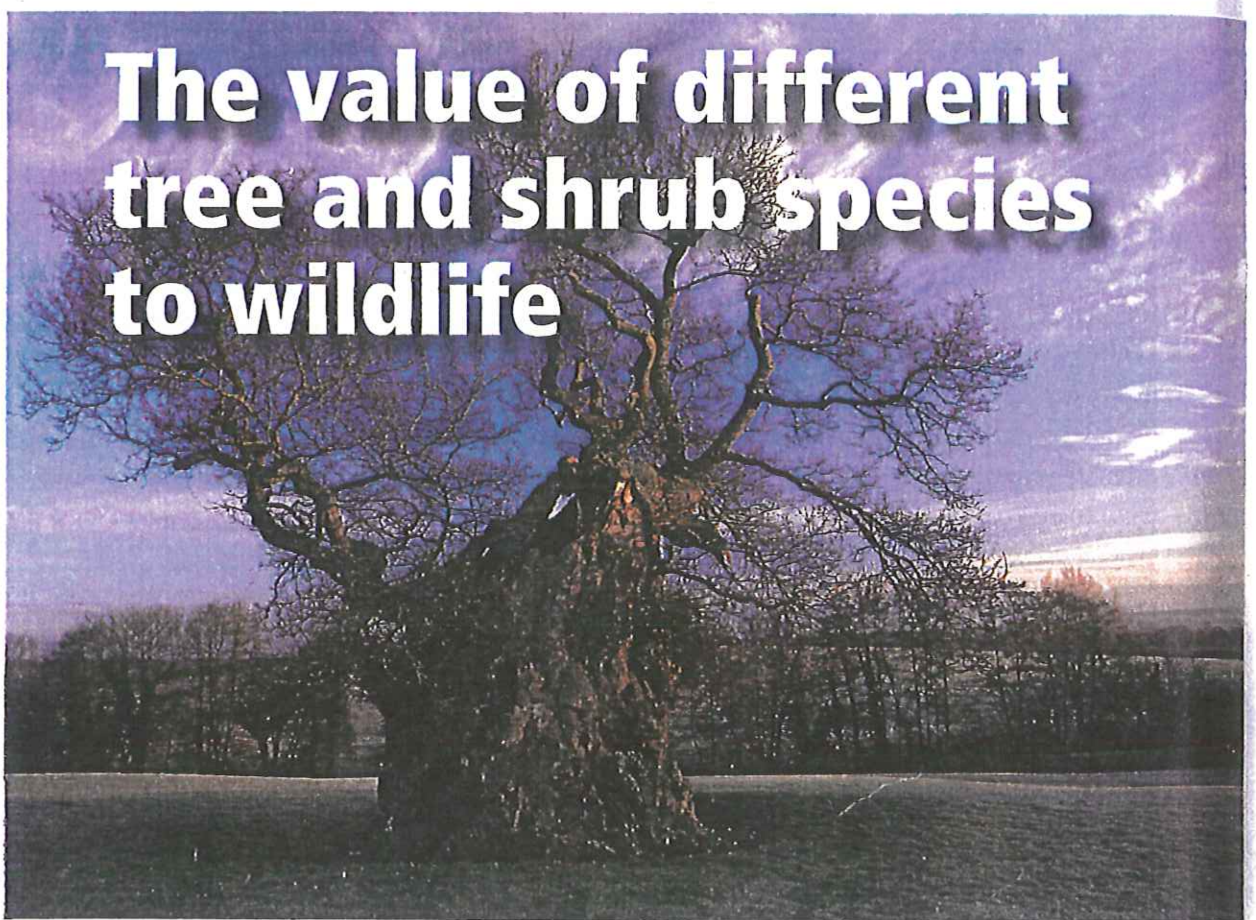
The value of different tree and shrub species to wildlife



Keith Alexander, Jill Butler and Ted Green

An ancient hollowed-out Pedunculate Oak still providing a wealth of niches for wildlife. Bob Gibbons

'The power of observation is the basis of all science'

Which trees are the most valuable to wildlife? Are tree and shrub species not native to Britain of any value for wildlife? These are two common and fundamental questions, but neither has been satisfactorily answered. The natural history and nature conservation literature is full of partial attempts, some well informed, some less so.

The first scientific comparison of the value of different tree and shrub species to wildlife was made by Professor Richard Southwood (Southwood 1961). His hugely influential paper focused on only the insect species that feed on foliage. This was updated some 20 years later (Kennedy & Southwood 1984), incorporating data on mites as well as other material which had subsequently become available. There is, of course, considerably more to woody plants than their value to foliage-feeding insects and mites. We offer here a preliminary assessment of a wider range of values of trees and shrubs to wildlife in general.

A key reason for expanding Southwood's work is the extent to which it is being misapplied by many of its readers. How often have we seen statements such as 'oak is the most important tree to British wildlife', based on Southwood's insect species-richness data? The statement may well be true, but Southwood never claimed to show that!

