conditioning may make the substrate more favorable to insects (e.g., adjustment of the C/N ratio). Growth of fungi may create new additional “habitats” (mudguts, etc.) or resources (fungi itself as food). Removal of secondary compounds may “homogenize” wood of different species (e.g., the characteristics of oak and maple wood converge) which acts to increase the amount of available wood across the landscape (less fresh-oak is available than all well-decayed hardwood combined). And finally less-sound wood may offer protection from parasites and predators because vibrations are dampened and tunnels collapse.

The question of diversity across successional stages is complicated by (1) how many stages are recognized; (2) the study system and scale in question (diversity within a particular dead tree, within members of a particular tree species, or across all deadwood types in the landscape); (3) poor taxonomic coverage, especially for flies which may have a different successional diversity profile than beetles (see Brauns 1954; Hövemeyer and Schauermaun 2003); and (4) most importantly, lack of studies cataloging species in final decay stages of wood (veteris).

22.10.2 “Wood” and “Soil” Fauna

As was pointed out above, no quantitative (or even qualitative) definition for the “end” of deadwood exists. Presumably a “log” becomes “soil” when certain qualities of the ground where the log was match qualities of the ground where the log was not. However, the impact of deadwood on soil characteristics begins soon after it touches the soil and lasts long after the log is no longer recognizable (see Lodge et al. (2016), and references therein).

The ambiguity of deadwood disappearance also greatly affects the question of when does soil fauna replace wood fauna. Ferro et al. (2012a) found two distinct beetle communities when they compared veteris wood and the surrounding leaf litter. However, in their study, the pieces of decayed wood were still large (liter scale) and not mixed with the soil. Communities associated with dead logs that have fragmented into smaller pieces (cubic centimeter scale) and mixed with the soil have not been sampled, except, perhaps, as “soil fauna.” Clearly a spectrum exists where

saproxyllic and soil fauna overlap and replace one another, but the character of that spectrum is unknown.

22.10.3 Big Beetles!

Some of the largest insects (by weight) are beetles with immature stages that live in veteris wood (Acorn 2006). Most of the biggest are within a few lineages in the families Lucanidae (stag beetles), Scarabaeidae (scarabs) (both in the superfamily Scarabaeoidea), and Cerambycidae (long-horned beetles) (superfamily Chrysomeloidea). Using phylogenetic reconstruction, McKenna et al. (2015) showed that Scarabaeoidea living in logs today transitioned into them from leaf litter-dwelling ancestors, and that once in logs, lineages have not transitioned out into other lifestyles. While most cerambycids today feed on damaged, dying, or (rarely) healthy plant tissue, ancestral cerambycids were probably deadwood feeders, a habit still prominent in several subfamilies including those with the largest species (Svacha and Lawrence 2014). It is speculated that consuming deadwood next to living wood (e.g., in a tree hole or veteran tree) may have led to consumption of live wood.

Why gigantism would arise in beetles associated with veteris wood is unknown. However, all things being equal, large-bodied beetles need more time, food, and protection from enemies while developing than small-bodied beetles. As Ferro et al. (2012b) pointed out, large pieces of deadwood (especially veteris) are a unique habitat. They represent large, stable, long-term resources in the presence of plenty of oxygen that are not actively metabolically defended. Perhaps giant beetles are in veteris wood simply because it is one of the few places where giant beetles could develop. Or, as vertebrates do not eat rotten wood, lack of competition may have left a size-related niche open that beetles were the first/best to fill. Despite the potential for very large quantities, deadwood is finite, and large body size may be the result of competition among individuals of the same species over resources within a log [e.g., Tanahashi and Togashi (2009) reported larval cannibalism in the stag beetle *Dorcus rectus* (Motschulsky)]. Whatever the reason, veteris wood and structures (e.g., tree holes) are an important habitat for giant beetles and important for conservation concerns.

22.11 Study of Invertebrates in Veteris Wood

Deadwood is an opaque habitat, and while chemical and fungal attributes can generally be sampled and analyzed quickly, the study of invertebrates that reside within it can be difficult. Additionally, the time encompassing complete decay of woody debris generally takes longer than research timespans, whether artificial (degree, grant) or real (career, researcher lifetime). Studies of the early stages of

deadwood, from death until interest or funding runs out, are well suited for experimental manipulation and replication. However, generally that research requires a complete expanse of time (studying 1 year after death requires waiting 1 year after death), and, when invertebrate taxa are involved, additional time (months to years) is required for adult emergence. Therefore the benefit of studying early stages of deadwood is the increased control over starting circumstances and replication, but the costs are the time required to carry out the study and inability to perform extended studies.

