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Chapter 9
Tree abundance, density and age structure: the key factors which determine species-richness in saproxylic invertebrates

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Introduction

Conservation should be based on practical observation rather than unstable theory (Rackham, 2006). This is a critically important point - far too much woodland conservation is currently based on an unproven hypothesis of the structure of the forests which spread across Europe following the last Ice Age - the high forest hypothesis. This is especially the case with our most precious sites, the Special Areas of Conservation (SACs), where practical observation would suggest that current approaches to 'minimum intervention' management will inevitably lead to decreasing species richness as a result of decreased sun penetration and increased shading. This chapter will focus on the specialist invertebrates which depend upon the natural decay and degradation of the dead woody tissues produced by trees and shrubs as they develop and age. It will discuss the importance of the age structure of the tree population, the spacing between trees, and the total numbers of trees, as well as the importance of connectivity across the landscape. A basic understanding of the key aspects of tree biology and tree ecology - the aging and decay processes of trees as well as tree form and tree habitats - is an essential tool for people involved in the conservation management of wood-decay invertebrates. A good appreciation of tree terminology is also essential in order to successfully achieve conservation of tree-dependent wildlife

The secret of successful conservation of these wood-decay invertebrates is to think landscape scale - the largest sites support the greatest range of species (Alexander, 2004a, b). It is also important to appreciate that the widest variety of wood-decay habitats is produced by an open-grown tree, where the tree has space to develop its full potential of form and structure (Alexander, 2007; Green, 2010) (Photograph 1 and 2). Only an open-grown tree has good lateral branch development and the potential to support the full range of wood-decay fungi and invertebrates which need decaying wood in the lower crown (Alexander, 2002) (Photograph 3, 4 and 5). Only an open-grown tree can survive into old age, as natural crown retrenchment with age results in a reduced crown height and leaves the tree very vulnerable to over-shading by neighbouring younger trees. Retrenched trees are referred to as 'ancient trees' and support many of Europe's rarest wood-decay invertebrates. The term 'veteran tree' refers to trees which have substantial development of decaying woody tissues resulting either from natural ageing processes or from physical damage - an 'ancient tree' is a type of 'veteran tree' but not all 'veteran trees' are ancient (Ancient Tree Guide No.4) .

Photograph 1: Open-grown oak showing full lateral branch development. Glengarriff Woods, Ireland (K. Alexander).

If conservation of wood-decay communities is an objective of site management then it is vital to consider the long-term production of suitable deadwood habitats from the living trees. It is especially important to base conservation action on the trees, rather than on such abstract concepts as 'woodland' or 'forest'. Trees are real, but terms such as 'woodland' and 'forest' mean different things to different people (Alexander, 2008).

Photograph 2: Open-grown oak, Calke Park, England (K. Alexander).

Photograph 3: This line of trees was planted about 100 years ago; one of the middle trees has been felled; the left hand oak tree now clearly shows an open-grown lateral branch development while the right side has high forest form structure; the tree on the right also has high forest form structure with poor lateral branch development. Heavitree Pleasure Ground, Exeter, England (K. Alexander).

Photograph 4: An old oak tree growing in a more natural situation, but also showing open-grown form on the left side and high forest form on the right side where there is competition from neighbouring trees. Wye Gorge, Wales (K. Alexander).

Photograph 5: Open-grown oak, one on left with history of shredding, the one on the right typical natural open-grown form, the difference in lateral branch size is very clear, Bodfach Park, Wales (K. Alexander).

Wood-decay invertebrates – how many species are there and why are they important?

Few countries have carried out full inventories of their native wood-decay invertebrates. Britain and Ireland may be the only European countries able to quote simple statistics. Alexander (2002) provides a full listing together with basic information on their known ecology, distribution and conservation status: at that time Britain was believed to be supporting 1792 different wood-decay invertebrate species and Ireland 615 species. The figures are somewhat different today as knowledge of the ecology of the species has grown, but essentially Britain is currently believed to have about 2000 native species of wood-decay invertebrate. The best studied group is the Coleoptera (beetles), with 700 species. 54% of these beetle species have been assessed as being rare, and 23% feature on Britain's Red Data Book (Hyman and Parsons, 1992). Other European countries are much richer in species but the proportion of Threatened species and species of conservation interest generally is probably similar to that of Britain. There is abundant evidence that this fauna is of great importance to conservation across Europe – the IUCN European Red List of Saproxylic Beetles (Nieto and Alexander, 2010) has shown that, at a continental scale, 11% of saproxylic beetles are threatened. This compares with 9% of butterflies, 13% of birds and 15% of mammals. Almost 14% of the assessed beetles are thought to have significantly declining populations. The drivers for those declines are mostly still in place – habitat degradation and loss poses the main threat, either in relation to forestry practices or due to a general decline in veteran trees throughout the landscape.