We also regularly hear or read that oak 'supports more than 400 species of invertebrate', but, of course, no one tree – or even one site – supports each and every one of these invertebrate species. This is equally applicable to other groups of organisms. The presence or absence of species on a particular site is dependent on a whole host of factors, especially the mobility of the species concerned, and their ability to find and colonise places that are suitable for them. Representation of wildlife associated with a particular tree or shrub species will also vary around the year, for instance, according to the age of the individual plant and its condition. Kennedy & Southwood identified the most significant variables affecting species richness in foliage insects as host-tree abundance, time present in Britain, and whether or not the foliage is evergreen, with some significance resulting from taxonomic isolation, tree height and leaf size. Again, these are also significant beyond just foliage-feeding invertebrates.

Southwood's compilation is of species closely associated with a single host tree or shrub species, and he purposely omitted organisms which feed on a wide range of hosts. However, these comprise a very significant proportion of the British invertebrate fauna.

Defining the wildlife of trees and shrubs

Living trees and shrubs actually support and are supported by a very wide range of other organisms, including:

- mycorrhizal communities in the soil (the fungi, as well as organisms which feed on them);
- soil-inhabiting organisms (such as bacteria, yeasts, nematodes, mites) associated with both live and dead roots;
- decay communities within dead areas of wood (fungi, invertebrates, etc);
- decay communities which exploit fallen dead leaves (fungi, invertebrates, etc);
- epiphyte communities which exploit all surfaces, bark, wood and leaves (lichens, mosses, liverworts, algae, as well as species which shelter amongst them and feed on them);
- animals which feed on pollen, nectar, fruits and seeds, as well as the foliage-feeding communities;
- animals which feed on the fungi (mycelium and fruit bodies) and animals that live on the plants.

And this list is by no means complete.

The value of trees will also depend on whether they are of open-grown form or close-grown within groups, the former being by far the most valuable – as individual trees – for wildlife in general. The tree standing as an individual, usually in the shape of a hemisphere or cone, is able to realise its full potential of leaf area and flowering (we have called these 'pollen' trees). This therefore influences and maximises pollen and fruit production by comparison with a tree grown in competition with others, for example in high forest, where the development of individual tree canopies is significantly limited. The open-grown tree has been recognised across the world for perhaps millennia as the most productive form for producing fruit and tree seed. Scattered trees have also been recognised as keystone structures for wildlife and cultural landscapes, and even in modern landscapes. However, dense stands of trees do provide conditions of shade and humidity required by many other species, but this is outside the scope of this article.

Palatability and medicinal value of tree foliage to large herbivores is an area of growing interest not covered here. With the current interest in ancient trees, we are now more aware that the values also change as trees develop and age – a successional development, with older examples generally providing the greatest wildlife value. Other variables include altitude, microclimate, proximity of other tree species, region and genetic variation within the species. Thus, the wildlife value of a tree species is not a fixed attribute.

Constructing a simple presentation of the information

The authors decided to make a first attempt at presenting some of this huge array of information in a simple form which could then be used in a more sensible and constructive way by naturalists and conservationists without specialist expertise.

The resulting table was not easy to construct. The underlying data are dispersed widely in the scientific literature and would have been a monumental task to compile. A pragmatic decision was made: we would draw on our own experiences and recollections, with the help of many colleagues who have published elsewhere (see Acknowledgements), rather than make a detailed study of the literature. The table is therefore presented as a preliminary analysis in the hope that it will inspire others to tackle a full literature review in due course.

The next issue to address was criteria. The different trees and shrubs needed to be compared and contrasted in a systematic manner, so far as this is possible. In the table, we have tried to consider each woody species as growing under conditions where the fullest complement of associates might be expected. The trees and shrubs are assumed to be maidens, that is, without a management history

The quality and quantity of species assemblages associated with the widespread trees and shrubs of the British countryside

A single asterisk indicates an estimated low value to wildlife, while five asterisks indicate relatively high value. Trees and shrubs are listed in taxonomic order (Preston *et al.* 2002) to facilitate comparison of close species. Most tree species are ectomycorrhizal; the exceptions are indicated as G (glomalean endomycorrhizal).