Study of veteris wood offers the opposite costs and benefits. Invertebrates from most veteris wood can be obtained within days of sample collection if extraction with a berlese funnel or Winkler eclector is used (see Owens and Carlton (2015) for best practices; Ferro et al. (2012a) offer an example). Or if only adults are desired, samples can be placed immediately within emergence chambers after collection (see Ferro and Carlton (2011) for a review). For collection of invertebrates associated with fungi or veteris wood in living trees, including tree holes, emergence traps can be deployed. Most species that emerge and disperse will do so during the warmer months; therefore 4–6 months may be all that is required to conduct a meaningful survey/study of insects in veteris wood in living trees. However, the time required for veteris wood to form, which may take years, decades, or centuries, precludes any control over starting circumstances and replication. Therefore the benefit to study of veteris wood or veteris structures (tree holes, etc.) is the short timeframe needed to survey the substrate (~less than 1 year), but the cost is that studies tend to be more observational than experimental.

Several veteris wood types have received little or no attention and are of particular research interest. Bouget et al. (2011) found differences in saproxylic beetle assemblages based on vertical strata within a forest. Ulyshen (2011) reviewed vertical stratification of arthropods in temperate forests and saproxylic beetles in canopies (Ulyshen 2012) and came to the same conclusions. Heartrot not exposed by tree holes has received little attention, but Berry (1969) and Berry and Beaton (1972) showed that heartrot is quite prevalent in central and eastern North American forests. At the time of their study, most infection courts began at fire scars; how fire suppression has altered heartrot and other resultant saproxylic habitats is unknown. The review by Gange (2005) on sampling insects from roots makes no mention of the saproxylic insects or deadwood. In a rare study involving dead tree roots, Victorsson and Jonsell (2016) collected 47 species of beetles associated with early decay roots of Norway spruce (*Picea abies* (L.) H. Karst.), five of which were associated with roots and not aboveground stumps.

From a conservation standpoint, veteris wood warrants study and may be of as much conservation interest as large-diameter trees and woody debris. Dahlbeg and Stokland (2004) surveyed needs of all organisms (plants, animals, fungi) associated with deadwood in Sweden and found that 15% were dependent on veteris wood. Veteris structures, such as tree holes, are associated with numerous species of conservation concern (see below). Veteris wood requires time to form, and the lag between current and future resources needs to be taken seriously. While fresh deadwood can be artificially “created” within minutes (simply cut a tree; although

Komonen et al. (2014) found differences in polypore communities between natural logs and chainsaw felled logs, so be careful), we currently lack the ability to “create” veteris wood (but see pollarding and artificial habitats below). For example, *Euperipatoides rowelli* (Reid) (Onychophora: Peripatopsidae), which lives in south-eastern Australian forests, requires hollow *Eucalyptus* L’Hér. logs for shelter. Barclay et al. (2000) showed that suitability of a log was highest after 45 years of decay—nearly half a century *after* the time it took a tree to grow big enough to have a log that, after 45 years of rot, is still substantial enough to make suitable habitat. Veteris wood in one location will already be inhabited, so movement to another location (if that is even possible) to provide resources is not a reasonable option.

Thankfully the structural aspects of veteris wood allow for relatively rapid surveys of chemical properties and fungal and invertebrate inhabitants on time scales that match undergraduate to Ph.D. level research schedules. There is no reason why invertebrates in veteris wood could not be thoroughly surveyed across the globe within the next few decades, making veteris wood the best understood phase in the deadwood cycle. Because so many endangered species are associated with veteris wood, study of veteris wood and conservation will go hand in hand.

22.12 Conservation Related to Veteris Wood

There are no ‘pests’ in a natural forest.

