



Wyre Forest Study Group

TREES AND BIODIVERSITY: POST-MATURE TREES AND THE DEADWOOD HABITAT

Malcolm J. Smart

I was asked to write an article on Veteran Trees and their importance in maintaining biodiversity, but I have taken the liberty of modifying the suggested title to reflect what I perceive to be the true issues behind the significance of such trees in the struggle to preserve biodiversity.

Unfortunately, for practical reasons, the term 'Veteran Tree' has been defined in the literature purely in terms of age, but the latter does not necessarily always reflect the true value of a tree for biodiversity. Even the term 'Ancient Tree' may understate the value trees have that have just passed maturity. Put simply, trees that are past their maturity (defined for the sake of argument as about the age at which they would be harvested for timber in a commercial forestry environment) are always potentially important whatever their age. Such trees are often referred to as 'overmature' (e.g. Harding, 1986), but that term to me carries the implication of something bad (like 'over-ripe' fruit) so I have chosen to refer to them as 'post-mature' in this article.

Some species reach normal maturity much more quickly than others. Oak trees, for example, may reach maturity at about 120 years but can continue to thrive for more than 600 years, while some softwood trees mature in 50 years and thrive for less than 200 years in total.

Our natural forest flora and fauna evolved as an interdependent community long before interference, disturbance and 'management' by *Homo sapiens* became a significant factor in the forest habitat. To understand the importance of mature and post-mature trees for biodiversity in a modern managed environment, it is necessary to consider the ways in which the other living organisms interact with, and depend on them in a natural forest habitat.

The Anatomy and Life Cycle of an Undisturbed Natural Forest

Following the retreat of the glaciers at the end of the last ice, about 12000 years ago, mixed broadleaved forest spread over lowland Britain and neighbouring parts of Europe, with coniferous forest dominating in the more northern areas. With these forests came a complete balanced ecosystem with flora and fauna perfectly adapted to conditions within them. We can get some idea of what our unmanaged natural forests were truly like by studying extant primeval forest remnants like that at Bialowiesza in Poland (see figure 1). It is misleading to think of the ancient forests as dark places full of densely packed trees. The presence of large herbivores (now unfortunately all extinct) such as elks, aurochs and tarpans ensured that those forests had large open areas, clearings and tracks,

so greatly enhancing the range of habitat available with an associated contribution to overall biodiversity (Vines, 2002).

So what is the reality of life in a natural forest? A simplistic view of the basic life cycle of trees within a forest can be summarised as follows: seeds germinate and grow into young saplings which grow further into mature trees and produce fruit with seeds, then die, rot away and are replaced by new saplings. This view can of course be expanded to take into account some of the other life forms which humans routinely see and interact within a forest. The fruits from the trees serve as food for some birds and mammals and the trees themselves provide shelter for others. The forest floor, fertilised by nutrients from decaying leaves provides a substrate in which some invertebrates and fungi flourish and on which a number of flowering plants and ferns grow. The flowers of the trees and forest floor provide nectar as food for many flying insects like butterflies, bees and wasps. The live foliage and stems provide a home for a number of invertebrates such as leaf miners and gall causers. A number of others (e.g. caterpillars) simply eat the healthy foliage.

The true picture is, however, very much more complex than that. The fundamental part of the story, which has been omitted above, is that related to the post-mature, senile and dead trees. In a forest like Bialowiesza, roughly 17% of the total organic matter present is in the form of dead wood (Key, 1996, p21). The most numerous organisms present in terms of biodiversity are fungi and invertebrates, which in concert with bacteria, play a pivotal role in the breakdown and dispersal of the dead and decaying wood.