These species are much more than features of conservation interest however, as they are part of the natural decomposition processes of deadwood, they are instrumental in the release of the nutrients which are locked up in wood, and part of natural recycling of nutrients (Stokland et al., 2012). They enrich the soil and facilitate the return of nutrients to the trees. Many are active predators and parasites of pest species, which would otherwise have a more serious impact on the economics of human exploitation of timber. Others are important in the pollination of flowering plants. The benefits of these obscure invertebrates to human populations are actually manifold and discussion of these aspects alone would occupy an entire book.

The importance of age structure of the tree population, the spacing between trees, and the total numbers of trees

Although conservationists tend to get over-occupied with quantifying the volumes of deadwood available in particular areas, there are actually four key factors which determine the species-richness for wood-decay invertebrates (Alexander, 2008) and volumes of deadwood do not feature:

- Total number of trees which make up the population
- Age structure of those trees
- Density of those trees
- Connectivity in the landscape

The first three will be discussed further in this section, with connectivity discussed separately in the following section. The first three relate to physical structure, but the fourth is as much about connectivity in time as in space and is best considered separately. Analysis of the tree population – the living trees – is much more important to wood-decay conservation than trying to quantify the volumes of deadwood. It is the living trees which generate the deadwood and it is by understanding the population dynamics of the living trees that conservationists can conserve the wood-decay fauna most effectively.

How many trees are needed to maintain population viability for the dependent wildlife? There have been attempts at answering this question for a very few species, notably Hermit Beetle *Osmoderma eremita* (Bergman, 2006; Ranius, 2006) but the question is really too all-encompassing to be completely answerable. What is very clear, however, is that the larger sites, the sites with the largest populations of trees, are the most species-rich. The obvious implication is that the more trees that are accessible the better.

It should be very obvious that sustainable conservation of decaying deadwood habitats requires the continual input of freshly dead woody material. This is only feasible where there is a diverse age structure of the trees. Young trees only generate small quantities of small dead branch and root material, but the production of a wider variety of dead woody tissues increases with age. As an individual tree matures it begins to accumulate an increasing volume of dead heartwood tissues as well as producing the occasional dead branch and/or root. As the volume of dead heartwood tissues increases with age it will eventually be colonised by specialist heartwood-decay fungi which are able to exploit the situation and start the recycling process. While it is at this later stage that the value of the tree is greatest to wood-decay wildlife, there is a continual need for new generations of trees developing in order to provide future replacements for the older trees as they eventually die and decay. This requires a diverse age structure. Little or no research has however been carried out on the complexity of tree population age structure that is required to ensure long-term viability of the various decay stages.

Tree density is another very important aspect. It has already been pointed out that only an open-grown tree has the potential of developing the full range of wood-decay situations, especially from the point of view of the important lateral branch habitat and the heartwood decay process that requires the retrenched ancient stage to complete the process. In the case of a *Quercus robur* tree, the lateral branch spread may extend up to 15m from the trunk centre, which means that a similar-sized neighbouring tree should be no closer than 30m, from trunk centre to trunk centre. This has enormous implications in tree planting programmes as very wide spacing is required if the desired end product is an ancient oak. Typically tree-planting schemes in forestry and landscaped developments employ commercial forestry planting densities, often at 2 to 4m spacing. Such plantings will never achieve significant wood-decay conservation, even where the expressed intention is to thin the trees as they grow (Ancient Tree Guide No.7). Experience has shown that thinning is all too often never carried out or carried out after the form of the new trees have already been damaged by the too dense planting and establishment stages – open-grown form lateral branch development in particular can be lost by overcrowded planting (Photograph 6). The need to rescue ancient oaks from competing growth has been demonstrated by Ranius and Jansson (2000); this has become standard practice in British forests (Alexander et al., 2010, 2011).