—Bobiec et al. 2005

One of the natural traits of the species *Homo sapiens* L. is modification of the environment, which may occur across multiple scales, from the bending of a twig to the straightening of a river. Despite misconceptions by the public and often misleading statements by parks and conservation organizations, modern conservation efforts are not and will not be able to return most localities to the *urwald* state. *Urwald* is currently a term loosely meaning *primeval forest before alteration by man* (Buckland and Dinnin 1993) but could easily be expanded to encompass any region of the Earth before human alteration. The reality is most of the landscape falls on a continuum from less altered to more altered. Modern conservation efforts need to recognize humans as a part and product of the Earth and strike a balance between the needs of human-related activities with the needs of other components of nature (Stone (1972) articulates this sentiment in a legal framework). The notion that some areas will be unaltered by nature (urban) and others unaltered by man (“protected” parks) is naive.

Conservation of saproxylic species and habitat has been the focus of many studies, and a variety of proposals and strategies have been suggested. At the landscape scale, most proposals fall within two categories, morticulture, actively managing for deadwood (Cavalli and Mason 2003; Harmon 2002; Key and Ball 1993), and “benign neglect” (noninterference, letting “nature” take its course) (Müller et al. 2010). Retention of veteris wood (a hybrid of the two) during logging

has been suggested by Ehnström (2001) (loggers should work to decrease fragmentation of existing logs at sites), and Hagan and Grove (1999) (down and hollow logs should be preserved during logging). Bergman et al. (2012) recommended retention of one hollow oak per 7 ha to optimize habitat for associated saproxylic beetles. At smaller scales, active management through pollarding to increase tree holes (Sebek et al. 2013) or use of seminatural areas in urban settings [e.g., golf courses; see Powell et al. (2016)] to enhance saproxylic habitat has been described. Conservation efforts will reach their pinnacle with the reintroduction of extirpated saproxylic species, similar to the concept of “Pleistocene rewilding” (Donlan et al. 2006). Reintroduction of the Lord Howe Island stick insects (see Phasmatodea above) is an important example.

Conservation of organisms associated with veteris wood has been the subject of much work and research, especially at very localized scales when considering ancient and veteran trees. Ancient trees are particularly old for their species, and veteran trees show signs of having “survived various rigors of life” including signs of decay and exposed deadwood (see Lonsdale (2013) for more complete definitions). Both are important for maintaining habitat for saproxylic species ranging from insects to rare lichens (Kirby 1992; Lonsdale 2013). Among the varieties of deadwood available in veteran trees, including tree holes, much would be considered veteris wood. Jonsell (2004) showed that a park with ancient trees harbored nearly as many red-listed saproxylic beetle species (20 spp.) as a high-value seminatural area (24 spp.) in Sweden. In a larger study across eight park sites, Jonsell (2012) found that old park trees were as valuable for maintenance of species in hollow trees and red-listed species as trees from more natural areas. In France, Parmain and Bouget (2018) compared saproxylic beetles between trees within forests and trees outside forests. They found similar alpha diversity and abundance, indicating the importance of retaining habitat trees in the landscape even if they are isolated. Sverdrup-Thygeson et al. (2010) found that hollow oaks in forests and parks were both rich in red-listed beetles but that assemblages differed between the two. Ranius et al. (2005), and references therein, showed the importance of tree hollows for the red-listed species *Osmoderma eremita* (Scopoli) (Coleoptera: Scarabaeidae). Lonsdale (2013), and references therein, offer guidance for management of veteran trees, which are considered important cultural elements across Europe. While not specific to veteran trees, Stone (1972) promoted the “unthinkable idea” that rights should be conferred to natural objects, including trees. The idea seems particularly applicable to ancient and veteran trees, especially those that may have a historic or cultural value.

However, large dead and dying trees can be a safety hazard. Lonsdale (2013) (Chap. 4) provides advice on balancing care for ancient trees and safety for people and property, and Watkins and Griffin (1993) provide advice specific to England and Wales. Carpaneto et al. (2010) found that 41% of surveyed trees in urban parks in Rome that harbored target beetle species, including red-listed species, were labeled as dangerous to citizens and needed to be cut for safety. They provide several recommendations to promote conservation and maintain safety, including leaving cut trunks and branches in the area for larvae.