As a tree passes 'maturity' (see definition above) parts of it begin to decay. This is a natural process and does not mean that the tree is unhealthy in any way. Left undisturbed, it will go on growing and thriving for many more years (our example oak tree reaching 'maturity' at 120 years may go on to ultimately reach five times that age before finally expiring). The tree may commonly develop a hollow lined with dead wood, sections of bark may separate and individual boughs, even large parts of the trunk, may break off or die in place. Rot holes, a very important habitat for invertebrates, typically form where natural cavities (usually at forks) fill with water and detritus. If the tree is injured in some way sap runs may develop; these form a very specialised habitat which is favoured by many rare species of invertebrate. When the tree finally succumbs, the trunk (standing or fallen), the fallen branches and, very importantly, the stump and roots continue to provide a very significant wildlife habitat for many years, particularly in the case of hardwood trees.



Figure 1. Primeval Forest at Bialowieza, Poland.

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Dead wood is quickly invaded by bacteria, fungi and other micro-organisms which initiate chemical changes. Sugars, other nutrients and softened decayed wood tissue are produced which can be utilised by a wide range of invertebrates. While some of these (particularly beetles) bore into the dead wood directly, others obtain sustenance by consuming the bacteria, fungi or decayed wood; yet others prey upon or parasitise the primary invaders or simply utilise their burrows. In the case of insects, it is often (but by no means always) the immature stages which are associated with these habitats.

A significant proportion of the invertebrates become prey to vertebrates, particularly birds and bats, which are in turn parasitised by other invertebrates or consumed by larger predators. Dung and dead bodies are returned to the soil where they join the decomposed remains of the original dead wood, creating a habitat for soil organisms. Ultimately, virtually all the dead wood biomass becomes nutrients for the development of new organisms within the forest.

A natural forest contains trees and wood at all stages of development, so that as decaying wood is used up it is replaced by dead wood from other maturing trees. The latter are not of course the only source of 'deadwood habitat' in the forest; many trees die (e.g. blown over) or get damaged (e.g. shed branches) before reaching maturity, adding dead wood to the general habitat pool. However, it is the oldest trees in the forest which contribute most to maintaining its biodiversity. They provide long term reservoirs of suitable deadwood habitat with its dependent organisms from which individuals can migrate to the new dead and decaying wood habitat as it appears and matures, so

dispersing the species. Stands of immature trees alone, even though they contain some dead wood, are a relatively sterile environment and support only a limited range of wildlife.

While some forest organisms live their whole life in dead or decaying wood, many others (particularly insects) have complex life histories which require them to spend part of their lives in other parts of the forest. Flowers of trees and ground plants are particularly significant as sources of nectar for food. Open glades and rides provide suitable habitats for many ground flora and as such form an essential and important part of the mature forest ecosystem.

Forests, Woodlands and Trees in Modern Britain

Our original forests have been hugely modified by human activity, and the damage has been increasing progressively with time.

Dead wood has been collected for fuel from the very earliest times. More recently, it has become victim of the 'tidy park-keeper' mentality. Well meaning woodland and park managers have deliberately cleared away dead wood and post-mature trees in pursuit of tidiness or in the (largely mistaken) belief that they are somehow 'unhealthy' or dangerous. Modern machinery such as chainsaws, chippers and particularly stump-grinders has greatly facilitated this destruction of the habitat.

More and more live wood has been harvested for timber, initially as a building material for housing, but increasingly through the centuries for ships (vast areas of mature hardwood trees were historically cut to build warships) and more



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recently for general construction. Maturing natural forest trees have increasingly been harvested and replanted with young trees long before reaching a stage favourable as invertebrate habitat. Worse still, many natural forests have been replaced by plantations of non-native fast growing species, particularly conifers, which have virtually zero value as habitat for our native wildlife.

The development of agriculture over thousands of years has resulted in gradual clearance of large areas for crop planting and livestock grazing. Huge tracts of natural woodland have totally disappeared, being replaced by relatively sterile crop fields or 'improved' grassland. Large cities and conurbations have sprung up on land that was originally forested. In those areas, trees are barely tolerated and generally managed only for their visual aesthetic value. However, many of those currently isolated trees are very old and some retain a valuable residual population of rare deadwood invertebrate species.