While open-grown trees are very important to the conservation of wood-decay wildlife, there are species which benefit from the decaying wood being situated in the moister conditions provided by shade. Shade is of course available beneath the canopy of open-grown trees, but this situation tends to be more exposed to drying winds and the desiccation caused by winter cold. There are undoubtedly wood-decay species which require relatively close-grown groups of trees, and this is especially the case with some invertebrates which favour stands of *Fagus sylvatica*, for example. 'Relatively' needs to be emphasised however, as the close-planting used by commercial forestry is often too close to favour these species as the trees tend to grow up relatively tall and thin and to have shortened life-spans as a result.

Trees vary considerably in their optimal requirements for light while developing. *Quercus robur* and *Pinus sylvestris* are examples of light-demanding trees while *Fagus sylvatica* and *Carpinus betulus* are examples

Photograph 6: Overcrowded pine, Feshiebridge, Scotland (K. Alexander).

Photograph 7: Open-grown pine in wood pasture, Sierra de Baza, Andalucia, Spain (K. Alexander).

of shade-tolerant trees. Open-grown conditions are therefore much more important for the light-demanding species, while the shade-tolerant species grow well under both light and shade conditions. The relationship of certain shade-preferring wood-decay invertebrates with *Fagus sylvatica* is therefore partly related to the ability of this tree to develop under conditions of relatively heavy shade.

In a given area there is clearly an optimal tree population which covers maximal tree numbers, optimal age structure, and variable tree density. What is lacking at present are models which can determine this optimal population for a unit area. Tree species of course adds a further dimension, as the same is equally true for each tree species (Alexander et al., 2006).

The importance of connectivity in the landscape

Each species of wood decay invertebrate potentially exhibits its own mobility characteristics, its ability to penetrate the landscape. This aspect has been little studied however. It is assumed that common and widespread species are highly mobile and able to cross relatively large distances of inhospitable habitat, ie areas lacking suitable trees. These are not species that require much conservation attention, if any at all. The rarest species appear to be the least mobile, which appear only able to move from one suitable tree to another if the intervening distance is relatively low and where there is good shelter and appropriate weather conditions for flight activity, ie the air is relatively warm, humid and calm. Between these two extremes is a full spectrum of variation between species. Conservation action becomes increasingly important as mobility decreases.

The basic principle of connectivity conservation is the provision of suitable trees throughout the landscape, which then may act as stepping stones between the relatively species-rich hot-spots. The richest sites tend to be those with the longest history of containing suitable tree populations – the oldest and largest forests and wood pastures (Alexander, 1998; Alexander and Butler, 2004) (Photograph 7). In the long-established cultural landscapes of Europe the rarest species are not necessarily confined to relatively undisturbed forests – these often remaining today as common wood pastures (Photograph 8). The species may have had time to colonise other situations such as tree-lined watercourses, some of which may actually be remnant old forest. Many historic forests have become mosaic landscapes, as the better agricultural land has become exploited by people, often leaving the old forest trees on the poorer land or retaining strips as field boundaries. Other situations which can be colonised by the rarer wood-decay invertebrates include traditional orchards and sweet chestnut groves, where fruit and nut harvesting is optimised by using concentrations of long-established open-grown trees. Where such cultural landscapes have developed alongside or close to old forest then the invertebrate are readily able to spread out into the cultural landscape. This is well-recognised in England where the Noble Chafer *Gnorimus nobilis* is largely confined to the traditional orchard landscapes alongside the medieval Forests of Dean and Wyre (Alexander and Bower, 2011).

With low mobility, connectivity in time is as important as connectivity in space – the rarer species become trapped in relict old forest areas through their inability to colonise new sites beyond the forest boundaries. Such species provide useful markers or indicators of old forest conditions (Alexander, 1998, 2003, 2004a). The primary conservation action for such species is to maintain habitat quality in the known sites, and encouragement of increased mobility through restoring habitat linkages should be a secondary action.