Tree type	Mycorrhizal fungi	Wood-decay fungi	Wood-decay inverts	Foliage inverts	Biomass of foliage inverts	Leaf litter	Blossom for pollen and nectar	Fruits and seeds	Epiphyte communities
Pinaceae									
Norway Spruce	*****	**	***	***	***	*	*	****	*
European Larch	*****	**	*	**	***	*	*	****	*
Scots Pine	*****	***	****	****	****	*	*	****	*
Taxaceae									
Yew	***G	**	*	*	**	*	*	****	*
Platanaceae									
London Plane	***G	**				*			*
Ulmaceae									
Elms	***G	****	***	***	***	****	*	*	*****
Juglandaceae									
Walnut	***G	**				***			*
Fagaceae									
Beech	*****	*****	*****	***	*	*	*	*****	*****
Sweet Chestnut	***	***	***	*	*	*	*	*****	*
Turkey Oak	*	***	****			***			*
Holm Oak	***	***	*	*	*	*	*	*****	*
Native oaks	*****	*****	*****	*****	*****	***	*	*****	*****
Betulaceae									
Birches	*****	****	****	*****	****	***	*	****	****
Alder	***	***	**	*	****	***	*	****	**
Hazel	**	***	***	***	***	****	*	***	****
Hornbeam	***	**	**	**	*	***	*	***	**
Tiliaceae									
Limes	****	***	**	**	***	****	****	*	**
Salicaceae									
Poplars	***	***	***	****	***	***	*	*	*
Goat and Grey Willows	***	***	***	*****	***	***	*****	*	****
Crack, White and other rough-barked willows	****	***	***	****	***	***	*****	*	*
Rosaceae									
Cherries	***G	**	*	***	**	****	****	*****	*
Plum	***G	**	***	***	***	****	****	****	*
Pear	***G	**	***	****	***	****	****	***	***
Apple	***G	**	***	****	***	****	****	****	***
Rowan and whitebeams	***G	**	*	*	*	****	****	****	***
Hawthorns	***G	**	***	****	***	*****	*****	****	*
Fabaceae									
False-acacia	***G	**	***	*	*	***	****	*	*
Aquifoliaceae									
Holly	***G	*	*	*	**	*	*****	****	**
Hippocastanaceae									
Horse-chestnut	***G	**	***	*	*	**	****	*	*
Aceraceae									
Field Maple	***G	**	**	**	*	***	****	*	***
Sycamore	***G	***	***	**	*****	*****	****	*	*****
Oleaceae									
Ash	***G	***	*****	***	*	*****	*	*	*****

as coppice or pollard. They are assumed to have had space to develop their full biological potential (i.e. not been constrained by commercial considerations).

The issue of native versus non-native and provenance is essentially avoided in our table. The use of these terms is too restrictive, especially in the context of the mobility of species as the climate changes. We have selected the most widespread species to be found today in the British countryside. Gardens, arboreta and commercial plantations were not considered. The term 'native' is widely used and abused, with little reference to its precise definition. The word actually refers to the place of birth, but is commonly used in natural history to refer to the range of a particular species which was established before it is believed that people had a significant impact. This is rarely a useful starting point. Reliable evidence is generally lacking, and the approach denies the natural dynamism of a species' range. Beech *Fagus sylvatica* is a classic example. This species would almost certainly have continued colonising Britain from its early range in the south-east, but people have distorted the natural expansion through widespread plantings. It is believed, for example, that Beech is not native in northern Britain and yet it may well have reached there by now under its own steam.

Introductions are not necessarily poorer for wildlife, as many species are not precisely tied to a particular tree or shrub species and can exploit others to some extent, especially where the introduced plant is taxonomically close to a native one, or where structural similarities are present. Often these introduced species can provide the necessary conditions when the normal host is not present. For example, quite a few invertebrate species associated primarily with Field Maple *Acer campestre* are capable of living on Sycamore *A. pseudoplatanus* and vice versa. The basic bark conditions found in Sycamore have proved very beneficial to many epiphyte species, including some that are nationally rare and threatened, particularly with the demise of elm trees *Ulmus*. Wood-decay communities exhibit many fascinating patterns among tree species. A good example is provided by the heartwood of Sweet Chestnut *Castanea sativa* and False-acacia *Robinia pseudoacacia*, which decays in a very similar way to that of oak *Quercus* and therefore supports some of the invertebrate species more associated with decaying oak. Here, the heartwood-decay fungus Chicken-of-the-woods *Laetiporus sulphureus* and not the species of host tree is the link. At many sites in the UK, Sweet Chestnut is the key species of tree associated with the mycorrhizal group known as the stipitate hydnoids (hedgehog fungi) and which are Priority Species under the UK Biodiversity Action Plan (BAP). Ectomycorrhizal associations which are usually linked with birches *Betula* and Beech have also been found with species of southern beech *Nothofagus*.

However, as Southwood has shown, a wider range of associates may be expected if the tree is within its native range. Equally, the representation of associates will vary across that range, as each associate will have its own range and mobility. Representation of associated species may perhaps be greater in the centre of the range, lower at the edge, and very restricted when the tree has been planted beyond its native range. In this article we have based our thinking at the biogeographical level of Britain alone, but there will be regional variations. A good example is Ash *Fraxinus excelsior* and its wood-decay communities. Ash tends not to be regarded as a tree which has many associated deadwood invertebrates. This to some extent may reflect regional patterns in the availability of ancient Ash trees. However, it is one of the most important trees in the Cotswolds, supporting a large array of British Red Data and Nationally Scarce insects, including the famous Violet Click Beetle *Limoniscus violaceus*. Another example demonstrating regional distribution is provided by two fungi that both decay the wood of birch: Birch Polypore *Piptoporus betulinus* predominates in the south, but Hoof Fungus *Fomes fomentarius* has a more northerly distribution.