It has not all been bad news, however. In many old estates and parks, woodland pasture has been generated by allowing stock to graze in woodland. Other areas have been managed as deer (hunting) parks. These activities result in an environment where there are relatively few widely spaced trees, but many of them attain an enormous age and so support a much richer fauna and flora than exists in more dense but less sympathetically managed and mature woodland. Woodland pasture likely bears more than a passing similarity to some areas of ancient natural forest grazed by large wild herbivores.

Amid all this exploitation, there is simply no undisturbed natural forest left in Britain. All woodland has become to some extent managed and indeed it is believed that true natural forest disappeared from virtually all of Europe well over 1000 years ago. Our largest old forests (e.g. Windsor, Epping, New Forest and Sherwood) are largely creations of man, derived from remnant areas by kings who gave them protection to develop their hunting potential (Buckland and Dinnin, 1993).

One of the most serious effects of forest clearance has been habitat fragmentation. Although deadwood habitat has been treated as a single entity in the discussion above, the term actually encompasses a vast array of different micro-habitats depending on the species of tree, degree of dampness, light, temperature and many other factors. Many of these micro-habitats are very scarce even within a large forest, so fragmenting that forest makes it very difficult for organisms dependent on those specialised micro-habitats to find new locations suitable for colonisation. The enormous longevity of some individual post-mature trees does to some extent ameliorate this effect by extending the time available for chance dispersal to succeed.

Two important traditional woodland management practices have arisen historically as a result of

commercial demand for particular forms (sizes) of timber and are worthy of further discussion. These are still practiced today and can have a significant impact on the biodiversity value of the habitat.

Pollarding is the practice of removing the top of a tree 2.5 to 4m above ground level (i.e. above the level browsed by grazing animals, figure 2). New shoots grow at or below the point of cutting. The process is repeated at regular intervals (typically from 5 to 30 years depending on the species of tree involved) and seems to act in a rejuvenating fashion. Many pollarded trees reach a considerable age, much older than maidens (untrimmed trees) of the same species. Their lower trunks typically grow very thick and gnarled with zones of dead timber, (figures 3 and 4). This technique was originally used as a means of obtaining a regular crop of light timber from trees while ensuring that the regrowing shoots were protected from damage by browsers. It has many advantages as a technique in management of trees for biodiversity preservation:

- it can be used to reduce crown size mature or post-mature trees considered potentially liable to fall and endanger passers-by;
- it encourages early maturity and development of post-maturity traits (such as dead wood production);
- it actually encourages trees to live longer.

In some managed ancient forests (e.g. Burnham Beeches in Buckinghamshire) virtually all the mature trees are pollarded. The practical application of pollarding and its value in nature conservation has been particularly well described in two excellent references (Read, 1991 and 1996) which are collections of papers covering many different aspects.

Coppicing is similar to pollarding, but the lopping is carried out close to the ground. Numerous small shoots grow out from the stool and can be harvested frequently or, more often, left to grow for many years. Old coppiced trees can be recognised by the presence of several 'trunks' growing from a single base at ground level. Harvesting is relatively easy, but new shoots must be protected from grazing animals during the early regeneration process. Coppicing is sometimes carried out as a way of maintaining open areas in woodland and can be very beneficial to certain forest floor plants and some particular species of insect associated with them (e.g. pearl bordered fritillary butterfly, *Boloria euphrosyne*) but because the coppice stool contains little volume of dead wood it does not benefit the overall forest biodiversity in the same way as pollarding.

Biodiversity in Post-Mature Tree Habitats of Britain and the West Midlands

The title of this section has been chosen with care! A number of animal species (particularly vertebrates) use trees and woodland as shelter or hunting grounds but are not necessarily dependent on them for survival. Similarly, many flowering



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plants live in woodland but are not dependent on the presence of dead wood or post-mature trees. A number of animals living in, on, or among trees are dependent on the live wood, leaves, flowers or fruits of immature trees rather than deadwood or post-mature trees. Some of those are considered endangered and may require special habitat management (e.g. pearl bordered fritillary butterfly, mentioned above), but that subject is not covered in this paper.

