ARTICLES

Wood decay, insects, palaeoecology, and woodland conservation policy and practice – breaking the halter.

Keith Alexander
59 Sweetbrier Lane, Heavitree, Exeter EX1 3AQ
(E-mail: keith.alexander@waitrose.com)

Summary

Research on fossil remains of beetles and other insects from the native forests of the current interglacial have the potential to change the current view of how our tree landscapes should be managed for nature conservation. It is vital that this work is underpinned by detailed knowledge of the ecology of the species concerned. Unfortunately the prevailing conservation paradigms are based on blinkered botanical interpretations of mostly pollen data, which have either ignored contrary evidence from other disciplines or manipulated it to actually support their closed canopy high forest model. A new champion for reformulation of our understanding of the native forest structure and dynamics has provided a different framework that is actually consistent with all of the evidence but the palynologists are intransigent. Importantly, the new wood pasture model also releases non-tree habitats such as calcareous grasslands and meadows from the stigma of being derived solely from the activities of people and therefore somehow un-natural.

Introduction

For much of the 20th century mainstream woodland conservation in Britain has been underpinned by assumptions about the structure of the 'Wildwood' of the Atlantic Temperate zone in Europe. The overarching assumption has been that closed canopy high forest covered most of the land (Peterken, 1996), opening up locally due to high water levels or high altitude. Glades were supposedly rare and caused by the occasional wind-blow, forest fire or pathogens. It followed therefore that it would be sensible for nature conservationists to be managing woodlands towards this same structure in order to effectively conserve our native species. "Minimum intervention" was invented as the way forward and has become something of a sacred cow and is chanted in just about every woodland conservation plan. But what does it actually mean? Precise definitions are elusive.

The high forest *hypothesis* – there is no proof that the idea is correct – has always confused me since the classic *'urwaldtier'* (species of primary forest before it was significantly altered by human activity) include a notably high proportion of species which require large old trees and decaying wood in open sunny situations (Alexander, 1998 & 2002). Lichenologists have also long argued that the high forest hypothesis must be incorrect as epiphytic lichens – including relict old forest species – also favour relatively high light levels.

Unfortunately, the world view in nature conservation has long been led by the vascular plant ecologists, and the fact that insect and lichen conservationists were confused by their concepts was seen as sad but inevitable. The highly respected lichenologist Francis Rose has been the main champion of the resistance movement (Rose, 1993; Harding & Rose, 1986), but even he has been marginalised by mainstream nature conservation. Interestingly the new champion to enter the arena is a Dutch plant ecologist, Frans Vera, who has written a wonderfully detailed and scholarly treatise on why the high forest hypothesis is incorrect and how the native forest would have been maintained in a dynamic openness through the grazing and browsing pressure exerted by large herbivore populations. His book has undermined the very basis of the high forest hypothesis by demonstrating that all of the so-called evidence is deeply flawed. Responses to this new enlightenment have either merely re-structured the same flawed evidence (Svenning, 2003; Mitchell, 2005) or else failed to grasp the full implications (Bradshaw et al, 2003).

The high forest v. wood pasture debate

At its simplest, the high forest hypothesis is based on the observation that areas of open ground go through a natural succession to closed canopy woodland when such areas are fenced off and left ungrazed. It is claimed that this is supported by the sub-fossil pollen record that shows high proportions of tree pollen throughout the natural forest period of the present interglacial. It is also claimed that sub-fossil remains of insects in those same deposits provides further evidence in favour of dense trees. But what the authors have failed to appreciate is that the presence of pollen and tree associates in the deposits only provides evidence for the presence of trees – extrapolation into forest structure is based on many assumptions and actual proof remains very elusive.

Of course, studies on bones in the dated deposits have demonstrated that large herbivores were present at the same time as the Wildwood over much of Europe. Indeed, some large herbivore species colonised the postglacial landscapes *before* the trees (Yalden, 1999) and so the native forest had to establish *alongside* grazing and browsing pressure, so the very basis for the high forest hypothesis is undermined – natural succession from open ground towards tree cover would have been influenced by grazing and browsing and that one cannot assume that closed canopy forest would have resulted. Enclosure to exclude grazing would certainly have resulted in closed canopy high forest, and that is precisely what the early peoples did in order to provide a sustainable supply of wood products near their settlements – thereby creating the coppice-with-standards woodlands that we value so highly today.