The special conditions provided by lateral branches on open-grown trees

Lateral branches in the lower crown of open-grown trees gradually die as they are shaded out from the developing crown above. They are a feature of relatively young and maturing trees rather than ancient trees. Their position is what makes them unique as wood-decay habitat – aerial dead branches sheltered and buffered from the wind by the crown above. These dead branches remain relatively humid, in contrast to dead branches high in the crown of the tree which are exposed to the full rigours of the local climate – sun in summer, frost in winter, and exposed to the drying air at all times. These aerial dead branches in the lower crown are colonised by specialist wood-decay fungi and this provides a unique habitat for wood-decay invertebrates. Such branches are however very vulnerable to the activities of people – in full view and so a subject for concern over public safety, and readily cut and removed from farm vehicles which can then get closer to the trunk for agricultural activities such as fertilising the pasture or ploughing, all with consequent damage to tree roots and tree health.

Photograph 8: Open-grown pine showing lateral branch development, Sierra de Baza, Andalucia, Spain (K. Alexander).

Heartwood decay and the rarest invertebrates

The heartwood decay succession is the latest of the broad types of woody decay to be found in trees. As a tree grows new annual rings of woody tissues are laid down beneath the bark and the tree gradually expands in girth. Only the outer annual rings remain alive and functional, the inner ones gradually die and form what is known as the heartwood of the tree. In the case of oak it is known that annual rings die after 25-30 years and so any oak tree that is say 100 years old will contain a core of dead annual rings – heartwood – of 70-75 years growth, and a tree 200 years old will contain a heartwood of 170-175 years growth. These dead woody tissues are not accessible to the living tree; before they die the tree extracts the more mobile nutrients present and deposits unwanted materials, as well as - in some cases – complex organic chemicals which will slow down any subsequent decay. Where these decay-resistant chemicals are laid down the dead woody tissues are referred to as durable heartwood – this is the case with oak (*Quercus*) for example but not beech (*Fagus*). In beech the death of the inner annual rings appears not to be so precisely genetically controlled as in oak, and sections of rings appear to die asynchronously, and without any decay-resistant chemicals being laid down; this type of death of the tissues is referred to as ripewood.

Eventually the dead woody tissues in the centre of the tree become colonised by specialist wood-decay fungi which break down the cellulose and – in some cases – also the lignin content. Different fungi may cause different types of decay, eg *Laetiporus sulphureus* typically specialises in durable heartwood and breaks down the cellulose, leaving the lignin behind as brown-rot (also known as red-rot) – hard and dry material which is brittle - whereas *Ganoderma australe* breaks down the lignin and then the cellulose, not quite simultaneously, causing what is referred to as a white-rot by leaving soft and moist cellulose towards the end of the process. Whichever type of heartwood decay takes place, the

Photograph 9: Overcrowded secondary woodland on former open wood pasture, Goehrde, Germany (K. Alexander).

Photograph 10: Overcrowded young oaks, Hamilton High Parks, Scotland (K. Alexander).

trunk is eventually hollowed and the base accumulates debris which composts to form a black soil-like material generally referred to as wood mould. The whole process may continue while the tree is alive and healthy, and the tree actually benefits from the process through the nutrients previously locked up in the dead woody tissues being released through the process of fungal decay – aerial roots may be produced by the tree and grow down into the wood mould to extract nutrients.

The process of decay of these woody tissues provides a wide range of niches for invertebrates to exploit. These invertebrates live inside the hollowing tree and are protected from extremes of weather outside. Invertebrate colonisation usually follows the death of the fungal mycelium within the tissues, with a whole succession of species specialising on the different stages of the process – some feeding on the fungal mycelium itself, others on the products of the decay, some favouring brown-rot others white-rot, and eventually at the end of the process are invertebrates which live in the wood mould in the base of the cavities created by the fungi. Given that wood mould is the end product of the decay of the woody annual rings, the host trees are generally old for the tree species by the time this stage is reached. As the habitat takes a long time to develop it is naturally the rarest of the wood-decay habitat types and one which few individual trees will reach during their lifetimes.