Despite the above, the vast majority of forest/woodland species other than flowering plants are in some way dependent on the presence of dead wood or are otherwise associated with post-mature trees. These include viruses, bacteria, mosses and liverworts (Bryophytes), algae, ferns and horsetails (Pteridophytes), fungi, invertebrates and a few vertebrates.

Among the vertebrates are woodpeckers, which are predaceous on insect dead wood insect larvae, willow tits, tawny owls, nuthatches and several species of bats (particularly the noctule bat) which rely on cavities in tree trunks for nesting or roosting. They represent altogether only a very small proportion of our total vertebrate fauna (308 species comprising 210 breeding birds, 48 mammals, 12 reptiles/amphibians and 38 freshwater fish).

Of the remaining groups, the fungi and invertebrates are by far the most numerous in terms of species and are relatively the best known - even if rather poorly recorded. At present almost 5,000 (13% of the total 38000+) British species of these two groups alone are known to be dependent on deadwood habitat, but as explained below, the true species total is likely to be far higher. The populations of some of these species are extremely large and they can form a significant component of the total woodland food chain, but many others are highly specialised in their micro-habitat requirements and therefore very local and scarce. Many of Britain's rarest and most endangered species are amongst the latter and they are particularly susceptible to fragmentation or loss of habitat. Because of their overwhelming species diversity, the remainder of this article is devoted to these two dominant groups.

Fungi

Fungi are remarkable in that there is very little visible evidence of the existence of the greatest part of their biomass. When a fungus spore lands on wood and germinates, it sends fine thread-like strands (hyphae) into the dead wood forming a network known as the mycelium which gradually breaks down and softens the wood, producing suitable habitat for invertebrates. This mycelium is the main vegetative body of the fungus and is always present within the wood, aiding its decomposition. Fruiting bodies are produced when suitable conditions arise. These are the obvious visible signs of the fungal activity and may be quite

large in the form of brackets and toadstools (macrofungi) but in many cases are smaller and insignificant (microfungi). The fruiting bodies may be hard and resilient with an almost woody texture, remaining permanently attached to the deadwood substrate (e.g. brackets) or they may decay and disappear very quickly once they have ripened and their spores dispersed. In either case, they also provide specialised habitats for invertebrates.

Invertebrates

Many invertebrates have complex life cycles which involve more than one stage, each having particular habitat requirements, while others spend their entire life cycle within a single habitat. Those known to be dependent on habitats associated with post-mature trees at one or more stages of their development include representatives of such groups as worms (Annelida), slugs and snails (Mollusca), copepods (Crustacea), millipedes (Diplopoda), centipedes (Chilopoda), false scorpions (Pseudoscorpiones), spiders (Araneae), mites and ticks (Acari), springtails (Collembola) and insects (Insecta). Many other groups are common in such habitats (e.g. woodlice) but also live in other habitats.

The vast majority of invertebrate species involved are flying insects, particularly beetles (Coleoptera), flies (Diptera) and bees/wasps/ants (Hymenoptera). Many of these (e.g. hoverflies) spend their immature stages (egg, larva, pupa) in dead wood, but their adult stages (those most familiar to non-naturalists) are found in a wide variety of habitats (e.g. at flowers).

Species Statistics

The statistics presented below are based on research carried out during the production of the Birmingham and Black Country (B and BC) Deadwood Habitat Biodiversity Action Plan (BAP) for which the author acted as facilitator and editor (Anon, 2000b). The tables are reproduced here by permission of the B and BC BAP Steering Group. The figures for deadwood invertebrates were based on a draft species list which has since been published (Alexander, 2002). In the interests of time, no effort has been made to update the table to reflect the slight differences in species numbers in the published version.