Pollen data certainly shows that trees such as oak and hazel were producing abundant pollen throughout the Wildwood period, but it is well accepted that these species do not regenerate under closed canopy conditions and even fail to do so in glades. So their continual presence through thousands of years actually demonstrates that there was extensive open ground in which they could regenerate (Vera, 2000). So the pollen data does not imply closed canopy conditions, as the palynologists would have us believe but actually open conditions.

The insect assemblages found in dated deposits

Palaeo-entomologists have made similar serious mistakes in their interpretation of fossil faunas. Dinnin and Sadler (1999) suggest that up to 20% saproxylic representation amongst insect assemblages – mostly beetles - found in deposits suggests "closed ancient woodland" while values of less than 2% wood and tree taxa have been interpreted as open, largely treeless landscapes. The authors acknowledge that these figures are intuitively rather than empirically derived, but modern field entomologists will be surprised by these interpretations. A high percentage of saproxylic beetles actually suggests open old growth type tree cover (Alexander et al, 2003 & 2004; Alexander, 2004), as found in Windsor Great Park and the New Forest. A lower figure might actually suggest closed canopy woodland since such shady conditions are unlikely to produce large timber of anything other than shade-tolerant trees such as beech.

Another important aspect of the saproxylic insect assemblages in the deposits is that some of the species actually require large old or even ancient trees as habitat (Alexander, 1999, 2002, 2003), and yet such trees must have been very rare under the high forest hypothesis – trees characteristically develop lower canopies as they age (this is termed retrenchment – e.g. stag-headed oaks) and such trees would be suppressed and eliminated by younger more vigorous growth under closed canopy conditions. The existence of such old tree insects in the deposits therefore demonstrates that large old trees existed at the same time and so the forest canopy was actually open enough for such trees to develop.

Studies of the same saproxylic insects under modern conditions suggest that these species have very poor mobility, which is how they have become increasingly confined to a small number of refugia. Buckland (2002) comments that, having evolved through the mid-Tertiary in a landscape of continuous forest, it is hardly surprising that most saproxylic species have a low dispersal potential. Kirby (2003) suggests that the composition of the modern fauna will be biased by centuries of human exploitation of trees for wood products and so the requirements of the modern old growth fauna cannot be used to imply the structure of the former tree cover.

The saproxylic insects which were present in the deposits from the time of the postglacial forest, but which became extinct as people pressure increased, might however provide useful evidence for the forest structure – would closed canopy or open wood pasture species predominate? Information on the forest structure in which particular species occur is very difficult to find in the literature, but preliminary analysis suggests a strong bias towards open forest with high light levels and the presence of large old trees with advanced decay (Table 1) – a result inconsistent with closed high forest but very consistent with the Vera model of large herbivore driven forest structures[1]. This effect is most obvious with the beetles developing in the decay of broad-leaved trees. It is particularly instructive just how few species require the combination of high humidity and low sunlight that would have characterised the closed canopy high forest that the palynologists hypothesise was the predominant tree cover throughout the period.