The advice above highlights another stumbling block in the conservation of saproxylic habitats. Veteran trees and deadwood in general have to overcome the current fad of considering decaying logs, limbs, and stumps unaesthetic. Whitehead (1998) describes the “grafting” of a cut decaying limb onto a nearby tree to prolong the life of the “discriminating arboreal invertebrates” within but warned of the public perception that those “efforts may compromise the appearance of the landscape at large.” Education (see below) may help to reverse this trend. Thankfully some instances of retaining dead trees as “features of the historic landscape” do exist; see Lonsdale (2013: 11) for examples.

The stag beetle, *Lucanus cervus* (L) (Lucanidae), is a beetle of conservation concern across Europe and represents one of the “enigmatic megafauna” (flagship species) associated with veteran wood. Harvey et al. (2011a) reported that it was declining across Europe and “absent or extinct” from 13 countries. Their survey found that larvae are generally on decayed oak stumps but have been collected from a dozen other tree species, and it may use other substrates, such as oak fence posts, provided the wood is sufficiently decayed. Several monitoring studies have been conducted: Hawes (2008) developed and tested a mark and recapture technique; Harvey et al. (2011b) tested several noninvasive monitoring techniques including road transect surveys, acoustic detection, and adult lures; and Campanaro et al. (2016) used a standard transect walk technique to detect populations within eight countries. Sprecher (2003) studied the life cycle of *L. cervus* in northern Switzerland and noted that adults will eat sap from wounded trees or ripe fruit including cherries, illustrating that adults have resource needs not just larvae. She also described habitat enhancement by creating oak stumps and mounding wood chips on the shady side of the stump. In the UK, the People’s Trust for Endangered Species currently coordinates several types of monitoring for *L. cervus*, including the “Great Stag Hunt” and advocates creation of log “pyramids” and “piles” as artificial habitat for the species (PTES 2017).

The hermit beetle, *Osmoderma eremita* (Scarabaeidae), is another relatively well-studied flagship species associated with tree holes (see Ranius et al. (2005), and references therein). Creation of artificial tree holes for *Osmoderma* and other species has been attempted and is reminiscent of Fager’s (1968) “synthetic logs.” Green (1995) re-erected the hollow trunk of a dead tree and filled it with sawdust, guano, and a few dead animals in a successful attempt to create additional habitat for the violet click beetle (*Limoniscus violaceus* (Müller), Elateridae). A simple pilot study by Whitehead (1998) found a compost bin and a plastic bag each filled with coarse beechwood sawdust attracted saproxylic species. Birtele (2003) made artificial habitats consisting of wooden boxes filled with sawdust to study the saproxylic fauna of Bosco della Fontana Nature Reserve in Italy. In a twist, Hilszczański et al. (2014) created artificial tree cavities and seeded them with larvae of *Osmoderma barnabita* (Motschulsky) to test the efficacy of the design. They found a high survival rate and successful recolonization within the boxes.

Jansson et al. (2009) conducted a large study of artificial tree holes in Sweden. In total, 47 boxes simulating artificial tree holes, each 60 l in volume, were created. All containers were filled with oak sawdust, leaves, and one of four additional

ingredients, including a dead hen to simulate a hollow used by birds. After 3 years, 105 saproxylic beetle species were recovered from the boxes representing 70% of the total species known from tree hollows in the area. Boxes with a dead hen had a higher number of beetle specimens. The substrate volume decreased by 15–30% over the 3-year period, possibly because of the “fresh” quality of the sawdust used. Probably many years of processing by fungi and invertebrates would be necessary before the substrate more fully mimicked true tree hollows. Micó et al. (2011) and Sánchez et al. (2017) studied chemical changes in wood eaten by the tree-hollow-inhabiting beetle *Cetonia aurataeformis* Curti (Scarabaeidae). They found a higher concentration of nitrogen and other changes associated with tree hollow substrates and concluded that wood processing by *C. aurataeformis* facilitated use by other saproxylic organisms. Presumably laboratory-reared beetle larvae could be used to condition fresh sawdust and convert it into veteris wood for future artificial habitats.

In the USA, few if any specific saproxylic species are of conservation concern. It is not clear if this is accurate or due to ignorance. A review of insect conservation in the USA by Bossart and Carlton (2002) did not mention any deadwood species. A recent study by Powell et al. (2016) about suitability of deadwood habitat on golf courses was interested in reducing the general degradation of the environment, not increasing habitat for a specific species or guild. Ulyshen et al. (2017) studied the North American *Lucanus elaphus* F. (Coleoptera: Lucanidae), a relative of the European red-listed *L. cervus*, but found that it is probably not immediately threatened.