The different wildlife assemblages have been ordered across the table, starting with the group of organisms which really drive ecosystems, the fungi, followed by the invertebrates which exploit the trees and the fungi, and then moving to the complex associations with leaf litter, blossom, and fruits. Epiphytes come next. We considered including a final column dealing with the very complex associations with birds and bats, but we have decided to cover this topic with just a brief discussion.

We have chosen to present the degree of value of each feature on a scale of one to five. A single asterisk indicates an estimated low value to wildlife, while five asterisks indicate relatively high value. It is important to stress that these are provisional rankings, or suggestions, and are not intended to be the last word on the subject.

Mycorrhizal fungi

'*A tree without mycorrhiza is a dead tree.*' James Merryweather (2001)

As mycorrhiza have been an integral, formative component of all biological communities since life on land began – and the partners are interdependent – it is difficult to consider the fungi alone and separate from the plants which they support (J Merryweather pers. comm.). To give them a star-rating lower than the full five when they are essential to the majority of plants could also misrepresent their importance. However, we are attempting to compare species-richness and uniqueness of the composition of the mycorrhiza, and so it seems sensible to score down some tree and shrub species which are thought to have fewer species associations with mycorrhizal fungi and those which are associated with fungi which have a wide range of hosts. Merryweather (2001) and Spooner & Roberts (2005) provide modern reviews of the association between the different tree species and their mycorrhizal fungi, while Allen (1991) provides a useful introduction to mycorrhizal ecology.

Merryweather (2001) also provides a useful description of the two different types of mycorrhiza. The ectomycorrhizal fungi ensheathe roots but do not penetrate root tissue, and many produce recognisable mushrooms (many of which are favoured foods of invertebrates and mammals). The endomycorrhizal fungi actually penetrate root cells to exchange nutrients and are invisible without a microscope. Most trees and shrubs are actually ectomycorrhizal, and so the exceptions – the glomalean endomycorrhizals – are indicated by a 'G'. This in itself is an oversimplification as some – birch and willows *Salix* – seem to be endo- when young and ecto- when mature, although it is possible that they are both types sometimes, or in some circumstances. The situation may change over time, or perhaps be continually changing.