Wood-decay beetles informing hypotheses of natural forest structure

The rationale for minimum intervention management is that the original forests which developed after the last Ice Age and before people began to have a significant impact on forest structure were of a continuous closed-canopy 'high forest' nature. This hypothetical forest structure is based both on an interpretation of pollen assemblages preserved in peat and other dateable deposits, and the observation that when people abandon an area of land it is gradually colonised by trees and shrubs and eventually forms a closed canopy. However, the modern landscape can hardly be considered 'natural' - by the definition of the supporters of this hypothesis - the truly 'natural' processes that would have operated in the distant past are no longer the natural processes which will occur today Photograph 9 and 10). A key factor is that wild large herbivore assemblages are no longer present within the landscape. Where deer are present – natural or naturalised – this succession may not actually occur, as evidenced by the current fashion for deer eradication due to their observed impacts on woodland structure. 'Minimum intervention' management is a peculiar approach in that it is rarely properly defined, if ever. The best definition that the author has heard is 'the minimum needed to protect, maintain and enhance the intrinsic values' (John Deakin, Head Forester, The Crown Estate at Windsor, UK). Where an intrinsic value is forest structure and where that structure is becoming increasingly uniform under the natural processes that are currently operating, then intervention is justifiable in order to conserve the special associated interests.

There are actually two alternative hypotheses about the structure of the original forest cover of Europe: the closed canopy hypothesis (as promoted in the final quarter of the 20th century by Peterken, 1993, 1996, and others) and the wood pasture hypothesis (Vera, 2000, 2013). Advocates of the former, earlier story, have manipulated data on sub-fossil beetle assemblages to support their case. Although a full and detailed analysis has not yet been carried out, a strong case has been made (Alexander, 2012) that, in reality, the sub-fossil beetle assemblages are completely at variance with the closed canopy hypothesis, but more or less consistent with the wood pasture hypothesis. The sub-fossil beetle record does demonstrate that the original forest contained widespread open-grown and ancient trees.

In a fully natural ecosystem with trees – as in the hypothetical original postglacial forest – it seems reasonable to expect the full suite of native wood-decay invertebrates, including those of open-grown trees. As people began to have an impact on the natural undisturbed tree cover then they would have initiated shifts in the representation of the wood-decay invertebrates – favouring some species while pushing others in the direction of rarity and even extinction. After thousands of years of people activity, Britain has 700 native wood-decay beetle species (Alexander, 2002). It is not known how many had colonised Britain before people began to have a significant impact but sub-fossil evidence has been found for just 18 species which are no longer found there (Buckland and Dinnin, 1993). This is a remarkably low percentage – 2.6% extinction – considering the stories of large-scale forest clearance that have been promulgated by the paleo-ecologists. The extinct species are a more or less equal mix of shade-loving species and species requiring open-grown trees (Alexander, 2003). Sub-fossil studies are relatively new, however, and so the figure of 18 is almost certainly an under-estimate of the losses; nonetheless, this really does not sound like a major shift in species-richness. Clearly habitat representation has not changed a great deal – the vast majority of saproxylic beetles are still able to live in the modern cultural landscape. It should however also be acknowledged that a large number are on the verge of extinction due to declining habitat availability through modern development pressure – 54% currently are of sufficiently restricted occurrence to have conservation status.

So, if the overall species-richness of wood-decay beetles has changed little since postglacial forest times, what changes have studies of the sub-fossil fauna demonstrated? The weevil *Dryophthorus corticalis* provides an instructive case study. It lives within moist brown-rotten heartwood inside exceptionally large old examples of open-grown oak trees. It is present within the modern British landscape at just one site, a very special site - Windsor Forest and Great Park - with the most extensive landscape of open-grown ancient oaks in the country. There appears to be a requirement for large concentrations of suitable host trees; the species has particularly low mobility under modern conditions. And yet the sub-fossil record demonstrates that this weevil was actually much more widespread in the postglacial forest period, and present at a site 250km to the north. This is strong evidence that open-grown conditions, suitable for the development of ancient oak trees, were not only widespread at this time but also sufficiently linked across the landscape, enabling the species to move freely from tree to tree (Photograph 11 and 12). The sub-fossil discoveries include many such species requiring open-grown conditions – *Prostomis mandibularis, Teredus cylindricus, Hypulus quercinus, Batrisodes venustus, Gastrallus immarginatus*, etc. The ecology of these beetles clearly demonstrates that open forest conditions were the norm, not exceptional, in the natural forests of Britain. The beetle assemblages demonstrate the very widespread occurrence of large, almost certainly open-grown trees, reaching ages that are not feasible under closed-canopy conditions. Heartwood decay is a strong feature of these trees, as is wood mould in hollow trunks, and even lateral branching allowing the development of rot-holes in the trunk. Basically the palaeo-entomological work on sub-fossil beetles has never before been examined objectively, separate from the closed forest hypothesis. W.G. Hoskins (1966) was thinking of industrial archaeology when he said: 'There are profoundly important discoveries to be made by those who have learnt to use their eyes intelligently. Most of us are visually illiterate, and our education has helped to make us so.' Unfortunately most scientists are blinded as part of their training'.