22.13 Education

*Verily, the most common things about
us are those of which we know the least.*
—W. S. Blatchley 1902

All conservation begins with education—the existence of that to be conserved must first be known. Whether the “knowledge” itself is emotional (“Save the whales!”—it doesn’t really matter why) or intellectual (water pollution causes general degradation to the environment) matters little at the first step. Books for popular audiences, such as *What a Plant Knows* (Chamovitz 2013), *Bark: An Intimate Look at the World’s Trees* (Pollet 2010), *Remarkable Trees of the World* (Pakenham 2003), *The Hidden Life of Trees* (Wohlleben 2016), *Oak: The Frame of Civilization* (Logan 2005), *Trees: A Complete Guide to Their Biology and Structure* (Ennos 2016), *The Secret Life of the Forest* (Ketchum 1970), and *Reading the Forested Landscape* (Wessels 1997), and innumerable field guides help to inspire (emotion) and educate (intellect) the public about plants, trees, and forests in general.

Other resources occupy a middle ground between popular and technical and are very important bridge between the two. A series of richly illustrated publications by the USDA help to explain tree wounding and decay: *A Tree Hurts Too* (Shigo 1974), *Compartmentalization of Decay in Trees* (Shigo and Marx 1977), *Tree Decay: An*

Expanded Concept (Shigo 1979), and *Wood Decay in Living and Dead Trees: A Pictorial Overview* (Shortle and Dudzik 2012). Not only do they provide a background for the processes that lead to veteran trees but also provide a template for similar publications.

Several public-friendly publications specific to the saproxylic habitat are available, including: *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington* (Thomas 1979); *The Seen and Unseen World of the Fallen Tree* (Maser and Trappe 1984); *From Forest to the Sea: A Story of Fallen Trees* (Maser et al. 1988); *Trees and Logs Important to Wildlife in the Interior Columbia River Basin* (Bull et al. 1997); and *The Afterlife of a Tree* (Bobiec et al. 2005). Additionally guides exist for maintaining and establishing saproxylic habitat from the scale of a landscape to individual trees: *Habitat Management for Invertebrates* (Kirby 1992); *Techniques for Re-Establishment of Dead Wood for Saproxylic Fauna Conservation* (Cavalli and Mason 2003); and *Ancient and Other Veteran Trees* (Lonsdale 2013, and references therein).

Educational information and materials for children and the public about the importance of deadwood and saproxylic fauna have been created. Possibly the first was Animal Inn (2003), initially created in 1985, it was an educational program with the motto “There’s life in dead trees” designed to inform the public about the importance of snags to wildlife. The program featured the character “Sally Snag” and at one time included a costume and merchandise as well as educational workbooks. It has since been suspended. The Australian Department of Environment and Water Resources created an educational program, including handouts and songs, called “Logs have life inside” about inappropriate firewood collection (AU 2002). Minari et al. (2003) undertook a 3-year project to educate the public about deadwood at Bosco della Fontana Nature Reserve in Italy (see Cavalli and Mason 2003). They specifically created distinct lessons for school-aged children, high schoolers, university students, and adults. Bobiec et al. (2005) provide several interesting educational activities in Appendices I and II of their book. They also suggest creation of an interpretive deadwood trail—“a living museum of dead wood!” (p. 192)—which is an immensely appealing idea. The Slovenian Forestry Institute’s Forest of Experiments group has created the “Handbook for Learning and Play in the Forest” (Vilhar and Rantaša 2016) (not yet available in English) which contains numerous forest-related activities for school children.

Finally, two popular “advocates” for deadwood must be mentioned. The Marvel Comics superhero Groot is a saproxylic-like character resembling a snag. Groot is an individual of the species *Flora colossus* Lee and Kirby from Planet X and has numerous plantlike superpowers, including totipotency. While Groot has appeared in several guises, he is currently best known as a member of the group Guardians of the Galaxy (<https://en.wikipedia.org/wiki/Groot>). Botanical gardens and forest preserves could capitalize on the popularity of the character among children—“Watch for Groot on the trail!”, “Can you find Groot?”, etc.