Wood-decay fungi

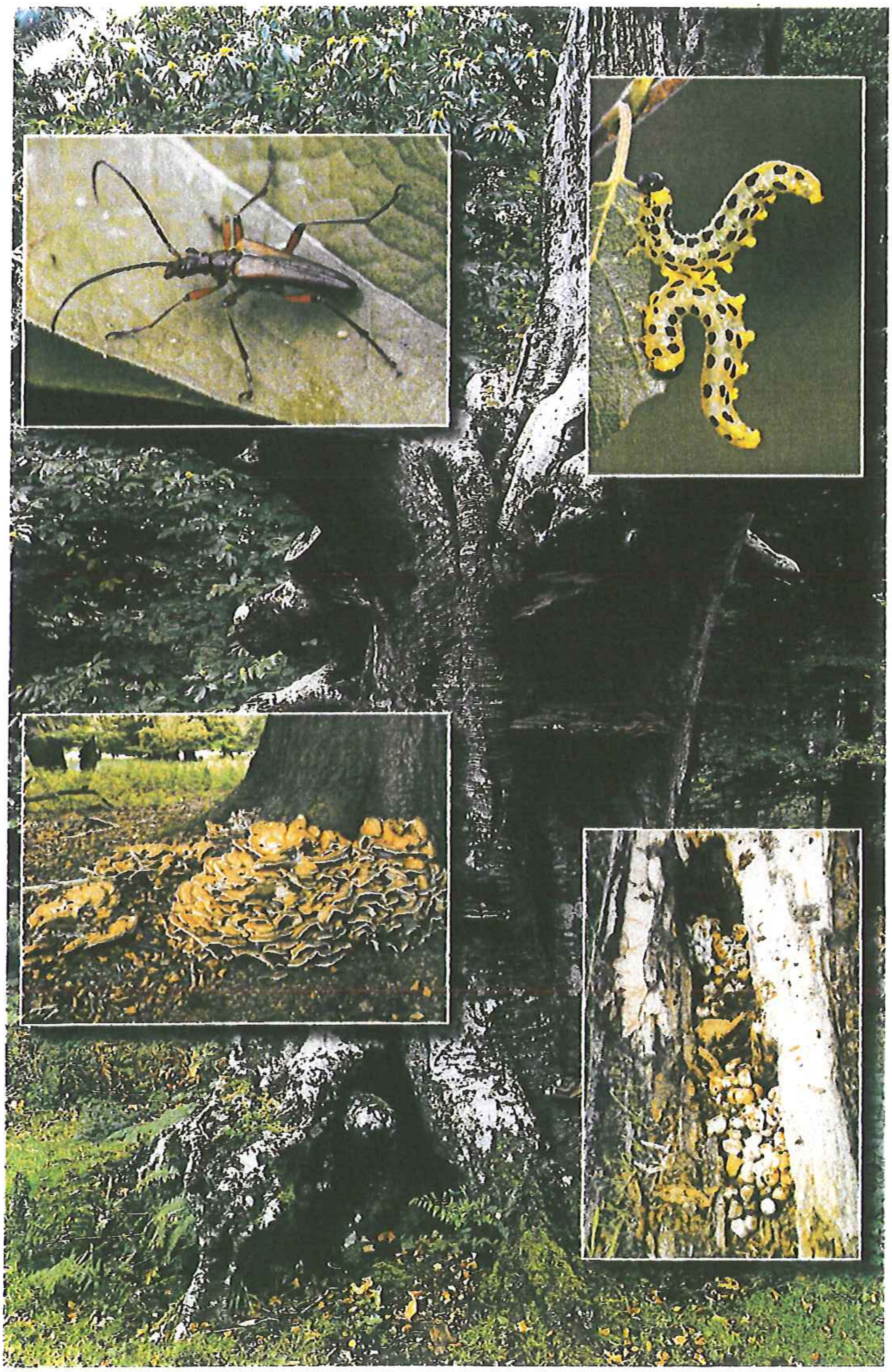
Trees and shrubs are woody plants, laying down additional wood each year as an annual ring. The inner and older rings gradually die, and therefore this dysfunctional (dead) woody tissue accumulates with age. These are eventually colonised by fungi and other micro-organisms and decomposition progresses. Other dead woody tissues begin to develop and accumulate in parallel, for example, in shaded-out twigs and branches, and areas of damage, etc. Tree species differ in whether they have true heartwood, e.g oak and Sweet Chestnut, or ripewood, e.g. Beech, Ash and birch, although it is thought that this distinction probably has little impact on the actual wildlife values of the tree species concerned. All tree species are assumed to hollow naturally at some time in their life through the activity of fungi and other micro-organisms, as a result of which the older stages of any particular tree or shrub species will support a wider range of wood-decay associates. Spooner & Roberts (2005) include a tree-by-tree review of decay fungi, and more detail can be found in Rayner & Boddy (1988) and Schwarze *et al.* (2000).

Fungal fruit bodies, both the soft fleshy ones produced annually and the woody-textured ones, which can be present for many years, provide habitat and food for a wide range of animals. As they are more abundant in late summer and autumn, the resultant associated invertebrate biomass is a resource for other animals at a time of the year when other food supplies are in decline.

Wood-decay invertebrates

The wood-decay invertebrate fauna has been reviewed recently (Alexander 1999, 2002), and so it has been relatively straightforward to categorise the various tree and shrub species according to the range of invertebrates which exploit their decaying wood habitats. It is important to be aware that the key determining factor for the presence or absence of a particular invertebrate species is the condition of the decaying wood, which is largely a result of the species of fungus rather than the species of tree. While the invertebrates attracted to freshly dead wood are more closely associated with tree species, the majority of timber invertebrates

Main photograph **An ancient Beech pollard covered in bracket fungi.** Bob Gibbons Top left **Long-horn Beetle *Stenocorus meridianus*, the larvae of which are found in stumps and roots of various tree species.** Richard Revels Top right **Dusky Birch Sawfly *Croecus latitarus* larvae, foliage-feeders.** Richard Revels Bottom left **Giant Polypore *Meripilus giganteus*.** Richard Revels Bottom right **The eggs of Grass Snake in a hollow stump.** Richard Revels



The heartwood-decay fungus Chicken-of-the-woods *Laetiporus sulphureus*. David Woodfall/Woodfall Wild Images

exploit *decaying* wood, and their species composition at any one time reflects fungal activity. The fauna splits into those species which are associated with brown-rot (also referred to as red-rot), those with white-rot and those with either.

Whether wood decays along a brown route (with the lignin remaining undecayed) or the white route (lignin and cellulose broken down) is determined by the fungus species which is causing the rot. The dead heartwood of a live oak tree, for example, may be colonised by Chicken-of-the-woods (a brown-rot fungus) and the Oak Bracket *Inonotus dryadeus* (a white-rot fungus) at the same time, and therefore has the potential to attract specialist invertebrates which favour both types of decay.

Species-richness of foliage invertebrates

This topic is covered in detail in the Southwood references. Kennedy & Southwood (1984) updated an earlier (Southwood 1961) list of the numbers of foliage-feeding insects and mites associated with 28 British tree and shrub species. A breakdown was provided on the numbers of species in selected insect and mite foliage-feeding groups that are specific to one species or genus of tree and/or shrub as host. The species counts ranged from 450 for willows, 423 for the two native oak species (Pedunculate Oak *Quercus robur*, Sessile Oak *Q. petraea*) and 334 for birches, down to six for Yew *Taxus baccata*, five for the evergreen Holm Oak *Q. ilex*, and just two for False-acacia. The authors went on to analyse the influence of various factors on the species totals per tree or shrub species, as discussed earlier.