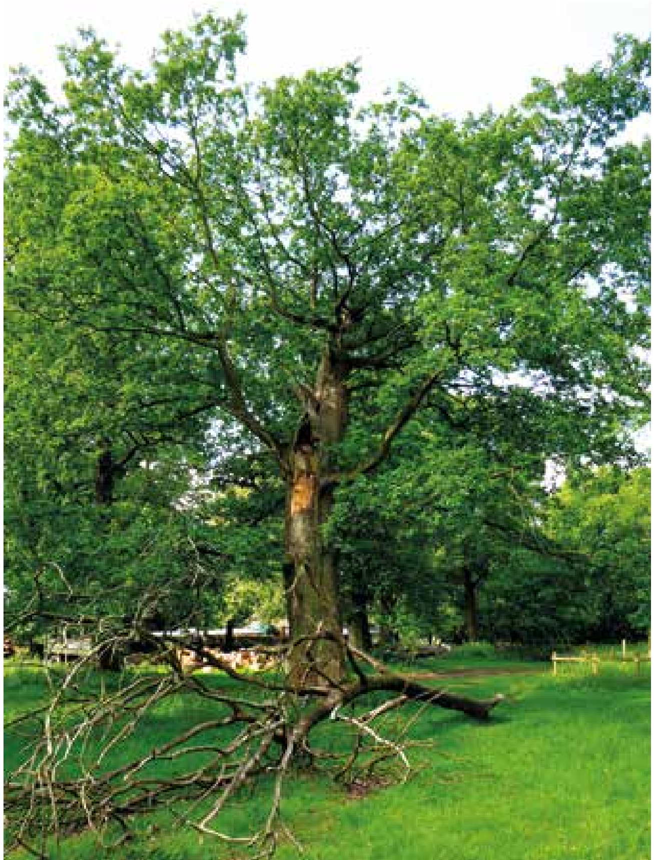
Photograph 11: Good spacing of trees, Calke Park, England (K. Alexander).

Photograph 12: Ancient oak, fully retrenched crown, Calke Park, England (K. Alexander).

The consequences of minimum intervention management that excludes large herbivore grazing

It has been shown by Vera (2000) that large herbivores have a very significant impact on forest structure. Native forests have evolved alongside wild large herbivore populations; one without the other is an artificial and man-made situation. Wood-decay invertebrates have evolved to exploit the wide variety of decaying wood situations which develop under the relationships between trees and

Photograph 13: Death by non-intervention management - veteran oak killed by over-shading secondary woodland in former wood pasture, Hasbruch, Germany (K. Alexander).



Photograph 14: Veteran oak, crown collapsed through wind damage rather than retrenchment, Levens Park, England (K. Alexander).

large herbivores. The removal of large herbivores from a forest creates an imbalance that is disadvantageous to a high proportion of wood-decay invertebrates and is especially damaging to those species which require advanced development of heartwood decay, the development of lateral branching and the availability of trees retrenching naturally through old age (Photograph 14). In cultural landscapes, domestic livestock may have replaced the wild large herbivores and maintained suitable conditions for long periods of human history, and tree exploitation such as shredding and pollarding may have extended the lifespan of trees and kept them free of competing woody growth.

In the absence of large herbivores it becomes necessary to consider direct and active management of forest in order to conserve wood-decay beetles. Working methods need to be devised to enable trees to have sufficient space and to develop into large open-grown form trees. Removal of the suppression of seedlings and saplings will inevitably lead to the development of thickets of young growth (Photograph 15). Cutting management becomes highly advisable – coppice!