Species	Wood-decay Succession	Humidity	Light	Host trees
Broadleaf forests				
Batrisus formicarius Aube*	Late	Low	High	*Quercus*
Cerambyx cerdo (L.)*	Early	Low	High	*Quercus*
Dromaeolus barnabita (Vil.)*	Late	Low	High	*Fagus, Quercus* etc
Isorhipis melasoides (Cast.)*	Late	High	Low	*Fagus*
Platycerus caraboides (L.)*	Late	High	Low	*Fagus* preference
Porthmidius austriacus (Schrk.)*	Late	High	High	Broadleaves?
Prostomis mandibularis (F.)*	Late	High	?	*Quercus* & *Fagus*
Pycnomerus terebrans (Ol.)*	Late	Low	High	*Quercus* etc
Rhopalodontus baudueri Ab.*	Late	Moderate	Moderate	*Fagus* & *Quercus*
Rhyncolus punctulatus Boh.	Late	Moderate	High	Broadleaf preference
Rhyncolus sculpturatus (Walt.)	Late	?	?	Broadleaf preference
Rhysodes sulcatus (F.)*	Late	Moderate	Moderate	Fagus preference
Strangalia attenuata (L.)	?	?	?	*Quercus* etc
Broadleaf or conifer hosts				
Bothrideres contractus F.*	Mid	Low	Moderate	Plastic
Zimioma grossum (L.)*	Late	Low	High	Plastic
Conifer forests				
Cryptolestes corticinus Er.	Late	?	?	Conifer
Mycetina cruciata (Schall.)*	Late	High	Low	Conifer preference
Pissodes gyllenhali Gyll.	?	?	?	*Pinus*
Rhyncolus elongatus Gyll.	Late	?	?	Conifer
Rhyncolus strangulatus (Perr.)	Late	?	?	*Pinus*
Temnochila coerulea (Oliv.)*	Early	Low	High	*Pinus*

Table 1. Saproxylic Coleoptera species represented in British Holocene but subsequently lost (species from Dinnin & Sadler, 1999; habitat association from BUGS and other sources) [* refers to species which are considered part of the *Urwaldtier*.]

italics

[1] An earlier version of this analysis was presented at the British Ecological Society's Annual Meeting at Manchester Metropolitan University, September 2003.

While palaeo-ecologists have tended to overlook the true significance of the saproxylic beetle data, a few have recognised the difficulties in explaining the presence of grassland and dung beetle remains. Buckland (2002) comments that the presence of old grassland species in fossil insect assemblages dating from before the opening up of the forests for agriculture during the Neolithic suggests a more varied mosaic than the pollen might at first portend; and that old grassland faunas have followed saproxylics into decline. Whitehouse and Smith (2004) have also pointed out that grassland and dung beetles contribute about 10% of the assemblage when tree pollen is at its peak abundance in the deposits. This is clearly not closed canopy forest. They also cite Eriksson et al (2002) who have highlighted the fact that many semi-natural grassland species were present in the peak tree pollen period. They conclude that the fossil insect evidence hints that beetles associated with open taxa are a constant feature in these early Holocene assemblages, whilst species usually associated with the dung of grazing animals are persistent. They go on to say that they believe that fossil beetle specialists have an important role to play in further exploring the structure of European native forests.

It is very clear that analysis should focus on the species level as all have precise and very different requirements and this can provide very detailed information on the habitat structure, which produced the particular species assemblage. The lumping of all saproxylic species together and trying to draw conclusions based on the percentage representation in the whole fauna is seriously counter-intuitive to a field ecologist – as should the same approach for tree pollen data to plant ecologists. And dangerous too, since the palynologists have jumped on these entomological misinterpretations as evidence in support of their favoured high forest hypothesis (e.g. Svenning, 2002).

The latest study (Mitchell, 2005) takes the pollen extrapolations to new and even more tenuous lengths, suggesting that the absence of large herbivores from Ireland (unproven) makes it an ideal place for testing the hypotheses, and that, because the Irish pollen record is virtually indistinguishable from that in Britain and other European counties, then it follows that large herbivores make no detectable difference to gross forest structure. This presupposes of course that pollen composition in deposits provides suitable data for such sophisticated analysis. It might just mean that pollen data is too coarse to detect such differences in canopy structure.

Examined from a multi-disciplinary viewpoint the mistakes of the past interpretations are all too obvious. The key problems appear to be that the different disciplines have been working in isolation and that plant palaeoecology has been acknowledged as the lead discipline – not to be challenged unless the contrary evidence is incontrovertible, a virtually impossible situation given the nature of the study medium. The debacle that has followed Vera's inspirational book has demonstrated the need for wider debate, for a new leadership in palaeoecology , and more importantly a review of current conservation policy and practice.