While host-tree/shrub abundance was found to be the best predictor of total insect species-richness, Sycamore, Ash, Hazel *Corylus avellana*, Holly *Ilex aquifolium* and Horse-chestnut *Aesculus hippocastanum* came out poorest as having fewer species associated than might be expected from their abundance in the countryside. Of course, the number of species associated is not static in time. Parsons & Greatorex-Davies (2006) point out that over 70 moth species have been recorded feeding on Sweet Chestnut, whereas Kennedy & Southwood (1984) cited only nine.

Some of the sap-sucking insects, e.g. aphids and scale insects, generate large quantities of honeydew as a waste product. This is an important source of sugars, etc, exploited by many other insect species. The surplus is converted by bacteria and fungi and returned to the tree.

Biomass of foliage invertebrates

We have included the 'biomass option' because it is clearly important for foliage-feeding fauna. To say that Sycamore, for example, is not good for wildlife because it does not support a species-rich foliage fauna is nonsensical when it does have a superabundance of aphids on which aphid-feeders can feast. Using biomass also enables other non-foliage-feeding invertebrates to be taken into account, e.g. predators, parasites, hyperparasites, microfungi-feeders, etc. We are not aware of any publications on the invertebrate biomass of trees – and indeed have heard vertebrate ecologists bemoan this lack of knowledge!

The biomass also changes throughout the year, this varying among tree and shrub species. Thus, oak has an abundance of invertebrates within the first few weeks of coming into leaf, but this rapidly tails off. It usually coincides with the build-up and therefore continuity of the aphid biomass on Sycamore.

Leaf litter

Of course, all leaf litter is good for wildlife in some way. The annual fall of conifer needles or seasonal fall of leaves is part of natural recycling which returns nutrients into the soil, where they can be absorbed by fungi and passed on to the tree roots. But the speed of the breakdown and release of nutrients varies with the tree and shrub species which produce the litter. Beech and Sweet Chestnut leaves are notoriously slow to break down, while those of Ash and Sycamore are relatively fast. Sycamore leaf litter is well known to support a large worm population. The slower degradation of Beech provides a deep leaf-litter layer which provides extensive cover for organisms, while the fast degradation of Sycamore does not. The basis for the quality-scoring which we decided on is the premise that faster recycling is more beneficial to the system as less nutrient is locked away at any one moment in time.

There are many publications which discuss the leaf-litter communities, and any selection has to be a personal choice. Spooner & Roberts (2005) are once again a good modern source on fungal decomposition, while Charles Elton's classic *The Pattern of Animal Communities* (1966) still has one of the most useful discussions of leaf-litter fauna.

Blossom

Pollen and nectar are two distinctly different resources for wildlife. Pollen is rich in protein and is believed to be important for egg-production in flower-visiting insects. Nectar is basically a sugar solution and provides an immediate source of carbohydrate for fuelling flight in insects. Early-flowering trees and shrubs are especially important for a large number of spring-flying nectaring insects, and the annual sequence of Blackthorn *Prunus spinosa*, sallow, Hawthorn *Crataegus monogyna*, etc. is followed by a succession of insect species. It is important not to equate flower size with wildlife value. The small flowers of Holly are very attractive to a wide variety of flying insects. One of the great strengths of Sycamore as a wildlife tree is its flowering in high summer, when little other tree blossom is available. Most large trees are wind-pollinated and do not attract many insects to their flowers, although some are strongly attractive to insects as a result of honeydew production by sap-sucking insects (covered under the foliage category).