The Ents, a race of creatures created by J. R. R. Tolkien in his Middle Earth universe, were ancient shepherds of trees tasked with protection of the forests from overharvesting by Dwarves, an apt allegory for veteran trees today (

wikipedia.org/wiki/Ent). Much like the Ent, veteran trees are tasked with sustaining biodiversity until adequate forest resources can be reestablished. One could easily imagine an “Ent Trail” where participants travel across the country visiting multiple veteran trees, especially within the UK and Europe. Around the world, the concept to the Ent could be used to personify veteran trees for conservation purposes.

22.14 Future Research into Veteris Wood

Virtually all types of saproxylic research are currently being held back by the lack of taxonomic resolution and the inability to accurately characterize substrates in an agreed upon, repeatable manner. When researchers are willing, taxonomic resolution issues can be overcome or reduced using techniques, such as DNA barcoding, which allow unrecognizable forms (egg, immature, pupae, females, etc.) to be associated with described forms (typically an adult male) (e.g., Caterino and Tishechkin 2006). MicroCT scans of immature insects identified with DNA barcoding would allow for morphological recognition of additional imaged specimens not available for barcoding (e.g., imaged during nondestructive sampling). The same or similar techniques could be used to “define” an undescribed or unnamable species and track its presence, absence, and abundance over multiple independent studies.

Characterizing deadwood substrates will be much more difficult. Seemingly at least six measures need to be made: physical properties of the wood (volume, diameter, structural aspects, etc.), “chemical” profile (e.g., lignin content, C/N ratio, etc.), fungal profile (which species and in what proportions), water content (significant factor in determining extent of fungal activity), immediate abiotic environment (sun, shade, temperature, humidity, etc.), and landscape factors (see Franc et al. 2007). If implemented, the above approach would seek to define all existing deadwood “types.” However, as has been pointed out (Stokland and Siitonen 2012b: Sect. 11.3.1), the possible number of deadwood types would exceed the actual number of saproxylic species by several orders of magnitude. However, “habitat” defined by nature and defined by humans is two different things. If the focus was reversed, and deadwood types were defined through their use by saproxylic species, then a reasonable list of a few hundred “functional” substrates could be created and still be described by the measures listed above. We already do something similar in a qualitative manner when we talk about species that are subcortical, only in the fermenting stage, or associated with veteris wood.

Above all else, detailed natural history of saproxylic organisms is needed. Increased accuracy and precision of how material is cycled and energy and genes flow at the species level must be known to protect species from extinction and connect the saproxylic habitat with the rest of nature. However, there is little fame in these endeavors.

New technology, tools, and techniques will allow study of the saproxylic habitat in extraordinary ways. The current smuggling/terrorism paradigm is driving improvements in technology in noninvasive scanning techniques, a boon for

deadwood researchers. A variety of technologies are being developed and implemented: large arrays for scanning huge items such as cargo containers, hand-held X-ray devices for smaller items, and nanoCT scanning with microscopic resolution. The result is that researchers can now obtain noninvasive images ranging from the interior of a 4 m thick log loaded on the back of a truck to micron-scale images of the interior of a twig.

Veteran trees with multiple types of wood and cavities are very complex, and measuring internal and external features is daunting. However, Lidar (“light detection and ranging”), which uses lasers to measure distances, can be used to create three-dimensional images of small to large complex forms. Omasa et al. (2008) combined on-ground and airborne Lidar scanning to create complete three-dimensional models of standing trees. Their models allowed for quantitative measurements of volume and length of any aspect of the tree. Photogrammetry is a technique that extracts geometric information from multiple two-dimensional images of a particular item and creates a three-dimensional model. Whereas Lidar can use UV light and create high-resolution scans, photogrammetry using visible light captures true-to-life colors. A combination of the two could create a high-resolution model of a veteran tree and allow for identification of lichens growing on its surface.

The internal attributes of live trees can also be imaged in a number of ways. Niemz and Mannes (2012) review techniques for nondestructive testing of wood artifacts, including sound tomography and electromagnetic radiation, which could be used on live trees. Allison and Wang (2015) provide practical examples of the use of acoustic devices to evaluate tree decay and create three-dimensional models of tree interiors. It is not inappropriate to expect that over the next few years techniques will be developed to scan and model an entire veteran tree and image artifacts within it, including adult and immature insects, that are as small as a few millimeters. Imaging techniques coupled with faunal surveys could make veteris wood and veteran trees one of the best understood keystone habitats on Earth.