The total number of species quoted is likely to be a significant underestimate since there undoubtedly remain many undiscovered species (either new to science or new to Britain). Amongst the Diptera alone 84 species have already been added to the British list since publication of the latest checklist in 1998 (Chandler, 1998, 2002), an average of 20 species each year!. Similarly, the immature stages of many species of the groups represented are very poorly known, so the proportion of species dependant on deadwood habitat is also likely to be an underestimate.

Table 1. Approximate Numbers of Invertebrate and Fungus Species Associated with Dead Wood

Group	Total Species Count		Dead Wood Associated		% Dead Wood Associated	
	UK	B&BC	UK	B&BC	UK	B&BC
Beetles (Coleoptera)	4114	514	754	62	18.3	12.1
Flies (Diptera)	6668	1082	737	154	11.1	14.2
Bees, Wasps, Ants etc (Hymenoptera)	6549	264	178	12	2.7	4.5
Butterflies & Moths (Lepidoptera)	2768	900	46	6	1.7	0.7
Other Insects	1973	317	33	6	1.7	1.9
Non-Insects	1724	420	25	4	1.5	1.0
Invertebrates Total *	23796	3497	1773	244	7.5	7.0
Toadstools etc. (Agaricales)	1633	821	204	140	12.5	17.1
Bracket fungi (Aphylophorales)	702	216	519	194	73.9	89.8
Jelly fungi (Tremellales S.L.)	105	21	75	5	71.4	23.8
Stomach fungi (Gasteromycetes)	116	27	8	5	6.9	18.5
Ascomycetes	5100	904	1680	284	32.9	31.4
Slime moulds (Myxomycetes)	300	158	267	111	89.0	70.3
Lichens	1355	141	223	71	16.5	50.4
Rusts & Smuts	360	111	0	0	0.0	0.0
Coelomycetes	643	259	40	16	6.2	6.2
Hyphomycetes	1113	196	200	55	18.0	28.1
Others	3573	32	0	0	0.0	0.0
Fungi Total **	15000	2886	3216	881	21.4	30.5
Invertebrates + Fungi	38796	6383	4989	1125	12.9	17.6

* Includes species associated with sap runs and a few species also associated with live timber.

** B&BC columns include fungus species recorded from the whole of Warwickshire

Table 2. Red Data Book Categorisation of the Dead Wood Associated Invertebrates

Red Data Book Status	Total Species Count		Dead Wood Associated		% Dead Wood Associated	
	UK	B&BC	UK	B&BC	UK	B&BC
Presumed Extinct - No recs. since 1900	148	0	25	0	16.9	0.0
K - Insufficiently Known to categorise	456	1	56	0	12.3	0.0
1 - Endangered	587	4	95	0	16.2	0.0
2 - Vulnerable	397	5	54	1	13.6	20.0
3 - Rare (found in <16 10km squares)	811	15	95	1	11.7	6.7
Notable - Known from 15-100 10km sq.	2739	129	356	17	13.0	13.2
Unclassified ***	18658	3343	1092	225	5.9	6.7
Total	23796	3497	1773	244	7.5	7.0

*** Includes species not known at time of compilation of the Red Data Books

Besides the total numbers of known British species in each category, the tables also show the number of species recorded from the Birmingham and Black Country area. In a more local context the statistics show that roughly 1/4 of the 5000 known British invertebrate and fungus species have been recorded there. The proportion of species associated with dead wood is roughly similar to the national average at 7% of insects and 20+% of fungi.

Although most of our original native flora and fauna arrived at a time when Britain was largely forested, many of those species would have been generalists not dependent on trees or deadwood (e.g. woodlice). Areas of heath, grassland and other non-forest habitats would have supported their own specialist populations and there are likely to have been many later arrivals as those habitats increased in area as a result of forest clearance. Enormous disturbance has been wrought on our forests and

woodlands, so many deadwood species have undoubtedly already been lost.