There are a few examples available where long-term minimum intervention can be seen to be causing this damage. The Forêt de Fontainebleau in northern France had domestic livestock removed over a hundred years ago and - without browsing animals to provide a selective advantage to oak over beech – ancient oaks have now largely been eliminated by crown competition with beech and any new oaks developing are overcrowded and developing as high forest form trees. The specialist wood-decay fauna of old oaks is now under severe threat here. Similar problems are evident elsewhere eg the Hasbruch in Lower Saxony, where old oaks are in severe decline through minimum intervention management (Photograph 13). The decline in oaks has been explained as a ‘natural process’ and part of ‘natural cycling’ by Peterken (1996) who advocates leaving management to natural processes, but these are no longer natural systems, they are cultural modifications. There is no evidence that beech dominance will return naturally to oak dominance in due course, as Peterken says. In reality this is the dominance of shade-tolerant species over light-demanding species in the absence of large herbivores, as explained by Vera (2000). The hypothetical cycling of Peterken is leading to the extinction of many rare and threatened invertebrates. He has provided no reliable evidence in support of his hypothesis. In contrast, the Vera process is well-established in ecology and can be seen in action at many sites, eg the New Forest and other sites in England. At Ashton Court Park, Bristol, removal of large herbivore browsing and grazing has resulted in ancient oaks becoming engulfed in ash and sycamore woodland – tree species which are very palatable to large herbivores and

Photograph 15: Dense secondary growth in former wood pasture at Bialowieza Forest, Poland (Photo: K. Alexander).

which would have been suppressed by them (Alexander, 2013). Active cutting has now been carried out and plans expressed for restoring deer to the area with the ancient oaks in order to conserve them.

Approaches to conserving dead wood

Conventionally, invertebrate specialists tend to emphasise the importance of leaving dead wood to decay naturally in situ, largely ignoring the population of living trees which generate that dead wood. It is much more important – in the author's opinion – to focus first on managing the tree populations and ensuring that they can provide sustainable quantities of deadwood and in the full variety that an open-grown tree can generate; quality of decaying wood is very important, and in many ways more so than quantity. Measuring gross volumes of deadwood that are available is a very coarse way of assessing site value for wood-decay invertebrates, but it may be better than nothing. Ideally those gross volumes should be broken down by type of deadwood and stage in the decay process. By type of deadwood I mean reflecting the full suite of dead wood habitats, incorporating whole trunks, branches, twigs, stumps, and roots, and considering broad girth ranges. The more that can be left and the greater the variety then the conservation effort will be more worthwhile. Speight and Good (2003) have demonstrated that maintenance of quantities of coarse woody debris in European forests is largely irrelevant to the maintenance of biodiversity in wood-decay hoverflies (Diptera: Syrphidae) as many of these develop in rot-holes in living trees, and so the wood-decay conservation effort needs to focus much more on those living trees.

Within commercial forestry operations, there is clearly a need to retain whole living trees with space to grow on into old age and to continue the process of generating wood-decay habitats (Humphrey et al., 2004). Ideally these should be retained throughout the forest rather than be concentrated and thereby isolated from other such groups of trees. But scattered trees would be very vulnerable to incidental damage during forestry operations. The best option is probably to retain groups of such conservation trees as identified stands or compartments, away from the main centres of commercial activity, but also in sufficient quantity to provide a network of stepping stones across the forest.

Guides to good management of old tree populations have been produced (Read, 2000; Lonsdale, 2013). While these are written in English, versions in other European languages are currently being developed.

Conclusions

Conservation should be based on practical observation rather than unstable theory (Rackham, 2006). If landscape planners and forest managers desire to conserve wood-decay invertebrates as part of their operations then they need to rely on knowledge of tree biology and tree ecology rather than hypothetical woodland ecology. The four key factors which determine the species-richness for wood-decay invertebrates are:

- Total number of trees which make up the population – the more trees the better, but not at the expense of individual space;
- Age structure of those trees, with not only old trees with their important full suite of wood-decay situations, but also cohorts of new generations to provide continuity over time;
- Density of those trees, ensuring that trees with an open-grown form – lateral branches well developed - are as well-represented as closer grown trees with more of a high forest form;
- Connectivity in the landscape, enabling movement of the invertebrates, with scattered trees providing the essential stepping stones.

The range of tree species adds a further complication as each tree species that forms part of the local landscape needs to be considered in the same way. It goes without saying really that the dead woody tissues that these trees produce should be retained to decay naturally, preferably in situ, but at the very least displaced only the minimum required to maintain access, ensure public safety, etc. It is important that the conservation of decaying wood habitats should be treated seriously and sustainably, and not be treated as tokens.

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