22.15 Conclusion

The study of the saproxylic habitat has undergone a grand expansion, and necessarily a certain amount of specialization and atomization of research topics has occurred. With the concept of veteris wood, the relatedness of studies that have otherwise been treated as independent can be illustrated. For example, a living veteran tree may have more fauna in common with a severely decayed log than a fresh windfall. Expanding the scope of study is important too—studies by foresters on heartrot and wood stain in living trees cascade into studies on tree cavity nesters, veteran trees, and eventually mudguts.

The study of veteris wood suffers from being far removed from economic issues; few faunal elements are shared between fresh-cut timber and veteris wood. And it suffers from issues with experimental design and repeatability. Ferro et al. (2012b: 17) proposed a scheme to create “legacy” coarse woody debris where descriptions of

trees (species, size measurements, etc.) were recorded immediately after death and available for researchers in the future. A century from now, a researcher standing over a faint line on the forest floor would know it originally was a 60 cm diameter red maple killed by wind during a particular week. However, as that plan would not bear fruit for several decades after initiation, it is unlikely to be implemented.

Nevertheless, the study of veteris wood benefits greatly by its association with large scarab (Scarabaeidae) and stag beetles (Lucanidae) which serve as nonthreatening mascots and flagship species for their habitat (Huang 2018; see Chap. 4). Some hoverflies (Syrphidae), Mydas flies (Mydidae), and the crane fly genus *Ctenophora* Meigen (Tipulidae), with the right ad campaign, could also become insect advocates for veteris wood conservation. Veteris research also benefits from veteran trees, which are important for biodiversity conservation and, due to their age, can serve as inspirational rallying points in a community. Finally, because veteris wood is removed from structural wood, it can be incorporated into private and public spaces like gardens and parks (a massive redwood log is on display outside the northeast corner of the Oregon Convention Center, Portland, USA). Allowing the public to participate in conservation issues and habitat enhancement is important for raising awareness of all saproxylic habitats.

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Journal titles should not be abbreviated (Ferro and Mayor 2016). The following is a key to the abbreviated journal titles given: Adv Ecol Res = Advances in Ecological Research; Agr Forest Entomol = Agricultural and Forest Entomology; Am Ent = American Entomologist; Am Nat = American Naturalist; Anim Biodiv Conserv = Animal Biodiversity and Conservation; Ann Entomol Soc Am = Annals of the Entomological Society of America; Ann Mo Bot Gard = Annals of the Missouri Botanical Garden; Annu Rep Dept Geol Nat Resour Indiana = Annual Report of the Department of Geology and Natural Resources of Indiana; Annu Rev Ecol Syst = Annual Review of Ecology and Systematics; Annu Rev Entomol = Annual Review of Entomology; Arch Hydrobiol = Archiv für Hydrobiologie; B Am Mus Nat Hist = Bulletin of the American Museum of Natural History; B Illinois St Lab Nat Hist = Bulletin of the Illinois State Laboratory of Natural History; B Mus Comp Zool = Bulletin of the Museum of Comparative Zoology; Behav Ecol Sociobiol = Behavioral Ecology and Sociobiology; Biodivers Conserv = Biodiversity and Conservation; Biol Conserv = Biological Conservation; Biol Rev = Biological Reviews; Bollett Di Zoologia Gen E Agr = Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricoltura in Portici; Br Wildl = British Wildlife: The Magazine for the Modern Naturalist; Can Entomol = The Canadian Entomologist; Can J Forest Res = Canadian Journal of Forest Research; Can J Zool = Canadian Journal of Zoology; Coleopt Bull = The Coleopterists Bulletin; Cretaceous Res = Cretaceous Research; Crop Forage Turfgrass Manage = Crop, Forage & Turfgrass Management; Curr Biol = Current Biology; Ecol Appl = Ecological Applications; Ecol Bull = Ecological Bulletins; Ecol Bull = Ecological Bulletins (Stockholm); Ecol Entomol = Ecological Entomology; Ecol Evol = Ecology and Evolution; Ecol Monogr = Ecological Monographs; Ecol Res = Ecological Research; Entomol Exp Appl = Entomologia Experimentalis et Applicata; Entomol Fennica = Entomologica Fennica; Entomol Gaze = Entomologist's Gazette; Entomol Mon Mag = Entomologist's Monthly Magazine; Entomol News = Entomological News; Entomol Obozr = Entomologicheskoe Obozrenie; Environ Entomol = Environmental