So are the figures in the table significant? I believe that they are. Both the total numbers of species present and the proportion of those dependent on dead wood are likely to be underestimates. The deadwood habitat contributes enormously to Britain's overall biodiversity and its preservation should be a prime target of any programmes to preserve that biodiversity.

The fact that an essentially urban area like Birmingham and the Black Country still retains a similar (actually higher, if the statistics are correct) proportion of deadwood habitat dependent species to the entire British Isles indicates that all may not be lost. Urbanisation alone has apparently (amazingly) not yet wiped out a disproportionate number of these species. There is hopefully still time to prevent or reduce further losses in our area.



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The Importance of Post-Mature Trees for Biodiversity in Britain.

In the discussion presented above I have tried to show how the value of an individual forest tree as a habitat and refuge for wildlife increases with age, and does not cease with its death. I have described how the increase is related principally to the development of zones of dead and dying wood within (or attached to) the living tree or shed and lying around it and have introduced the term 'deadwood habitat' in connection with it. I have also described how other important wildlife habitats develop within a tree as it ages: particularly rot-holes (which may be just cavities in healthy wood filled with water and rotting vegetation) and sap runs. These are usually considered to be part of the general 'deadwood habitat' even though not actually or necessarily consisting of dead wood.

It may appear that I have used the terms 'post-mature trees' and 'deadwood habitat' almost interchangeably, but it should be noted that the bulk of the deadwood habitat in a woodland or forest actually consists of dead fallen branches or completely dead trees. Heavily managed areas such as parks, village greens, gardens and urban roadsides often support widely spaced or isolated post-mature trees. However, the intervention of man usually results in deliberate clearance of fallen branches or removal of attached deadwood - dramatically reducing, but most importantly not eliminating, the volume of valuable wildlife habitat present.

Colonisation of deadwood habitat depends largely on chance migration of specimens from existing sites of similar suitable habitat. Many species have very specific micro-habitat requirements and exist in only very small numbers. The number of species harboured by any particular tree at a particular time depends on the range of micro-habitats present, the proximity of the nearest reservoir of similar micro-habitat, and the time that those similar microhabitats have coexisted. The older the tree, the more chance that any given species will have become established. Hence the older the tree, the more species it is likely to harbour and hence the more important it is for biodiversity. Another reason why old trees are important is that they may support relict populations of species which have otherwise disappeared completely from the area due to habitat loss during their (post-mature) lifetime. They represent a small but potentially viable source of individuals which might be able to recolonise restored habitat. I have often heard it stated (but don't ask me the reference) that the value of a tree for biodiversity increases by a factor of ten for each time its age doubles (i.e. a 600 year old tree is 10 times as valuable as a 300 year old tree in the same place).

Obviously, an old tree in a forest has a greater potential for harbouring wildlife than an isolated tree of similar age on a village green or city street, but it is surprising how many species an apparently quite isolated tree can support. The value of a tree should never be totally discounted, however isolated it is.

Most of the discussion above has focussed on existing post-mature trees, but it should be remembered that the habitat can only be maintained in the long term if young trees are planted and nurtured until they become post-mature so that they can take over from older trees which are eventually lost due to old age.

What can be done to preserve the Habitat?

The primary factor affecting the deadwood habitat is lack of appreciation of its importance by both woodland managers/workers and by the general public. Mature and ageing trees are often felled and removed, and fallen/cut dead wood cleared away, without understanding of the magnitude of the impact that this has on the wildlife in the area. The increasing use of chainsaws, chippers and particularly stump-grinders has greatly accelerated the impoverishment of our wildlife habitat in recent years.

Relatively minor changes to attitudes and procedures could result in an enormous reduction in the damage being caused at very little cost. So what can be done?

Objectives

Because of the large number of species involved, maintenance and ultimately expansion of Britain's current deadwood habitat must play an important part in maintaining our overall biodiversity in the long term. Old trees can be preserved and nurtured by sensible non-destructive management wherever possible.