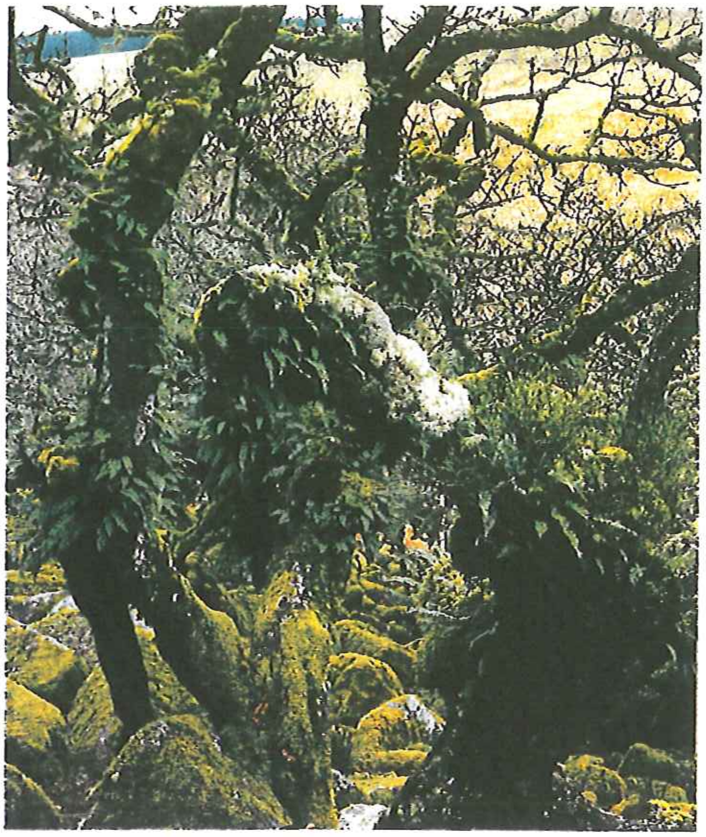
Again, there are many books which deal with pollination as a wildlife resource, but Proctor *et al.* (1996) is the best modern treatment.

Fruits and seeds

This section is one of the more difficult to assess. It aims to bring together and summarise a large and disparate variety of organisms that benefit from the fruits and seeds produced by the various tree and shrub species. These include fungi and invertebrates which parasitise those fruits and seeds, as well as the mammals and birds which feed on them and contribute to their dispersal. Annual productivity is very variable. Seasonality issues are also important – pine *Pinus* and larch *Larix* release seeds in March and April and are especially important for seed-eating birds, when other food sources are scarce. Some birds – notably Hawfinch *Coccothraustes coccothraustes* and Greenfinch *Carduelis chloris* – specialise in the hard seeds, whereas soft fruits are more generally accessible. For information on the value to birds of different berry-bearing trees and shrubs, see Snow (2002).

Epiphyte assemblages

Positive features of tree bark which favour epiphytic lichens are texture, relatively high porosity and absorptive capacity, and also higher pH. These features may change during the life of a single tree. Rose (1974) points out that young oaks and the smaller branches and twigs of older trees have relatively smooth bark and can support lichens characteristic of smooth-bark trees such as Beech. Older oaks develop a more rugged bark, and support rough-bark species. Other features that can increase the species-richness of a tree are aspect (e.g. a leaning tree has many more niches for epiphytes than an upright one) and damage, with sap-runs providing important additional micro-habitats. Salts in dust and splash derived from animal excreta and urine, and even particles from car tyres, may also enrich absorptive and porous barks and enable lichen species characteristic of high-nutrient barks to be present. Conifer bark tends to be acid and the dense foliage of these trees reduces light levels on their trunks, making the bark a poor place for epiphytes. While conifers have poor epiphyte floras in southern Britain, Coppins & Coppins (2002) record 220 species of lichen on Scots Pine *Pinus sylvatica* in its native



Pedunculate Oak covered in epiphytes, including ferns, bryophytes, lichens and even Bilberry, at Wistmans Wood on Dartmoor. Bob Gibbons

Scottish range.

A numerical comparison of the lichens of different tree species has been attempted by Rose (Rose 1974; Harding & Rose 1986). He found that in most cases there were no marked differences in the epiphyte floras on the species within most genera, the main exception being between Field Maple and Sycamore. The richest trees for epiphytes – with the species totals from Harding & Rose (1986) – are the native oaks (326 species), Ash (265), Beech (213), the native elms (200) and Sycamore (194), followed by Hazel (162), Goat and Grey Willows *Salix caprea* and *S. cinerea* (collectively 160), birches (134), Field Maple (101), Alder *Alnus glutinosa* (116), Holly (96), the limes *Tilia* (83) and Hornbeam *Carpinus betulus* (44). However, Rose also pointed out that, while it is clear that the native oak species have a considerably greater number of lichen epiphytes recorded on them than do any other tree species or genera occurring in Britain, no species of epiphytic lichen is actually specific to oaks in Britain. Because epiphytes are partially dependent on aerial sources of nutrients, they are particularly sensitive to pollution effects. Therefore, tree species which may buffer these, e.g. the basic bark of Ash, can support a wider range of species than can others in more polluted regions, where, for example, the more acid bark of Beech can be very poor for epiphytes.

Bryophytes are more difficult to tie down to tree associations, but Rose (1974) comments that more bryophytes appear to occur on oak than on most other trees. No bryophyte epiphytes appear to be strictly host-specific. Elms and Ash were picked out as other rich trees.

Of course, as with the other groups, species-richness is only one feature of the wildlife value. So far as epiphyte invertebrates are concerned, the quantity of epiphyte plants is perhaps more important than the quality. In areas which would formerly have had species-rich lichen epiphytes but where air pollution has caused severe impoverishment, the invertebrates associated can still be surprisingly species-rich as they appear much less affected by the air pollution. Another feature of invertebrate communities is the importance of structure, especially areas bare of vegetation, so that a dense cover of epiphytes will favour some species, while a sparse cover will favour others.