Implications to insect conservation

Restoration of large areas of wild herbivore maintained "wilderness" might be a twinkle in the eye of a few academic ecologists but it is unlikely to be a realistic proposition for much of the modern landscape and isn't necessarily a key priority for conservation. Indeed, Buckland (2002) comments that the baseline of conservation is not the (re-) creation of past environments, 'for it is impossible to return to that foreign country, of which we seek to create idealised impressions'. For saproxylic insects we need sensitive management of core areas and wide availability of diverse tree populations in between, linking and extending the available habitat (Alexander, 2004). Saproxylics are an important group of insects which can be actively conserved in the face of global climate change as open-grown trees can be welcomed and encouraged in all landscapes – in contrast with say calcareous grassland species which are confined by the realities of geology.

The problem tends to be the way that conventional forestry techniques are still used for tree regeneration schemes. Trees are capable of regenerating themselves – they have been doing so for millennia without humans to plant them! Frans Vera has now shown us that trees can be grown by manipulating plant competition through low level grazing and browsing by large herbivores. This is indeed how trees are being grown in the inspirational Hatfield Forest in Essex, where the managers periodically release open-grown trees from the thorn scrub which has nursed them.

"New woodlands" are a distraction from the real conservation of saproxylic insects. These organisms need large open-grown trees at landscape scale. Trees need space to develop a full canopy, to grow large, and develop diversity of decay as they age. Trees drawn up tall in close plantings will not survive in an increasingly stormy world. We need short squat trees in high winds and tree protection measures throughout the landscape not just in a few scattered sites.

So, should conservation management then perhaps consider re-establishing grazing regimes in the enclosed woodlands? Woodlands that were enclosed many hundreds of years ago and which have developed their own special interest of ground vegetation and associated phytophagous insect assemblages are not a priority for saproxylic conservation, contrary to the view of Speight and Hambler (1995). Their saproxylic faunas have mostly been severely depleted by centuries of exploitation for wood and timber. The richest examples of saproxylic faunas are today confined to a few old wood pastures – sites where the cultural landscape is not so different structurally to the early native forest and where sensitive livestock grazing provides a direct link with the natural grazing of the now extinct large herbivores. Buckland & Dinnin (1993) comment that elements of the *Urwald* fauna survive today in poor analogues to their primary habitats, the ancient wood pastures, and describe our historic parklands as "a managed habitat which is perhaps the oldest in Britain".

The discredited high forest model

Minimum intervention has been provided as a more scientific expression for "leaving it to nature" in our tree habitats, but 'minimum' is a loaded word which implies limited intervention, whereas the loss of large herbivores to the system is actually a major intervention and one which is rarely acknowledged let alone attempts made to rectify the situation by restoring grazing. The enclosed and ungrazed ancient semi-natural woodlands that have dominated woodland conservation in Britain are long-established but man-made artefacts of centuries of exploitation for wood products. Conservation of their special features requires continued active intervention. Minimum intervention will result in declines in those features as shading becomes increasingly predominant, and is unlikely in the longer term to encourage species-rich old growth assemblages unless the wood is linked with an old wood pasture.

Minimum intervention has been advocated as a means of restoring natural processes to our woodlands, but is based on the discredited high forest model; without restoration of free-ranging large herbivores a vital natural process is missing and the results will be a travesty of nature, a new man-made cultural artefact!

Rose and Sanderson (1997) have pointed out that natural history interest and conservation value are much more closely linked to old-growth woodland than to natural woodland; all old growth woodlands should be treasured. The cultural use of old-growth woodlands is an integral feature of these sites and probably has been since people first colonised these forests.

Vera's wood pasture hypothesis is important not only to tree interests but suddenly brings other habitat types away from the stigma of "man-made or cultural artefacts". Calcareous grasslands and meadows are no longer relatively recent phenomena but part of the post-glacial landscape, their insect faunas just as significant (in gross terms) as those of old forest. It is interesting that *Grazing Ecology and Forest History* was published at the turn of the millennium, ushering in "open ecology" as the way forwards and consigning the misguided 20th century "dense ecology" to the history books.