Replacement of existing post-mature trees, in the long-term, can be ensured by planning their replacement. While it takes as much as 120 years to grow a post-mature oak tree from a seedling, we can in some cases look to preserving and maintaining suitably located existing immature trees to ensure that they reach maturity and beyond. Maturation of such trees may, in some cases, be accelerated by careful use of pollarding.

Fallen wood contributes very significantly to the deadwood habitat. A very great contribution can be made to habitat maintenance by halting or reducing unnecessary removal of deadwood. Fallen trees and branches should, as far as possible, be left to rot where they lay (or nearby). While this may not be possible on urban road verges, it can generally be achieved quite easily elsewhere with no cost and no loss of public amenity.

Education

Public awareness is essential. If the public can be made aware of the importance of old trees and dead wood for biodiversity there would be far less pressure to 'tidy' it away or to cut down old trees unnecessarily. Enlightened managers would automatically choose options which would maximise preservation of the habitat within their jurisdiction.

The B and BC Deadwood Habitat BAP (Anon, 2000a) has an appendix entitled "Principles of Deadwood Management Guidelines" which contains many useful suggestions about ways in which woodland and trees can be managed to maximise the value of the deadwood habitat.

Survey

Identify and list/map all 'significant' old trees in a particular neighbourhood. Bring them to the attention of the managers/owners and target them particularly in the awareness campaign. This process is already being carried out in some areas as part of local Biodiversity Action Plans.

Bring the same trees to the attention of local specialists and establish plans for surveying the wildlife (particularly fungi and invertebrates) present in the areas concerned so that the importance of the trees as a biodiversity resource can be assessed in the longer term.

Identify local areas where rare or important deadwood habitat species have already been recorded (data from local recording schemes). Arrange for the local specialists to resurvey those areas to ascertain whether or not these important species are still present. This can be a long process (several seasons = years) because the species concerned are often extremely elusive.

Acknowledgements

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Figure 2. Old pollarded willow showing old trunk and numerous younger shoots.

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Figure 3. Deadwood habitat in main trunk of tree in Figure 2. Malcolm J. Smart



Figure 4 Close up of deadwood habitat showing invertebrate and other animal bores. Malcolm J. Smart

References and Additional Reading

A remarkable amount has been written on this subject over the years, so it is surprising that there is still so much ignorance of the subject amongst the general public and even among woodland managers.

The references given here include several collections of papers. Although only a few are referred to directly in the text, the vast majority of those individual papers are very interesting and masterly works in plain English, which provide a fascinating insight into numerous aspects of the subject. They generally make quite easy reading and are to be recommended. All the references given contain substantial lists of further references. When reviewing literature on organisms living on

wood (including the references given below), particularly dead wood or post-mature trees, one is likely to encounter a number of special terms that have been coined to describe them. Although I have avoided using them in this article I believe that it may be helpful to introduce two particularly common terms before you proceed further.

- Saprophytic:** Organisms living on dead organic matter. Typically used in reference to species of fungi.
- Saproxyllic:** Species that depend on wood, usually but not always dead wood, for some part of their life-cycles. Typically used in reference to invertebrates.

- ALEXANDER, K.N.A., 2002. The invertebrates of living and decaying timber in Britain and Ireland. English Nature Research Reports No. 467, 142pp, Peterborough, ISSN 0967 876X
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[A plan for the conservation of deadwood and post-mature trees in the urban West Midlands with proposed deadwood management guidelines as an appendix]
- ANON, 2000b Birmingham and Black Country Biodiversity Action Plan - Deadwood Habitat Action Plan Tech. Appendix (only in the Internet version). Birmingham and Black Country Biodiversity Action Plan Steering Group (only in the Internet version)
Internet: <http://www.wildlifetrust.org.uk/urbabwt/ecorecord/bap/html/deadwda.htm>
[A detailed description of deadwood habitats and their associated Invertebrates and Fungi]



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