Birds and bats

Trees and shrubs provide a wide variety of resources for birds and bats, which are highly mobile exploiters of food supplies. The cavities caused by fungal decay offer suitable places for hole-nesting birds and roosting bats, while physical splits in the timber are preferred by certain bats. The rare Barbastelle *Barbastella barbastellus* is said to favour loose, thick bark on the trunks of large old trees. The variety of insect life is preyed upon by insectivorous birds and the bats, while buds, seeds and fruits provide other nutritious feeding for specialist and generalist birds alike. The value of a particular tree or shrub species to birds and bats is therefore assumed here to be a product of longevity, cavity provision and food resources.

The literature on birds is vast and only a scant review was feasible. Nonetheless, few authors directly address the issue of the different values of tree and shrub species. Fuller (1995) provides a useful general discussion, but points out that prey selection by woodland birds has not been adequately studied (R Fuller, pers. comm.). Peck (1989) is one of notably few authors to have investigated the differences in bird usage between tree species, with an interesting study of the feeding behaviour of six species of arboreal passerine in a forestry plantation. The birds showed a marked preference for feeding in European Larch *Larix decidua* and Sycamore and tended to avoid Beech and Western Hemlock *Tsuga heterophylla*. Each bird species, however, showed a preference for a different combination of tree species. Both bird density and the number of bird species were positively correlated with the number of tree species present. The author comments that there is virtually no recognition of tree preferences in European studies on avian foraging behaviour, the main distinction being made between broadleaved and coniferous tree species. The availability of quantities of insects and other foods, not the prey species-richness, is almost certainly of prime importance to the birds. It does seems likely, though, that the Southwood data have no direct bearing on which tree species are more valuable to birds for feeding.

A male Pied Flycatcher. These summer visitors are associated with western Sessile Oak woodlands. However, the woods' open nature and sparse shrub layer as a result of grazing are thought to be the key features of the habitat for this species. Frank Blackburn/Nature Photographers

Longevity

Tree longevity is difficult to ascertain for any individual tree. The only way conclusively to age a tree is to count its annual rings, and in hollow trees these will have long since decayed away. The girths of the largest trees in the UK and Ireland can be found on the Tree Register of the British Isles (www.tree-register.org).

The life expectancy of a tree is an important feature as regards the wildlife which it supports during its lifetime. The larger-girthed trees will inevitably contain greater volumes of dead heartwood or ripewood than smaller trees, and therefore have a potential to support a wider variety of wood-decay fungi, invertebrates and other microorganisms, and also a greater biomass. Generally speaking, they will have the potential to provide a greater variety of roost and nest sites for bats and birds, as well as a greater abundance of insect food for these animals.

Hollowing of tree trunks and limbs, which can occur in all species of tree, has been shown in some cases to prolong the lives of trees. The debris or mulch in the base of an old hollow tree is believed to be one of the original sites for the incubation of reptile eggs, such as those of Grass Snakes *Natrix natrix*.

Conclusions

An inescapable conclusion from this study is that most species are of significant value to wildlife, irrespective of whether or not they are native in a particular area of Britain. No one species in the table has fewer than three asterisks in at least one of the categories. The least valuable species in general do, however, come out as Walnut *Juglans regia* and Turkey Oak *Quercus cerris*, both of which have become naturalised in Britain relatively recently.

This conclusion should not be taken as a *carte blanche* to plant non-native tree species anywhere and everywhere. That would seriously erode the uniqueness of our plant and animal communities. The areas of our countryside least affected by human intervention, and where the tree species composition reflects undisturbed soil conditions rather than the whims of people, do have very special wildlife values and considerable interest to us humans. But in areas not constrained by these considerations, it does not make sense to emphasise one particular species in plantings just because it supports the widest range of foliage-feeding invertebrate species. More diverse plantings – in terms of spacing and pattern of planting, as well as variety of tree and shrub species – will provide more varied wildlife habitat.

We have found that the process of compiling the wildlife-trees table and writing this article has expanded our own knowledge and understanding of the wildlife value of trees and shrubs. We hope that readers will find the article equally useful and stimulating. We are sure that strong feelings will be aroused by our personal – and undoubtedly idiosyncratic – analysis of the subject matter, and look forward to the debate which will inevitably follow.

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The first draft of the table was circulated amongst a selection of ecologists, entomologists, mycologists, lichenologists, etc, for their reactions. On the whole, it received a strong and warm welcome. Wherever possible their criticisms have been addressed, but we take full responsibility for the final presentation. Especial thanks are given to Martyn Ainsworth, Sandy Coppins, Mick Crawley, Fred Currie, Alan Feest, Adrian Fowles, Rob Fuller, Roger Key, Keith Kirby, James Merryweather, Neil Sanderson and John White, and of course to Dick Southwood for his constructive interest and support.

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