Acknowledgements

I must acknowledge the inspiration of Ted Green who transformed a mere saproxylic entomologist into a tree ecologist, and also the membership of the Ancient Tree Forum who have proved such a fertile ground for debate and support in the face of so many uncaring conservation professionals. Christophe Bouget, Peter Sprick, and Dmitry Telnov provided useful ecological data on our extinct saproxylic beetles.

References

Alexander, K.N.A. 1998. The links between forest history and biodiversity: the invertebrate fauna of ancient pasture-woodlands in Britain and its conservation. Pp73-79 in: Kirby, K.J. & Watkins, C. (eds.) *The Ecological History of European Forests.* CAB International, Wallingford.

Alexander, K.N.A. 1999. The invertebrates of Britain's wood pastures. *British Wildlife* **11**: 108-117.

Alexander, K.N.A. 2002. The invertebrates of living and decaying timber in Britain – a provisional annotated checklist. *English Nature Research Report* No **467**.

Alexander, K.N.A. 2003. The British saproxylic invertebrate fauna. Pp9-11 in: Bowen, C.P. (ed.) *Proceedings of the second pan-European conference on Saproxylic Beetles.* People's Trust for Endangered Species, London.

Alexander K.N.A. 2004. Revision of the Index of Ecological Continuity as used for saproxylic beetles. *English Nature Research Report* No. **574**.

Alexander, K.N.A. 2004. Landscapes with ancient trees: invertebrate mobility and population viability. Pp107-114 in: Smithers, R. (ed.) *Landscape ecology of trees and forests.* International Association for Landscape Ecology (UK).

Alexander, K.N.A. & Butler, J.E. 2004. Is the US concept of 'old growth' relevant to the cultural landscapes of Europe? A UK perspective. Pp 233-246 in: Honnay, O., Verheyen, K., Bossuyt, B. & Hermy, M. (eds.) *Forest Biodiversity. Lessons from history for conservation.* IUFRO Research Series No 10. CABI Publishing, Wallingford.

Alexander, K., Smith, M., Stiven, R. & Sanderson, N. 2003. Defining 'old growth' in the UK context. *English Nature Research Report* No **494**.

Bradshaw, R.H.W., Hannon, G.E., & Lister, A.M., 2003. A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management* **181**: 267-280.

Buckland, P.C., 2002. Conservation and the Holocene record, an invertebrate view from Yorkshire. *Bulletin of the Yorkshire Naturalists' Union* No **37**: 23-40.

Buckland, P.C., & Dinnin, M.H., 1993. Holocene woodlands, the fossil insect evidence. Pp 6-20 in: Kirby, K.J., & Drake, C.M. (eds.) *Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain.* English Nature Science No. 7.

BUGS2000 – Coleopteran Ecology Package. http://www.bugs2000.org/

Dinnin, M.H., & Sadler, J.P. 1999. 10,000 years of change: the Holocene entomofauna of the British Isles. *Quaternary Proceedings* No. **7**: 545-562.

Harding, P.T., & Rose, F. 1986. *Pasture-Woodlands in Lowland Britain.* Institute of Terrestrial Ecology, Huntingdon.

Kirby, K.J. 2003. What might a British forest-landscape driven by large herbivores look like? *English Nature Research Report* No **530**.

Mitchell, F.J.G., 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* **93**: 168-177.

Peterken, G.F. 1996. *Natural Woodland: Ecology and Conservation in Northern Temperate Regions.* Cambridge University Press.

Rose, F. (1993) Ancient British woodlands and their epiphytes. *British Wildlife* **5**: 83-93.

Rose, F., & Sanderson, N. 1997. Book Review: Natural Woodland by George Peterken. *British Wildlife* **8** (6): 405-406.

Svenning, J.-C., 2002. A review of natural vegetation openness in north-western Europe. *Biological Conservation* **104**: 133-148.

Vera, F.W.M. 2000. *Grazing Ecology and Forest History.* CABI Publishing, Oxon, UK.

Whitehouse, N.J., & Smith, D.N. 2004 'Islands' in Holocene forests: Implications for forest openness, landscape clearance and 'culture-steppe' species. *Environmental Archaeology* **9**: 203-212.

Yalden, D.W., 1999. *The History of British Mammals.* T. & A.D. Poyser, London.