Entomology; Environ Modeling Asses = Environmental Modeling and Assessment; Environ Rev = Environmental Reviews; Eur J Soil Biol = European Journal of Soil Biology; Fla Entomol = Florida Entomologist; Folia Fac Sci Nat Un Biol = Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia; Forest Ecol Manag = Forest Ecology and Management; Forest Sci = Forest Science; Front Biol China = Frontiers of Biology in China; Glob Change Biol = Global Change Biology; Illinois Nat Hist Surv Bull = Illinois Natural History Survey Bulletin; Insect Conserv Diver = Insect Conservation and Diversity; Insect Soc = Insectes Sociaux; J Anim Ecol = Journal of Animal Ecology; J Arboric = Journal of Arboriculture; J Chem Ecol = Journal of Chemical Ecology; J Cult Herit = Journal of Cultural Heritage; J Forest = Journal of Forestry; J Insect Conserv = Journal of Insect Conservation; J Insect Physiol = Journal of Insect Physiology; J Insect Sci = Journal of Insect Science; J Kansas Entomol Soc = Journal of the Kansas Entomological Society; J N Am Benthol Soc = Journal of the North American Benthological Society; J Nat Hist = Journal of Natural History; J Torrey Bot Soc = Journal of the Torrey Botanical Society; J Veg Sci = Journal of Vegetation Science; J Wash Acad Sci = Journal of the Washington Academy of Sciences; J Zool = Journal of Zoology; J Zool Syst Evol Res = Journal of Zoological Systematics and Evolutionary Research; Linzer Biol Beitr = Linzer Biologische Beiträge; Mem Am Acad Arts Sci = Memoirs of the American Academy of Arts and Sciences; Mem Entomol Soc Can = Memoirs of the Entomological Society of Canada; Murrelet = The Murrelet; Nat Area J = Natural Areas Journal; New Sci Sci J = New Scientist and Science Journal; North J Appl For = Northern Journal of Applied Forestry; Northwest Sci = Northwest Science; Occas Pap Calif Acad Sci = Occasional Papers of the California Academy of Sciences; P Acad Nat Sci Phila = Proceedings of the Academy of Natural Sciences of Philadelphia; P Entomol Soc Wash = Proceedings of the Entomological Society of Washington; P Minn Acad Sci = Proceedings of the Minnesota Academy of Science; P Mont Acad Sci = Proceedings of the Montana Academy of Sciences; P US Natl Mus = Proceedings of the US National Museum; Pearce-Sellards Ser = The Pearce-Sellards Series; Philos T R Soc B = Philosophical Transactions of the Royal Society B; Polish J Entomol = Polish Journal of Entomology; Rec Aust Mus = Records of the Australian Museum; Rev Écol (Terre Vie) = Revue d'Écologie (Terre et Vie); Rev Soc Entomol Argent = Revista de la Sociedad Entomológica Argentina; Scand J Forest Res = Scandinavian Journal of Forest Research; Silva Fenn = Silva Fennica; Southeast Nat = Southeastern Naturalist; Sov J Ecol+ = The Soviet Journal of Ecology; Syst Entomol = Systematic Entomology; T Am Entomol Soc = Transactions of the American Entomological Society; T Kans Acad Sci = Transactions of the Kansas Academy of Science; Tasmanian Naturalist = The Tasmanian Naturalist; Univ Calif Publ Entomol = University of California Publications in Entomology; Us Dep Ag Biol Surv Bull = US Department of Agriculture Biological Survey Bulletin; Verh Internat Verein Limnol = Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie; Wilson Bull = The Wilson Bulletin; Z Angew Entomol = Zeitschrift für Angewandte Entomologie; Z Morph U Ökol Tier = Zeitschrift für Morphologie und Ökologie der Tiere; and Zool J Linn Soc-Lond = Zoological Journal of the Linnean Society.

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